Università degli Studi di Milano
PhD in Environmental Sciences
XXXV Ciclo

Plant and arthropod communities of Alpine ice-related landforms: ecological and biogeographic importance

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Overview of the Thesis

This PhD thesis is mainly organised as collection of research papers published, submitted, and in preparation.

Chapter 1 outlines the state of the art, the main aims of the PhD project and the approaches used for reaching these objectives on peculiar study areas

Chapter 2, "Vanishing habitats", presents, as a first result, a scientific call for studying and monitoring glacial and periglacial habitats – refugia for a cold-adapted and threatened biodiversity - because of the lack of knowledge that still affects these habitats (Gobbi et al. 2021). The study points out the urgency in planning this research due to the risk of total disappearance of these habitats in the current scenario of global warming.

Chapter 3, "Glacial and periglacial biodiversity", is focused in analysing with multiple approaches the glacial and periglacial biodiversity. Studies **3.1-3.2** (Valle et al. 2022a-b) describe plants and arthropod communities of threatened glacial sites (Peirabroc, Clapier and Calderone glaciers) in peripheral mountain chains (Maritime Alps and Apennines, Italy, respectively). In these studies also important environmental parameters (e.g. debris thickness, soil temperatures and chemical parameters) have been correlated with biological communities. Study **3.3** focuses on glacial springtails and regards the description of a new species of ice-dwelling springtail from Calderone glacier (3.3, Valle et al. 2021). Studies **3.4-3.5** (Valle et al. 2020, Ornaghi et al. submitted) analyse the efficacy of cryophilic ground beetles (Carabidae: Nebrini) as ecological indicators of sub-superficial ice presence, through community, demographic (3.5) and morphometric (3.6) approaches. The paragraph **3.6** focuses on the biodiversity hosted by two of the few Dolomitic debris-covered glaciers, Sorapiss glaciers (Bernasconi et al. 2019). The last study (**3.7**, Fugazza et al. in submission) is a glaciological analysis that lays the foundations for studying in detail how the thickness of the stony debris accumulating on the glaciers influences the distribution of the biological community on debris-covered glacier.

In **chapter 4, "Toward a synthesis of glacial ecology"**, we move from the detail spatial scale (i.e. the glacier) of the previous chapter to a regional scale (e.g. Alpine), that could be useful for global considerations. The first study (**4.1**, Valle et al. in preparation) gives a complete overview on taxonomy, ecology and biogeography of ice-dwelling cryphilic springtails from European Alps. The second study (**4.2**, in preparation) aims to answer the question "what is the fate of cold-adapted species during global warming and glacier retreat?"; in order to do this, a comprehensive database with abundance data of 513 species of plants, ground beetles and spiders sampled in 463 glacial and periglacial plots has been analysed. The second paper (**4.3,** Hågvar et al. 2020) is a review of ecological studies performed in Europe (Svalbard, Scandinavia and European Alps) and points out the ecological features of young environments close to retreating glaciers: these "virgin" soils are colonised by a pioneer peculiar biological community in which springtails results a key taxon of the early trophic chain and consequently the early successional stages.

In **chapter 5** are presented conclusions and perspectives of the research.

Chapter 6 reports the comprehensive Curriculum Vitae of my PhD, including all papers published, in submission and in preparation, congresses, teaching activity, grants, awards, dissemination, education activities and other projects which I joined.

Chapter 1

Introduction, aims and methods

1 INTRODUCTION, AIMS AND METHODS

The reduction of the mountain cryosphere – i.e. glaciers and permafrost - is among the most visible effects of climate change (Beniston et al. 2018; D'Agata et al. 2019, Hock et al, 2019) that causes a fast melting of the ice masses (Biskaborn et al. 2019, Diolaiuti et al. 2019) and, for glaciers, an evident front retreat. Another visible effect of climate change is the increase of supraglacial stony debris, due to freeze-thaw processes delivering large volumes of debris from the surrounding slopes to the glacier surface (Azzoni et al., 2018; Janke et al., 2015; Kirkbride, 1993; Kraaijenbrink et al., 2017; Tielidze et al., 2020).

Biological responses to glacier retreat and increase of debris coverage of glaciers and permafrost melting are still only partially known (Stibal et al, 2020; Fickert et al. 2022; Brighenti et al. 2021). Generally, species could react to unfavourable environmental changes in different ways, and clearly at different time-sclaes, evolving and getting more adapt to changing condition – and, maybe, speciating –, migrating, getting extinct or finding a refugium (Merila et al., 2013; Bellard et al., 2014; Rull, 2009; Stewart et al., 2010). A refugium is a site to which a species retreat, persist in and potentially expand from under changing environmental conditions (Keppel et al. 2012).

Ice-related landforms, in particular clean-ice glaciers (i.e. with ablation area mostly free from stony debris), debris-covered glaciers (i.e. glaciers with the ablation area covered by debris for more than 50% of the surface; Fickert e al. 2022) and active rock glaciers (periglacial landforms of stony debris with interstitial ice; Brighenti et al. 2021), could host an extreme specialised biodiversity and cover a very important ecological role as refugia during this climate change scenario. A peculiarity of debris-covered glaciers and rock glaciers is that they are more conservative systems than clean-ice glaciers, reacting more slowly to induced stresses from the climate (Seppi, 2006; Nakawo & Rana, 1999).

1.1 Glacial biodiversity: its global threats and local refugia

On the base of the most widespread human perception, glaciers and ice-related landforms are harsh environments where there are no living organisms. Even the Habitat Directive (adopted in 1992 in Europe, it ensures the conservation of a wide range of threatened or endemic habitats and species), that include glaciers and rock glaciers with the Code 8340 "Permanent Glaciers" [Council Directive 92/43/EEC (1992)] considers these habitats almost abiotic.

In contrast, a multitude of studies (e.g. Brighenti et al. 2021, Zawierucha et al. 2020; Fickert et al. 2022; Gobbi and Lencioni 2020) have demonstrated that they are ecosystems in their own right and are a habitat - permanent or temporary - for a large variety of cold-adapted organisms, from bacteria to vertebrates. These landforms that host peculiar biodiversity of cold-adapted organisms were defined by Cauvy-Fraunie and Dangles (2019) "cold-spot" of biodiversity.

Clean-ice glaciers (i.e. glaciers with the tongue uncovered, or only partially covered, by rock debris) are able to host the so called "cryophilic (or glacial) biodiversity", that includes mainly bacterial and algal communities and some invertebrate groups (Zawierucha et al. 2015). Only in the Arctic also mosses have been found growing on the ice surface, which could be inhabited by species of Tardigrada, Nematoda, Enchytraeidae (Oligochaeta) and Acarina (Coulson & Midgley, 2012). Among invertebrates, only few groups seems to be able to complete their life cycle on the surface of the ice: Collembola (Fjellberg, 2010), Chironomidae (Gobbi and Lencioni 2021), Plecoptera (found only in Patagonian glaciers; Kohshima, 1985), and Enchytraeidae (found in Alaska; Shain et al., 2001).

Debris-covered glaciers (Fickert et al. 2022, Caccianiga et al. 2011) and rock glaciers (Gobbi et al. 2014) are more heterogeneous habitats than clean-ice glaciers, thanks also to the variable physical conditions of stony debris that cover the ice masses. This mosaic of environments hosts not only species able to live in direct contact with the ice but also organisms that need soils (usually lithosols) for surviving: vascular plants (even trees, in some glaciers), bryophytes and macroinvertebrates, in particular ground beetles (Coleoptera: Carabidae) and spiders (Arachnida: Araneae) (Fickert et al. 2022; Tampucci et al 2016, 2017a; Gobbi et al. 2014, 2017).

Recently deglaciated terrains (i.e. substrates ice-free since 1-10 years) attracted the interest of several mountain ecologists because they reperest perfect study areas to investigate the ecosystem birth and consequently the spatial and temporal biotic successions. Hodkinson et al. (2002) described the species co-occurences and interactions in the early successional stages via the "predator first paradox". This paradox consists in affirming that not plants, but hunting arthropods are the only visibile first colonisers able to live and reproduce in front of the glacier thanks to the airborne fallout. Only recently it has been understood that there are autochthonous food sources constituted by biofilms on which microarthropods (i.e. springtails) are able to feed (Hågvar & Gobbi 2022, Sint et al. 2019) triggering the first trophic chain (from primary producers to predators): biofilm (diatoms, cyanobacteria)-springtails-ground beetles/spiders. This is probably true also for supraglacial habitat, because of the similar composition of the biological communities - dominated by predator and detritivores - also if a trophic study on this habitat have never been performed.

The extreme morphological, physiological and behavioural specialisation of the organisms permanently living in these landforms makes them particularly threatened by the ongoing climate warming (Cauvy-Fraunié and Dangles 2019; Stibal et al. 2020). The ecological communities hosted by glacial and periglacial habitats are suffering deep alterations due to species turnover and local (or global) extinction.

In this warming scenario, environmental heterogeneity at different scales and the presence of a great variety of fragmented landforms with peculiar microclimatic conditions could play an important role in providing a suitable refugium for cold-adapted glacial biodiversity.

Periglacial and glacial landforms characterized by debris with underlying ice enhance microclimatic heterogeneity: the stony debris cover reduces the ice melting, allowing the fragmentary persistence of ice at low altitudes (Nakawo & Rana, 1999). In general, debris-cover glaciers could sustain cold-adapted species at altitudinal belt very different from the nival one (Caccianiga et al 2011, Tampucci et al. 2016). On European Alps, the tongue of some debris-covered glaciers even persists under the treeline (e.g. Miage Glacier, Belvedere Glacier).

Also macroclimatic heterogeneity is an important framework for studying glacial and periglacial biodiversity. A significant example of macroclimatic heterogeneity on European Alps is the contrast between the continental climate of inner Alps and the different climate in peripheral mountain chains, that is generally more oceanic (Tampucci et al. 2015; Körner 2003), but can also be Mediterranean-like. Glaciers and rock glaciers persist under different macroclimatic conditions: in continental areas rock glaciers are favoured by cold-dry climate (Millar et al., 2013), while glaciers persist in cold-wet oceanic regions (Warren and Aniya, 1999).

Peripheral mountain areas are crucial points for the studies on glacial communities, for different reasons. Firstly, they could show one of the plausible future scenarios for the whole inner glacial areas, given the occurrence of few, small and rapidly shrinking glaciers. Because of their role as microrefugia during glacial and interglacial periods, peripheral chains have contributed to the evolution of several endemic species (Muellner-Riehl, 2019; Steinbauer et al., 2016). Thus, they are hotspot of biodiversity, characterised by high richness of endemic species (Medail and Quezel 1999), often cold-adapted (Tampucci et al. 2015), since they were partially ice-free during glacial periods, acting as refugia (Schonswetter et al. 2005).

Peripheral mountain chains coincide with all the marginal mountain areas not affected by the Pleistocene glaciations (cold-stage refugia. e.g. Tampucci et al. 2015) and/or the areas that remained glaciated during the climatic Optimum (warm-stage refugia. e.g. Tampucci et al. 2017b); therefore, they include a great variability of areas with different climatic and biological features. However, their knowledge is still fragmentary, although some of them risk extinction and, with them, we will lose many biological, ecological and biogeographic information.

1.2 Collembola: an unexplored Alpine cryophilic world

Springtails are small, wingless arthropods living in almost all terrestrial habitats and particularly abundant in soils, where they can attain high densities (Hopkin, 1997; Balian et al., 2007; Gibert and Culver, 2009). They have a broad range of specialization and include species adapted to deep underground environments and species associated to surface and canopy environments (Gibert and Deharveng, 2002; Kováč et al., 2016; Greenslade et al. 2016; Zawierucha et al. 2015).

Springtails are positively linked to cold biomes (Potapov et al. 2022), being – with mites - among the few terrestrial invertebrates able to colonize Antarctic continent (McGaughran et al. 2011, Sømme 1981), surviving millions of years on isolated Nunatak. Their physiological adaptation to extreme cold conditions has been a long time object of studies (Holmstrup 2018, Sinclair & Sjursen 2001, Sømme 1981), since in springtails have been recorded very low supercooling point that could reach -32°C. Among Alpine arthropods, only for springtails of the family Isotomidae is known the existence of species living only in direct contact to the glacial ice – therefore really "cryophilic" – (Buda et al. 2020, Fjellberg 2010, Eisenbeis & Meyer 1999, Stoppani 1876). Among terrestrial arthropods, we have evidences that only springtails are able to live in contact to bare ice (Zawierucha et al. 2015). Eisenbeis & Meyer (1999) define these springtails "true ice-dwelling" cryophilic species, distinguishing them from other cryophilic species that occupy the habitat at the margin of the ice. The main period of activity of ice-dwelling springtails occurs during winter months: the microhabitat they occupy during cold season is the interface between the ice and the snow (Eisenbeis & Meyer 1999). Only when snow start melting, they move up to the snow surface and, during summer, when snow is completely melted, they lay on the ice and into the ice interstice, down to a depth of about 30 cm. They are obligate ice-dweller, unable to survive out of the ice.

Desoria saltans Nicolet, 1841 (Isotomidae) is a famous cryophilic springtail commonly known as "glacier flea" and was already cited by the geologist Antonio Stoppani in his early essay "Il Bel Paese" (Stoppani 1876) for its showy, swarming and large assemblages on Alpine glaciers. Nowadays there are indications that "glacier fleas" include multiple taxa of cryophilic Isotomidae, as suggested by Fjellberg (2010) for North America, but their taxonomy for European Alps is still unknown.

Springtails have, in general, an important functional role in soil as they affect organic matter decomposition and feed on dead organic matter, fungi, algae and microorganisms (Maaß et al., 2015; Potapov et al., 2016). However, in glacial ecosystems their importance seems to be even higher, by virtue of their very pioneer role in these environments which is well summarized in the "springtail first principle" (Hågvar & Gobbi 2022): before vascular plants establish near a melting glacier, chlorophyll is present in biofilms and pioneer springtails graze on these sources and on microorganisms and organic dead matter; on Alps, the numerous predators that inhabit glacial habitat feed mainly on springtails (Sint et al 2019).

Despite all these good reasons for studying ice-dwelling crypphilic springtails, their knowledge is still limited.

1.3 General aims

- The first aim of this PhD thesis was to describe the glacial and periglacial (i.e. of glaciers and active rock glaciers) biodiversity and ecology with a multitaxon approach (primarily vascular plants, bryophytes, springtails, ground beetles and spiders). Only implementing and completing the knowledge on these habitats will be possible to monitor and, hopefully, conserve them. In order to do this, it has been necessary to study areas important from a biogeographic point of view, thus the research was focused on peripheral mountain chains (that include glaciers of the Dolomites, still poorly studied) (see chapters **2-3**).
- Moving towards a synthesis for vascular plants, ground beetles and spiders, another aim of this study was to focus on the ecological features of periglacial and glacial landforms and to test if

they are acting as warm-stage refugia for cold-adapted species. In particular, I aimed to define the fate of all glacial and periglacial species, classifying them as “winner”, “neutral” or “losers” in relation to their ecological niche, the global increasing of temperature and their ability to find a suitable refugium on ice-landforms (see chapter **4**).

- An important and ambitious aim of this PhD project was to describe and clarify with integrative taxonomy the biogeography and distribution of ice-dwelling cryophilic springtails of European Alps and Apennines, since the great lack of knowledge on this group (Eisenbeis, & Meyer 1999) (see studies **3.3, 3.4**).

1.4 Study areas

The PhD project was carried out on European Alps, Apennines and Pyrenees, at different scale:

- The multitaxon ecological studies on glacial and periglacial communities were carried out on Calderone glacier (Apennines, Italy), on Peirabroc and Clapier glaciers (Maritime Alps, Western Alps, Italy), on Sorapiss and Agola glaciers (Dolomites, Eastern Alps, Italy) and Lazaun rock glacier (Eastern Alps, Italy). The glaciological work was performed on Amola glacier (Adamello, Eastern Alps, Italy). (Fig. 1, red points)
- The taxonomic and biogeographic study on ice-dwelling springtails, as well as the analysis on Alpine refugia, were performed at large scale. For studying ice-dwelling springtails, sampling was performed in European Alps, Apennines and Pyrenees, in order to compare all the known taxa of Europe and describe all this biodiversity (paper **3.4** for further details). For studying Alpine refugia, I implemented a database (Tampucci’s PhD thesis, 2017) that includes detailed studies on glacial and periglacial sites from European Alps. In particular, I implemented this database with five new studies from peripheral areas, still underrepresented in Tampucci’s database. New areas investigated are reported in Fig. 1 (yellow pin).

1.5 Methodological approaches

In order to reach the aims of this PhD project, several approaches have been used, from community to single-species, from biotic to abiotic, from morphological to molecular and functional trait approaches:

- Multi-taxa approach has been used for community analysis. For detecting each glacial and periglacial biological communities, different representative taxa have been selected and analysed together: vascular plants (primary producers), springtails (primary consumers), ground beetles (mainly nocturnal predators) and spiders (diurnal predators). For some sites also additional taxa have been analysed (chapter **3**). Species identification has been performed for each taxon with different method specified withing each specific chapter.
- In order to describe and analyse microclimatic heterogeneity, also soil chemical and physical factors (debris thickness, temperatures, soil chemistry) have been sampled and analysed (chapter **3**).
- For studying ice-dwelling springtails integrative taxonomy (Potapov et al. 2020) has been used (papers **3.3, 3.4**).
- In order to understand general pattern of cryophilic species responses to ice-presence in periglacial habitats, functional trait approach has been applied (paper **3.6**).

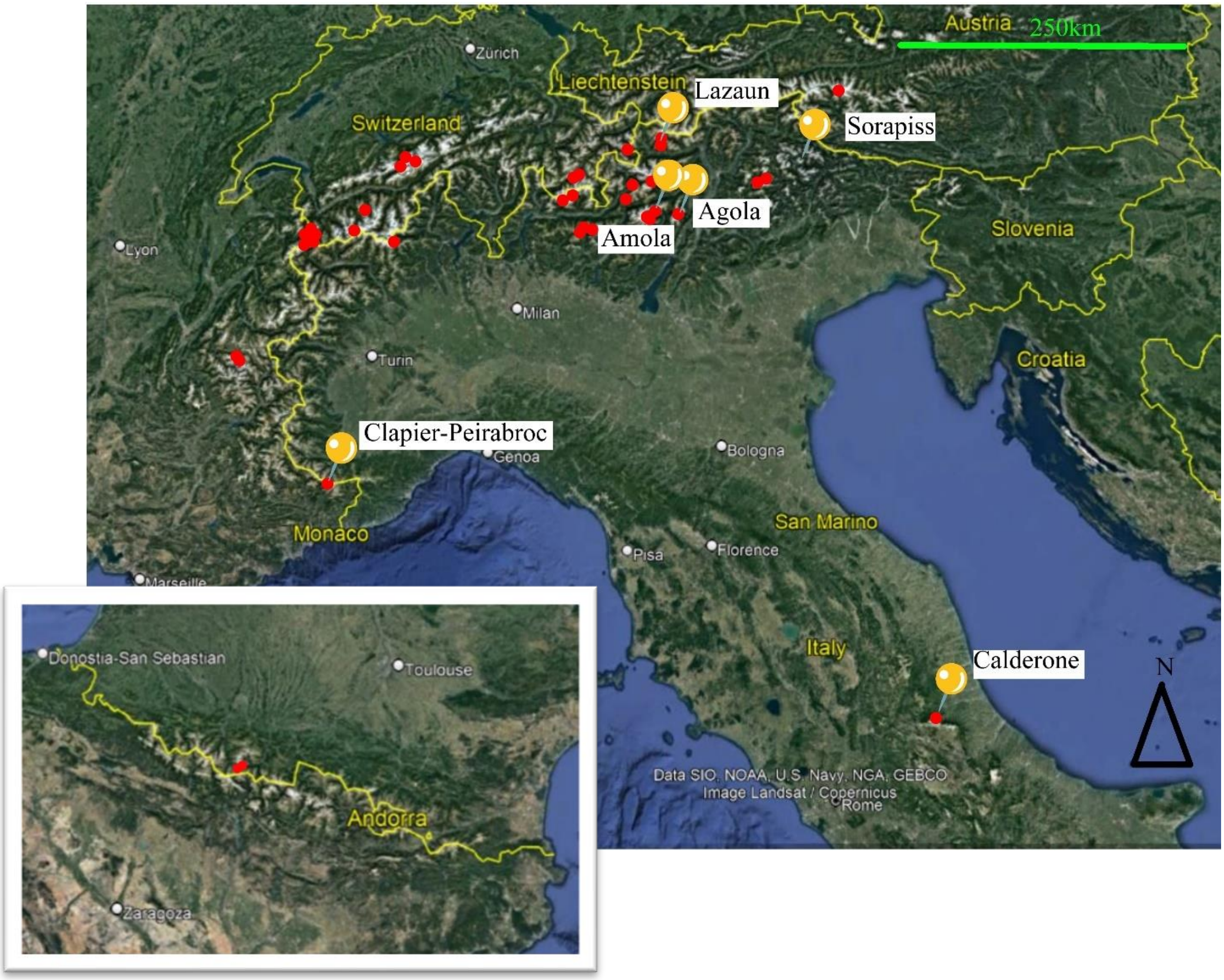

Figure 1*: All the sampling sites investigated during PhD project on European Alps, Apennines and Pyrenees. Yellow stylus: sites of multitaxon and multiapproach ecological studies; red point: sites in which ice-dwelling springtails have been samples (for details, see paper* ***3.4****)*

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Chapter 2

Vanishing habitats

2.1 Vanishing permanent glaciers: climate change is threatening a European Union habitat (Code 8340) and its poorly known biodiversity

Biodiversity and Conservation
https://doi.org/10.1007/s10531-021-02185-9

COMMENTARY

Vanishing permanent glaciers: climate change is threatening a European Union habitat (Code 8340) and its poorly known biodiversity

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Received: 27 November 2020 / Revised: 8 April 2021 / Accepted: 12 April 2021

Abstract

The cryosphere (i.e. glaciers and permafrost) and its related landforms offer a wide range of ecosystem services, thus they have strong relationships with human population. Even if these harsh environments have often been regarded as inhospitable, there is a growing amount of literature on glacial biodiversity, specifically concerning European mountains. Glaciers and permafrost-related landforms (e.g. rock glaciers) host a variety of cold-adapted taxa, from bacteria to vertebrates. They have been included in the Natura 2000 network, specifically in the habitat type: Permanent Glaciers (code 8340), but their biodiversity is still poorly known. Even if local extinctions and population reductions of cold-adapted species due to glacier and permafrost shrinking have been already documented, none of the species living in this habitat type are listed in the Habitat Directive Annexes. With this commentary, we call for urgent actions for an ecological characterization of this habitat type in order to plan monitoring and management of the biodiversity hosted by them. An increased knowledge of this no longer permanent habitat appears particularly urgent, because it is not replaceable and is likely to go extinct in the next decades.

Keywords Cold-adapted species · Cryosphere · Glacial biodiversity · Glacier retreat · Habitat monitoring programme · Permafrost

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Communicated by David Hawksworth.

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Commentary

International conventions are a cornerstone of biodiversity conservation, as they allow coordinated conservation and enforcement actions in several continents [e.g. CITES (1973); IUCN (2012); Council Directive 92/43/EEC (1992)]. The States belonging to the European Union have adopted the Habitat Directive [Council Directive 92/43/EEC (1992)] as one of the main tools to ensure the conservation of a wide range of rare, threatened and/or endemic plant and animal species and habitats. Over 1000 plant and animal species, as well as 233 habitat types listed in the directive's annexes are protected in various ways (https://ec.europa.eu/environment/nature/legislation/habitatsdirective/index_en.htm). The Directive also led to the creation of a continental-scale network of protected areas—the Natura 2000 network—for the conservation of species and habitats listed in it. Urbanization, habitat alteration, resource consumption and environmental degradation are some of the major threats for biodiversity, specifically in mountain areas, which are also particularly vulnerable to ongoing climate change (Hock et al. 2019).

Changes of the physiognomy of high altitude landscapes and reduction of the mountain cryosphere (glaciers and permafrost) and its related landforms (Box 1) are among the most visible effects of climate change (Beniston et al. 2018; Adler et al. 2019; D'Agata et al. 2019). Glaciers are perhaps the most sensitive witnesses of climate change, given their fast area reduction (Diolaiuti et al. 2019). Glacier retreat leads to cascade effects on surrounding ecosystems, such as altered hydrological, thermal and bio-geochemical cycles and changes in the extent of glacier-fed streams and glacier forelands (Finn et al. 2010; Robinson et al. 2014; Hotaling et al. 2017; Brighenti et al., 2019). Permafrost is degrading under the effect of climate change as well, for instance through the thickening of the active layer and the reduction of its extent (see UNEP 2016; Biskaborn et al. 2019).

Box 1: Mountain cryosphere and its related landforms

Glaciers are the most evident cryosphere feature in the European mountains. According to the amount of debris cover on their surface, glaciers can be divided into debris-free and debris-covered glaciers (Fig. 1) (Azzoni et al. 2018; Tielidze et al. 2020). Debris-covered glaciers are ice bodies where the largest part of the surface is covered by debris, which deeply influences glacier surface energy budget, ablation rates, long-term volume and surface variations (see Diolaiuti et al. 2019; Fyffe et al. 2019; Fugazza et al. 2019). Glacier-related landforms include glacier forelands and associated landforms (e.g. moraine ridges) and glacier-fed streams, ponds and lakes.

Fig. 1 On the left a vanishing debris-free glacier (Vedretta d'Agola, Brenta Dolomites—Italian Alps); on the right a debris-covered glacier with the tongue extending below the treeline (Miage Glacier, Mount Blanc Group—Italian Alps) (photos by M. Gobbi)

Rock glaciers (Fig. 2) are the most evident and widespread permafrost landform in many mountain areas, including the European mountains, particularly where the climate is cold and dry. A rock glacier is a lobate or tongue-shaped landform consisting of coarse debris with interstitial ice or ice-core, characterized by creeping movement due to ice deformation (Haeberli et al. 2006; Janke et al. 2013). The occurrence of subsurface ice in debris deposits is promoted by the prevalence of coarse blocks over the fine matrix, a grain-size distribution causing a cold thermal regime partially decoupled from that of the surrounding atmosphere (Juliussen and Humlum 2008; Tampucci et al. 2017a; Brighenti et al. 2021).

Fig. 2 A Rock glacier with its typical lobate tongue (Lago Lungo, Ortles-Cevedale Group, Italian Alps; photo by D. Tampucci)

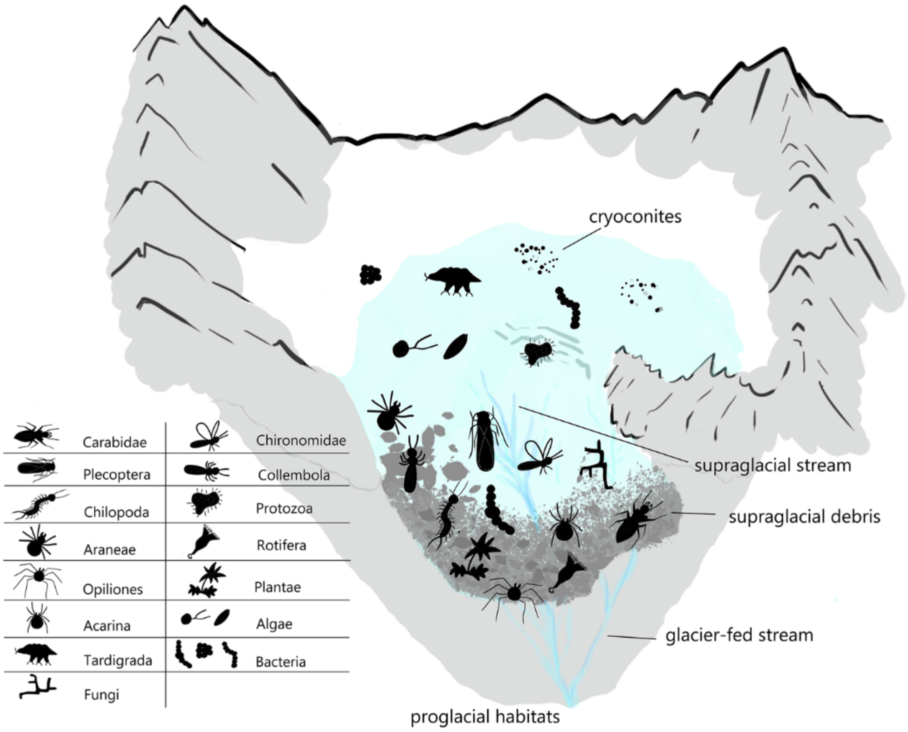

Fig. 3 Schematic representation of the organisms permanently living on a glacier (illustration by B. Valle)

Glaciers and rock glaciers are climate-dependent landforms protected by the Habitat Directive by the habitat type "Permanent Glaciers-Code 8340" [Council Directive 92/43/EEC (1992)]. However, their management is particularly challenging because, as all high altitude habitats, they are changing at an unprecedented rate (Hock et al, 2019) and the ecological communities they host are suffering deep alterations due to species reduction, turnover and local (or global) extinction. In addition, despite this habitat has been included in the Habitat Directive, only a fraction of the surface actually covered by permanent glaciers is protected in the Natura 2000 network, leaving a significant fraction of the Habitat 8340 unprotected. Currently, the total number of sites, belonging to the European countries, linked to the habitat code 8340 is 123; specifically, half of them (61) in Italy, 25 in France, 12 in Spain, 11 in Austria, 10 in Sweden, two in Germany and two in Slovenia (https://natura2000.eea.europa.eu/#).

On the base of the most widespread human perception, glaciers and related landforms are considered harsh environments not able to host living organisms. In contrast, a multitude of studies, many of them performed on the European Alps (see Brighenti et al. 2021), have demonstrated that they are ecosystems in their own right and are a permanent or temporary habitat for a large variety of cold-adapted organisms, from bacteria to vertebrates (Fig. 3).

The extreme specialisation of the organisms permanently living in these landforms makes them particularly threatened by the ongoing rapid climate warming

(Cauvy-Fraunié and Dangles 2019; Anesio and Laybourn-Parry 2012; Rosvold 2016; Gobbi and Lencioni 2020; Stibal et al. 2020). Glaciers are a habitat much more complex and heterogeneous than commonly assumed. Life forms are found on their surface (supraglacial habitat), into the ice (englacial habitat), under the ice (subglacial habitat), close to them (proglacial habitat) and in glacier-fed streams and proglacial lakes and ponds.

The biodiversity hosted by glaciers, rock glaciers and recently deglaciated areas, as well as in glacier-fed streams has been investigated generally by local-scale studies, which often focussed on some taxonomic groups like bacteria, yeasts, algae, plants, nematodes, rotifers, tardigrades, collembolans, insects and spiders (see. Gobbi et al. 2006; Caccianiga et al. 2011; Franzetti el al. 2013; Turchetti et al., 2013; Azzoni et al. 2015, Gobbi et al. 2017; Tampucci et al. 2017a; Lencioni 2018; Hågvar et al. 2020; Lencioni et al. 2021a; Tolotti et al. 2020; Zawierucha et al. 2019, 2021). However, our general knowledge of the biodiversity hosted by glacier environments is still incomplete from the taxonomical and biogeographical point of view.

The occurrence of Habitat 8340 is largely determined by climatic factors and is at risk due to the rapid ongoing climate warming. Some model projections showed that some glaciers are going to be extinct in a few years or decades (Aili et al. 2019; Hock et al. 2019), and with them, probably, the associated local biodiversity. The monitoring and reporting performed under Article 17 of the Habitat Directive, described the status of the Habitat 8340 as unfavourable-bad (U2-the lowermost grade of the Habitat Directive ranking level) for 2013–2018 in all the European countries where it is present, and the same evaluation was given in the previous reporting period (2007–2012). The negative evaluation was reported for all the indicators of habitat status (range, surface, structure and function, future prospects) (https://bd.eionet.europa.eu/article17/reports2012/habitat/report).

From the conservation point of view, we must be aware that this habitat type is not replaceable. Although none of the species living on it are listed in the Natura 2000 Annexes, most of them deserve to be considered threatened by the Habitat 8340 areal reduction due to their (i) small population size, (ii) patchy or restricted distribution (i.e. steno-endemic species), (iii) low dispersal ability, and (iv) ability of surviving only under a narrow range of temperatures (Hotaling et al. 2017; Gobbi and Lencioni 2020). For instance, local extinction of cold adapted aquatic (e.g. the Chironomid *Diamesa steinboecki*) and terrestrial (e.g. the Carabid *Nebria germari*) insect species typical of glacial habitats have been already observed in different areas of the Italian Alps (Lencioni et al. 2021a; Gobbi 2020; Valle et al. 2020). Furthermore, several taxa are likely still unknown, particularly in the least accessible high-alpine areas or mountain groups. In fact, many species living in this habitat probably have a much smaller distribution range than generally assumed, due to the presence of cryptic species (e.g. Bálint et al. 2011), and some endemic taxa are likely still not described and at the risk of extinction even before being described and having DNA sequences deposited (Lencioni et al., 2021b).

An ecological characterisation of Habitat 8340 is mandatory before glaciers and permafrost-related landforms become extinct or heavily reduced in Europe, and with them most of the associated biodiversity, which belongs to the naturalistic and cultural heritage at continental scale. Such characterisation should take into account the different landforms included within the Habitat Directive, such as debris-free and debris-covered glaciers, rock glaciers, proglacial environment, glacier-fed water bodies. Presently, following the interpretation manual of European Union Habitats (https://ec.europa.eu/environment/nature/

legislation/habitatsdirective/docs/Int_Manual_EU28.pdf), Habitat 8340 includes "rock and true glaciers". National monitoring guidelines (e.g. Angelini et al. 2016) provide a more detailed description of the habitat type, which includes glaciers, debris-covered glaciers and rock glaciers, but countries give different interpretations to Habitat 8340. This is evident from the heterogeneous lists of "typical species" provided by member states to assess the parameter of habitat's "structure and function". Some countries (e.g. Austria, Italy) only list strictly supraglacial organisms (mainly algae), suggesting a narrow correspondence of the Habitat with debris-free glaciers, while other countries (Germany, Spain) also include plant species linked to a much wider range of environmental condition, even subalpine shrubs like *Rhododendron ferrugineum* (http://cdr.eionet.europa.eu/help/habitats_art17). This highlights the need for a uniform, comprehensive and updated definition of the Habitat and of the species living in it.

We would like to draw the attention on glaciers, particularly debris-covered glaciers, and on rock glaciers. Debris-free glaciers are mainly colonised by bacteria, algae, arthropods (e.g. Coleoptera Carabidae, Diptera Chironomidae, Plecoptera, Araneae, Acarinae, Collembola), and are periodically or seasonally frequented by birds and mammals (Rosvold 2016, Gobbi and Lencioni 2020). In addition, whenever present, cryoconite holes (water-filled holes on glacial ice surface, in which dark-coloured aggregate of mineral particles and organic matter is deposited), are biodiversity hotspots where bacteria, algae, and several invertebrate taxa (e.g. Tardigrada, Annelida, Copepoda, Rotifera and Collembola) live (Zawierucha et al. 2021). Debris-covered glaciers host an even higher biodiversity also because their tongue, protected from intense ablation by the debris cover, can reach lower altitudes than that of clean-ice glaciers, even below the treeline. Indeed, besides the above-listed taxa, a diversified moss, vascular plant and invertebrate community is able to live on supraglacial debris (Caccianiga et al. 2011; Fickert et al. 2007; Pelfini et al. 2007; Gobbi and Lencioni 2020).

Rock glaciers are deeply different from glaciers as they are characterized by peculiar processes at their surface and inside them (Haeberli 1985) and by different biocoenoses on their surface (Cannone and Gerdol 2003; Burga et al. 2004; Gobbi et al. 2014; Tampucci et al. 2017b). Furthermore, there is an increasing agreement about the role of debris-covered glaciers and rock glaciers as potential refuge areas, in the present warming period, for some cold-adapted species threatened by summit traps in mountain areas (Fickert et al. 2007; Gentili et al. 2015a, 2015b; Tampucci et al. 2017a; Gobbi and Lencioni 2020).

Habitat 8340 is important also for humans, particularly for provisioning (e.g. tourism, industrial activities and "water tower" sensu Immerzeel et al. (2020)) and cultural (including recreational, e.g. mountain sport, and theatres of World War I) ecosystem services (Stewart et al. 2016; Milner et al. 2017; Palomo 2017). Being mainly a phenomenon due to global drivers, it is inconceivable to stop glacial retreat or permafrost thaw through local management strategies. To our knowledge, no action has been developed to mitigate the effect of climate change on this habitat type since the mechanisms driving its dynamics and ecology are still poorly known. Anyway, we cannot continue to ignore the crisis of this habitat type and its associated biodiversity, specifically when actions of habitat monitoring—in natural reserves—are in the planning phase. The poor knowledge we have of this no longer permanent habitat urges to increase the number of studies assessing the status and trends of this Natura 2000 habitat type and its connected biodiversity, in order to develop a European Glacial Biodiversity Monitoring Programme similar to the ongoing Circumpolar Biodiversity Monitoring Programme (see Christensen et al. 2020). Indeed, the spatial and temporal dynamics of the species assemblages linked to the Habitat 8340 is revealing a rapid turnover of species with the substitution of cold-adapted species with more eurythermal species (Lencioni 2018; Hagvar et al. 2020). This pattern deserves to be monitored for better planning conservation of this habitat type.

Funding GFF is funded by the European Research Council, Horizon 2020 Programme, Grant Agreement No. 772284 (IceCommunities).

Data availability Not applicable.

Code availability Not applicable.

Declarations

Conflict of interest The authors declare that there are no conflicts of interest regarding the publication of this paper.

Ethical approval This article does not contain any studies involving animals performed by any of the authors.

Consent to participate Informed consent was obtained from all individual participants involved in the study.

Consent for publication Informed consent was obtained from all individual participants involved in the study.

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Chapter 3

Glacial and periglacial biodiversity

3.1 Glacial biodiversity of the southernmost glaciers of the European Alps (Clapier and Peirabroc, Italy).

J. Mt. Sci. (2022) 19(8): 2139-2159 e-mail: jms@imde.ac.cn http://jms.imde.ac.cn
https://doi.org/10.1007/s11629-022-7331-8

Original Article

Glacial biodiversity of the southernmost glaciers of the European Alps (Clapier and Peirabroc, Italy)

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Citation: Valle B, Gobbi M, Tognett M, et al. (2022) Glacial biodiversity of the southernmost glaciers of the European Alps (Clapier and Peirabroc, Italy). Journal of Mountain Science 19(8). https://doi.org/10.1007/s11629-022-7331-8

Abstract: We applied a multi-taxa approach integrating the co-occurrence of plants, ground beetles, spiders and springtails with soil parameters (temperatures and chemical characteristics) in order to describe the primary succession along two glacier forelands in the Maritime Alps (Italy), a hotspot of Mediterranean biodiversity. We compared these successions to those from Central Alps: Maritime glacier forelands markedly differ for their higher values of species richness and species turnover. Contrary to our expectation, Maritime glacier forelands follow a 'replacement change model', like continental succession of Inner Alps and differently from other peripheral successions. We propose that the temperatures along these Mediterranean glacier forelands are warmer than those along other Alpine glacier forelands, which promote the faster species turnover. Furthermore, we found that early and mid successional stages of the investigated glaciers are richer in cold-adapted and endemic species than the later ones: we confirmed that the 'replacement change' model disadvantages pioneer, cold-adapted species. Given the overall correspondence among cold-adapted and endemic species, the most threatened in this climate phase, our results raise new concerns about the extinction risk of these species. We also describe supraglacial habitat of Maritime glaciers demonstrating that supraglacial debris represents an environment decoupled from the regional climate and may have an important role as refugium for cold-adapted and hygrophilous plant and animal species, whose survival can be threatened by climate change and by a rapid ecological succession in the adjacent forelands.

Received: 22-Jan-2022
Revised: 13-Jun-2022
Accepted: 15-Jul-2022

Keywords: Arthropod communities; Cold-adapted species; Glacier forelands; Plant communities; Primary succession

1 Introduction

Alpine glaciers are retreating globally due to climate change (Paul et al. 2015; Roe et al. 2017), freeing bare grounds - the glacier forelands - that are colonized by several micro- and macro-organisms (e.g. bacteria, plants, arthropods) giving an excellent opportunity to study an ecological succession triggered by climate changes (Cauvy-Fraunié and Dangles 2019; Ficetola et al. 2021).

The main driver of this succession is the time since deglaciation (Erschbamer and Caccianiga 2016; Hågvar et al. 2020), but its dynamics also depend on local climate (Matthews, 1992), biogeographic context (Tampucci et al. 2015) and by physical and chemical conditions at microscale (Castle et al. 2016; Hågvar et al. 2020). In addition, Rosero et al. (2021) recently demonstrated that the patterns of colonisation are taxa-dependent, i.e. different taxa can follow different models along to the same ecological succession.

Two main colonisation models were described (Vater and Matthews 2015; Ficetola et al. 2021): the 'addition and persistence' and 'replacement-change'. The former consists of the persistence of pioneer species (i.e. the initial colonisers) from the recently deglaciated sites (early successional stages) to late-successional stages. Conversely, with the 'replacement-change' process, mainly observed in the Alps, a group of initial colonisers (the pioneer community) is progressively replaced by other species; in this case, there is a species turnover. The two models can be distinguished through the persistence of pioneer species throughout the succession, which can be assessed by different indices (see Matthews et al. 2018) although fixed threshold values cannot be established.

A pilot study by Tampucci et al. (2015) performed in the Central Italian Alps highlighted how colonization dynamic is different in inner mountain chains with respect to peripheral ones, as a consequence of regional climate and altitude (see also Vater and Matthews 2013). In the peripheral chains of the Southern European Alps, the oceanic climate regime seems to allow the persistence of pioneer species along the glacier forelands and makes the succession slower than on glacier forelands at the same altitude under continental climatic regime, probably because of the harsher conditions during the growing season. This phenomenon is particularly evident for plants (Tampucci et al. 2015). This observation is consistent with the autosuccession concept tested by Matthews et al. (2018) along a climatic gradient in Norway, where a 'replacement change' model could be observed in the subalpine zone, progressively replaced by a pattern characterized by a longer persistence of pioneer species, ending with an autosuccession (overlap between pioneer and late successional stages) in the most-climatically-limited sites of the high-alpine zone.

The long-lasting persistence of pioneer stages is particularly important as, in some areas, it allows the survival and extended distributional area of many endemic species (Tampucci et al. 2015).

An additional effect of climate change observed is the increase of supraglacial stony debris due to the reduction of the pressure of the ice volume on the headwalls and the amplification of frost and heat weathering that increase their erosion (Paul et al. 2007). The supraglacial debris can hosts cold-adapted species currently threatened by global warming (Caccianiga et al., 2011; Gobbi et al. 2011, 2017; Valle et al. 2020; Valle et al. 2022) and reduces the ablation rate (Nakawo and Rana 1999), thus potentially acting as refugium for these species during the current warm climatic stage.

In the context of climate change, peripheral glacial areas deserve particular attention for at least three reasons: (1) they display one of the plausible future scenarios for the whole inner chain, given their overall low altitude and the occurrence of few, small and rapidly shrinking glaciers; (2) they are characterised by high richness of endemic species (Medail and Quezel 1999), since they were partially ice-free during glacial periods, acting as refugia (Schonswetter et al. 2005); (3) they could host threatened cold-adapted species in recently-deglaciated areas and on supraglacial debris (Tampucci et al. 2015; Valle et al. 2020)

Maritime Alps (maximum altitude: 3297 m a.s.l.) are the southernmost portion of the European Alps, and border the Mediterranean Sea. They host two small glaciers, Clapier and Peirabroc, the southernmost of the whole Alpine chain (Smiraglia and Diolaiuti 2015). A large amount of rainfall mainly concentrated in spring and autumn as snowfall allows

Maritime glaciers to persist at low latitude and relatively low altitude (Hannss 1970).

Maritime Alps represent the richest area in terms of biodiversity in the European Alps (Medail and Quezel 1999; Villemant et al. 2015) due to the peripheral position with respect to the ice sheet during the Ice Ages, the proximity to the sea, the high environmental variability due to the lithological variety and the high altitude of peaks that allow species of the Alpine altitudinal belt to persist within the Mediterranean region. Because of this peculiar climatic and biogeographic context, Maritime glaciers are unique within the European Alps.

This paper aims to analyse the ecological succession of plant and arthropod (Aracnida: Araneae, Coleoptera: Carabidae and Hexapoda: Collembola) communities along the glacier foreland and on the supraglacial stony debris of the Clapier and Peirabroc glaciers. We hypothesize that: i) different taxa colonise the glacier foreland and the supraglacial habitat, in relation to soil parameters and temperature, with different colonization patterns from each other; ii) succession model in Maritime glaciers are similar to those of other peripheral glaciers as reported in Tampucci et al., 2015; iii) as a consequence of hypothesis ii, cold-adapted species are distributed throughout the whole succession, from pioneer to late successional stages; iv) supraglacial habitat hosts cryophilic (i.e. cold-adapted and hygrophilous) species; v) supraglacial habitat of peripheral glaciers is a peculiar environment hosting a more endemic taxa with respect to supraglacial habitat of inner Alps.

2 Material and Methods

2.1 Study area

The Maritime Alps represent the southernmost part of the Alpine chain, and occur both in Italy and France. We studied Peirabroc (44°07'14" N, 7°24'53" E) and Clapier (44°06'51" N, 7°25'21" E), the last remaining glaciers of Maritime Alps (Smiraglia and Diolaiuti 2015) (Fig. 1, Appendix 1). The bedrock is siliceous, consisting of gneiss and amphibolite (Piana et al. 2017)

The studied glaciers showed an overall retreat following the end of the Little Ice Age (LIA, c. mid 19th century); an advance phase was recorded during the

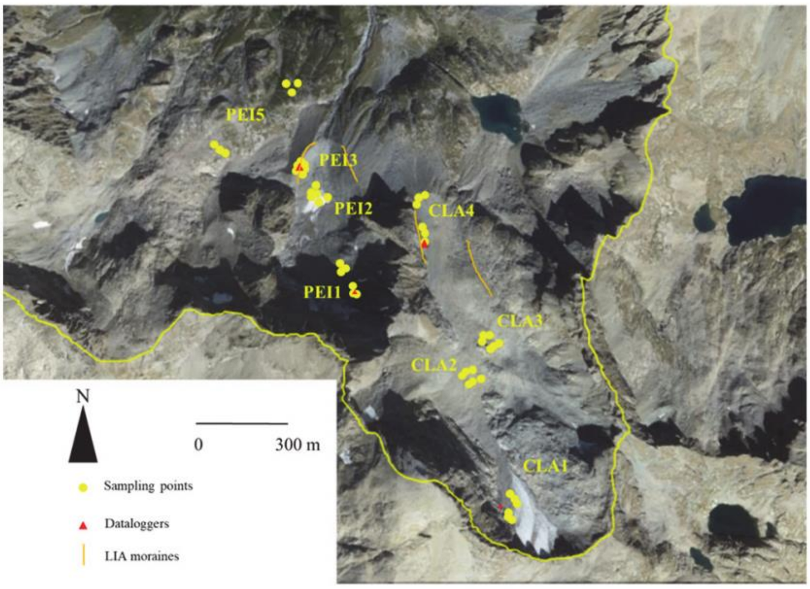

Fig. 1 Sampling plan. View of the environmental units investigated in each study area: Clapier "CLA" and Peirabroc "PEI". Yellow line indicates national border (Italy-France). Orthophoto from Google Earth. See text for details about the sampling design.

1930s and in 1951. The retreat pace increased after 2002 (Federici and Pappalardo 1995, 2010). However, no glaciological data are available for the period 1967-1989, in correspondence to the last consistent advance of Alpine glaciers. Thus, a further possible advance phase was not recorded for these glaciers and only approximate dating of the glacial deposits is possible (Table 1).

Smiraglia and Diolaiuti (2015) reported a surface reduction of 30% for Peirabroc (from 0.1 to 0.07 km^2) and of 77% for Clapier (from 0.3 to 0.09 km^2) for the period 1957-2010.

Approximately 1/3 of the surface of both glaciers is covered by supraglacial stony debris, which is located in the proximal part of the ice tongue (debris cover estimated with Agea 2015 Orthophoto). The minimum altitude of the glaciers tongue recorded in 2019 was 2430 m asl for Peirabroc and 2650 m asl for Clapier; the tongue of Clapier is separated from the accumulation basin at 2750 m asl.

2.2 Sampling design

Five environmental units were selected, three occurring on Peirabroc, four on Clapier, and one common to both glaciers. The environmental units correspond to a specific deglaciation or moraine deposition age, from the glacier front to terrains ice-freed since the Late Glacial Period (LG- c.10000 years BP) - (Table 1); the environmental unit corresponding to LG terrains (PEI5) is common to both glaciers, it ideally represents the late-successional stage of the succession. Terrain age was obtained from literature data reporting previous glaciological surveys (see previous paragraph). An environmental unit was selected also on the supraglacial debris of both glaciers (Fig. 1, Table 1, Appendixes 1 and 2). Two plots were placed in each environmental unit, each one consisting of three sampling points at least 10 meters apart from each other. For each sampling point:

(1) We performed a vegetation survey in a quadrat of 5 x 5 m^2. The cover of rock outcrop, debris, of the whole plant cover and of every single species was estimated with a resolution of 5%; a cover value of 3% or 1%, was assigned for rare (less than 5% cover) and sporadic (one individual) species (Table 2, Appendix 3).

(2) We placed a pitfall trap, to catch and preserve arthropods, consisting of a plastic glass (diameter 7 cm) filled up with a non-toxic and frost-resistant solution made by 2:1 water and wine-vinegar, with salt and few drops of soap (Gobbi 2020); pitfall traps were collected and re-set during two sampling sessions (Harry et al. 2011; Lencioni and Gobbi 2021): 20/21 August 2019 - 10/12 September 2019.

Among the sampled taxa, ground beetles (Coleoptera, Carabidae), springtails (Hexapoda, Collembola) and spiders (Aracnida, Araneae) were chosen for the analyses, because they are ubiquitous and good ecological indicators, particularly in glacial environment (Hågvar et al. 2020).

Table 1 Plot site data. For each glacier, plot codes, their relative environmental unit and deglaciation age are reported.

Glacier	Plot code	Successional stage	Environmental unit	Deglaciation age	Mean altitude of plots (m asl)	Datalogger altitude (m asl)
Peirabroc	PEI1.1 PEI1.2	SD	SD (PEI1)	-	2500	2549
	PEI2.1 PEI2.2	Early SS	Young moraine (PEI2)	1920-1980?	2460	-
	PEI3.1 PEI3.2	Mid SS	LIA Moraine (PEI3)	ca. 1850~	2420	2465
Clapier	CLA1.1 CLA1.2	SD	SD (CLA1)	-	2780	2771
	CLA2.1 CLA2.2	Early SS	Young glacier foreland (CLA2)	1980	2630	-
	CLA3.1 CLA3.2		Young moraine (CLA3)	1920-1980?	2640	-
	CLA4.1 CLA4.2	Mid SS	LIA Moraine (CLA4)	ca. 1850	2510	2552
Peirabroc Clapier	PEI5.1 PEI5.2	Late SS	LG terrains (PEI5)	>10.000 years BP	2450	-

Notes: Deglaciation age: time of deglaciation (foreland) or deposition (moraines). SD= Supraglacial debris ; SS= successional stage. See text for details about the sampling design.

Table 2 Species occurring in each environmental unit. X* = cold-adapted species, H*= hygrophilous species, V= endemic species of Western Alps, V° = endemic species of Maritime and Ligurian Alps, V* = stenoendemic species to Maritime Alps, U= endemic species to Maritime Alps and Tosco-Emiliano Apennines, U* = endemic species to Maritime Alps and Apuan Alps. For plants (p), it is indicated the mean cover value for each environmental unit, for ground beetles (b), spiders (s) and springtails (c) only presence is reported (+). For each environmental unit we indicated the species with the highest significant (indicator species analysis value (IndVal) (red > 90, orange 70<x<90, yellow 60<x<70, green 40<x<60, light blue 30<x<40). For sporadic species see Appendix 3.

Acronym	X*	H*	Endemic	Taxon	Species	PEI1	CLA1	CLA2	PEI2	CLA3	PEI3	CLA4	PEI5
Dor_clu	√			p	*Doronicum clusii (All.) Tausch (X) (*	.	.	.	0.2	0.5	.	.	.
Sax_aiz		√		p	*Saxifraga aizoides* L.	0.2	.	.	1	0.5	.	.	.
Sax_ped			V*	p	*Saxifraga pedemontana* All. sbsp. *pedemontana*	0.5	.	.	1	2	.	.	.
Sax_ret	√		V	p	*Saxifraga retusa* Gouan ssp. *augustana* (Vacc.) D.A.Webb	0.3	.	.	1	1	.	2	.
Poa_laxa	√			p	*Poa laxa* Haenke	0.3	.	.	1	1	2	.	.
Ade_leu	√	√	V	p	*Adenostyles leucophylla* (Willd.) Rchb.	0.2	.	.	3	3	6	3	1
Art_ gla	√			p	*Artemisia glacialis* L.	.	.	.	0.3	1	.	0.2	.
Epi_nut		√		p	*Epilobium nutans* F.W.Schmidt	.	.	.	0.3	.	.	.	.
Art_umb	√			p	*Artemisia umbelliformis* Lam. *ssp.eriantha*	.	.	.	.	1	.	.	.
Hor_alp				p	*Hornungia alpina* (L.) O.Appel	.	.	.	1	1	.	.	.
Lin_alp				p	*Linaria alpina* (L.) Mill.	.	.	.	1	0.5	.	.	.
Oxy_dig	√			p	*Oxyria digyna* (L.) Hill	.	.	0.3	3	3	.	.	.
Sax_opp	√			p	*Saxifraga oppositifolia* L.	.	.	.	1	.	.	.	.
Alc_alp				p	*Alchemilla alpina* L.	.	.	.	.	.	.	1	.
Min_rec				p	*Minuartia recurva* (All.) Schinz & Thell.	.	.	.	.	.	.	3	.
Sax_pan				p	*Saxifraga paniculata* Mill.	.	.	.	0.3	1	.	2	.
Sil_aca	√			p	*Silene acaulis* (L.) Jacq.	.	.	.	1	1	.	3	.
Ac_erb	√			p	*Achillea erba-rotta* All. subsp. *erba-rotta*	.	.	.	0.2	0.5	2	.	.
Ara_alp				p	*Arabis alpina* L.	.	.	.	1	2	1	.	.
Car_par				p	*Carex parviflora* Host	.	.	.	0.2	.	0.2	1	.
Luz_alp_pil	√			p	*Luzula alpinopilosa* (Chaix) Breistr.	.	.	0.3	1	.	1	2	.
Noc_cor	√			p	*Noccaea corymbosa* (J.Gay) F.K.Mey.	.	.	.	0.2	2	2	2	.
Poa_cen				p	*Poa cenisia* All.	.	.	.	2	1	2	1	.
Sax_bry	√			p	*Saxifraga bryoides* L.	.	.	1	2	3	2	3	.
Sax_exa	√			p	*Saxifraga exarata* Vill.	.	.	0.3	2	3	3	3	.
Sem_ara				p	*Sempervivum arachnoideum* L.	.	.	.	0.2	1	3	3	.
Ach_nan	√			p	*Achillea nana* L.	.	.	+	.	.	1	.	.
Dry_vil				p	*Dryopteris villarii* (Bellardi) Woyn. ex Schinz & Thell.	.	.	.	.	.	2	0.5	.
Eri_alp				p	*Erigeron alpinus* L.	.	.	.	.	.	1	2	.
Eup_alp				p	*Euphrasia alpina* Lam.	.	.	.	.	.	5	2	.
Fes_hal				p	*Festuca halleri* All. subsp. *halleri*	.	.	.	.	.	2	1	.
Hie_mor				p	*Hieracium pilosum* Schleich. ex Froel.	.	.	.	.	.	+	1.5	.
Gna_sup	√			p	*Omalotheca supina* (L.) DC.	.	.	.	.	.	1	1	.

(-To be continued-)

(-Continued-)

Table 2 Species occurring in each environmental unit. X* = cold-adapted species, H*= hygrophilous species, V= endemic species of Western Alps, V° = endemic species of Maritime and Ligurian Alps, V* = stenoendemic species to Maritime Alps, U= endemic species to Maritime Alps and Tosco-Emiliano Apennines, U* = endemic species to Maritime Alps and Apuan Alps. For plants (p), it is indicated the mean cover value for each environmental unit, for ground beetles (b), spiders (s) and springtails (c) only presence is reported (+). For each environmental unit we indicated the species with the highest significant (indicator species analysis value (IndVal) (red > 90, orange 70<x<90, yellow 60<x<70, green 40<x<60, light blue 30<x<40). For sporadic species see Appendix 3.

Acronym	X*	H*	Endemic	Taxon	Species	PEI1	CLA1	CLA2	PEI2	CLA3	PEI3	CLA4	PEI5
Jun_tri				p	*Oreojuncus trifidus* (Jacq.) Zav.Drabk. & Kirschner	.	.	.	.	.	2	2	.
Luz_spi				p	*Luzula spicata* (L.) DC.	.	.	.	.	.	2	3	.
Myo_alp				p	*Myosotis alpestris* F.W.Schmidt	.	.	.	.	.	2	3	.
Pil_lac				p	*Pilosella lactucella* (Wallr.) P.D.Sell & C.West	.	.	.	.	.	0.5	0.2	.
Poly_lon				p	*Polystichum lonchitis* (L.) Roth	.	.	.	.	.	2	.	.
Sag_sag				p	*Sagina saginoides* (L.) H.Karst. subsp. *saginoides*	.	.	.	.	.	1	1	.
Thy_oen				p	*Thymus oenipotanus* Heinr.Braun ex Borbas	.	.	.	.	.	1	2	.
Tri_tha				p	*Trifolium thalii* Vill.	.	.	.	.	.	4	5	.
Min_ver				p	*Sabulina verna* (L.) Rchb.	.	.	.	.	.	.	1	.
Tus_far				p	*Tussilago farfara* L.	.	.	.	.	.	1	.	.
Agr_rup	√			p	*Agrostis rupestris* All. subsp. *rupestris*	.	.	.	.	.	2	1	2
Agr_sch				p	*Agrostis schraderiana* Bech.	.	.	.	.	.	3	1	1
Alc_vul				p	*Alchemilla flabellata* Buser	.	.	.	.	.	1	4	2
Ant_alp				p	*Anthoxanthum nipponicum* Honda	.	.	.	.	.	6	1	6
Arm_alp				p	*Armeria alpina* Willd.	.	.	.	.	.	3	3	1
Cam_sch				p	*Campanula scheuchzeri* Vill.	.	.	.	.	.	4	2	3
Eup_min				p	*Euphrasia minima* Jacq. ex DC.	.	.	.	.	.	2	3	1
Fest_vio				p	*Festuca violacea* Ser. ex Gaudin subsp. *violacea*	.	.	.	.	.	1	.	3
Fes_var				p	*Festuca varia*	.	.	.	.	.	1	7	2
Lot_alp				p	*Lotus corniculatus* L. subsp. *alpinus* (DC.) Rothm.	.	.	.	.	.	2	3	4
Min_sed	√			p	*Cherleria sedoides* L.	.	.	.	.	.	1	3	2
Sen_inc	√			p	*Jacobaea incana* (L.) Veldkamp	.	.	.	.	.	3	.	2
Sil_rup				p	*Atocion rupestre* (L.) Oxelman	.	.	.	.	.	2	1	2
Tri_alp				p	*Trifolium alpinum* L.	.	.	.	.	.	2	5	2
Ped_ros_hel				p	*Pedicularis rostratospicata* Crantz ssp. *helvetica* (Steininger) O.Schwarz	.	.	.	.	.	.	3	1
Phy_glo_ped	√			p	*Phyteuma globulariifolium* Sternb. & Hoppe ssp. *pedemontanum* (Rich.Schulz) Becherer	.	.	.	.	.	.	1	2
Ast_min				p	*Astrantia minor* L.	.	.	.	.	.	.	.	1
Ave_ ver				p	*Helictochloa versicolor* (Vill.) Romero Zarco subsp. *versicolor*	.	.	.	.	.	.	1	2
Car_sem				p	*Carex sempervirens*	.	.	.	.	.	.	1	25
Leo_hel				p	*Scorzoneroides helvetica* (Merat) Holub	.	.	.	.	0.2	.	1	4

(-To be continued-)

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Table 2 Species occurring in each environmental unit. X* = cold-adapted species, H*= hygrophilous species, V= endemic species of Western Alps, V° = endemic species of Maritime and Ligurian Alps, V* = stenoendemic species to Maritime Alps, U= endemic species to Maritime Alps and Tosco-Emiliano Apennines, U* = endemic species to Maritime Alps and Apuan Alps. For plants (p), it is indicated the mean cover value for each environmental unit, for ground beetles (b), spiders (s) and springtails (c) only presence is reported (+). For each environmental unit we indicated the species with the highest significant (indicator species analysis value (IndVal) (red > 90, orange 70<*x*<90, yellow 60<*x*<70, green 40<*x*<60, light blue 30<*x*<40). For sporadic species see Appendix 3.

Acronym	X*	H*	Endemic	Taxon	Species	PEI1	CLA1	CLA2	PEI2	CLA3	PEI3	CLA4	PEI5
Lig_mut				p	*Mutellina adonidifolia* (J.Gay) Gutermann							.	2
Luz_lut				p	*Luzula lutea* (All.) DC.							2	1
Meu_ath				p	*Meum athamanticum* Jacq.								1
Nar_str				p	*Nardus stricta* L.								20
Phy_mic			V	p	*Phyteuma micheli* All.								2
Ran_mon				p	*Ranunculus montanus* Willd.								3
Rho_fer				p	*Rhododendron ferrugineum* L.								10
Sol_alp				p	*Soldanella alpina* L. ssp. *alpina*								2
Vac_myr				p	*Vaccinium myrtillus* L.							0.2	2
Vac_uli				p	*Vaccinium uliginosus* L.								4
Vio_cal				p	*Viola calcarata* L.								1
Sem_mon				p	*Sempervivum montanum* L.					1	0.5		
Sem_tec				p	*Sempervivum tectorum* L.				0.2	1		1	1
Car_res				p	*Cardamine resedifolia* L.				2	2	1	1	2
Cir_spi				p	*Cirsium spinosissimus* (L.) Scop.				0.2	.	1		1
Fes_mel				p	*Festuca nigricans* (Hack.) K.Richt.				2	2	6	9	3
Leu_alp	√			p	*Leucanthemopsis alpina* (L.) Heywood			0.3	1	0.2	0.3	2	1
Poa_alp				p	*Poa alpina* L.			1	3	3	4	5	4
Sag_gla				p	*Sagina glabra* (Willd.) Fenzl				0.3	.	1	1	1
Sed_alp				p	*Sedum alpestre* Vill.				2	2	3	3	2
Ver_alp		√		p	*Veronica alpina* L.				1	.	1	3	1
Ore_ang	√	√	V*	b	*Oreonebria angusticollis* ssp. *microcephala* (K. & J. Daniels)	+		+					
Neb_joc				b	*Nebria jockischii* Sturm. 1815								
Cic_gal				b	*Cicindela gallica* Brullé						+	.	
Lae_jan_coe				b	*Laemostenus janthinus coeruleus* Dejean. 1828							+	
Ama_car	√		V°	b	*Amara carduii* ssp.*psyllocephala* K. & L.							+	
Car_ped	√		V	b	*Carabus pedemontanus* Ganglbauer. 1891						+	+	+
Pte_mor	√		V*	b	*Pterostichus morio* ssp. *fenestrellanus* Csiki						+	+	+
Har_rub				b	*Harpalus rubripes* (Duftschmid. 1812)								+
Ore_mac	√		U	b	*Oreonebria macrodera* (K. Daniel. 1903)								+
Ent_sp				s	*Entelecara sp*			+				+	

(-To be continued-)

(-Continued-)

Table 2 Species occurring in each environmental unit. X* = cold-adapted species, H*= hygrophilous species, V= endemic species of Western Alps, V° = endemic species of Maritime and Ligurian Alps, V* = stenoendemic species to Maritime Alps, U= endemic species to Maritime Alps and Tosco-Emiliano Apennines, U* = endemic species to Maritime Alps and Apuan Alps. For plants (p), it is indicated the mean cover value for each environmental unit, for ground beetles (b), spiders (s) and springtails (c) only presence is reported (+). For each environmental unit we indicated the species with the highest significant (indicator species analysis value (IndVal) (red > 90, orange 70<*x*<90, yellow 60<*x*<70, green 40<*x*<60, light blue 30<*x*<40). For sporadic species see Appendix 3.

Acronym	X*	H*	Endemic	Taxon	Species	PEI1	CLA1	CLA2	PEI2	CLA3	PEI3	CLA4	PEI5
Dip_hel	√			s	*Diplocephalus helleri* (L. Koch. 1869)				+				
Mug_sp				s	*Mughiphantes sp*			+					
Ves_jug	√		V*	s	*Vesubia jugorum* (Simon. 1881)				+	+			
Coe_pab			V	s	*Coelotes pabulator* Simon. 1875				+	+	+		
Coe_pic_pas	√		V	s	*Coelotes pickardi pastor* Simon. 1875					+		+	
Par_nig	√			s	*Pardosa nigra* (C. L. Koch. 1834)					+		+	
Dys_cri	√		V	s	*Dysdera cribrata* Simon. 1882							+	
Xys_des	√			s	*Xysticus desidiosus* Simon. 1875							+	
Zel_gal				s	*Zelotes gallicus* Simon. 1914						🟦 .	🟦 +	
Dra_pub				s	*Drassodes pubescens* (Thorell. 1856)				+				+
Cen_pab				s	*Centromerus pabulator* (O. Pickard-Cambridge. 1875)								+
Coe_ose	√		U*	s	*Coelotes osellai* de Blauwe. 1973								+
Pal_pal				s	*Palliduphantes pallidus* (O. Pickard-Cambridge. 1871)								+
Par_bla				s	*Pardosa blanda* (C. L. Koch. 1833)								🟥 +
Orc_fro	√		V	c	*Orchesella* cf. *frontimaculata* Gisin	+		🟩 +	+	+			
Iso_sp.				c	*Isotomidae sp.*	+		.	+				
Deu_pal				c	*Deutherosminthurus pallipes* (Bourlet. 1843)	+		+	.	.	🟦 +	🟦	
Lep_cur gr				c	*Lepidocyrtus* gr *curvicollis* (sensu (Mateos. 2012)	+		+	🟦 +	🟦 +	+	+	+
Orc_alt				c	*Orchesella alticola* Uzel			+	🟦 +	🟦 +			
Tom_min				c	*Tomocerus minor* (Lubbock)				+				
Smi_sp				c	*Sminthurus* sp.				+			+	
Cer_arm				c	*Cerathophysella armata* (Nicolet. 1841/1842)							+	
Fas_sau	√		V	c	*Fasciosminthurus sauteri* (Nayrolles & Lienhard. 1990)						🟩 +	🟩	
Ent_lan				c	*Entomobrya lanuginosa* (Nicolet. 1842)						🟩 +	🟩	
Lep_cya gr				c	*Lepidocyrtus* gr *cyaneus* (sensu (Mateos. 2012))						+		+
Orc_qui				c	*Orchesella quinquefasciata* (Bourlet)								🟥 +

(3) We collected a soil sample of 200 g for analyse pH values, organic matter content (Walkley-Black method). In every plot (except plot CLA2, where it was not possible) a soil sample of approximately 2 kg was taken to estimate grain size distributions.

The considered taxa were identified to the species level or, whenever it was not possible, to the genus or family level. Plants were identified with Pignatti (2017), ground beetles with Pesarini and Monzini (2010, 2011), spiders with Roberts (1995), springtails with Bretfeld (1999), Gisin (1960), Jordana (2012), Mateos (2012), Thibaud et al. (2004). Only adult specimens of carabids and spiders were considered. Nomenclature follows Bartolucci et al. (2018); Jong et al. (2014) for plants and arthropods, respectively.

The sampled arthropods were preserved in ethanol and stored at Natural Science Museum of Bergamo, Italy (spiders), and at MUSE - Science Museum of Trento, Italy (ground beetles, springtails and other taxa not identified at the species level).

Two dataloggers (Tinytag plus 2) were placed, one in correspondence to supraglacial debris and one near the LIA Moraines of each glacier in order to analyse the patterns of mean daily ground surface temperature and humidity during the period 3 August 2019 - 13 September 2020. The devices were placed between stones at a depth of c. 10 cm, in order to shield them from direct solar radiation, and to obtain micrometeorological data about the substrate in which plant roots and arthropods develop. The recording was set at 30 minute intervals. Datalogger on Peirabroc supraglacial debris was downloaded in September 2019; afterwards, it was lost during winter due to avalanches and rockfalls; thus only data from one month (4 August 2019 - 11 September 2019) are available.

2.3 Data analysis

Vegetation data were expressed as cover values (%), while occurrence data of the considered ground-dwelling arthropods were expressed as presence/ absence, since the second sampling session was not available for all the sampling points because many traps were damaged by snow and wild fauna. Site (altitude, slope, aspect) and soil data were standardized ($y = (x - \text{mean})/$ standard deviation; Kreyszig 1979) and aspect was normalized with ($-\cos(X)$).

We defined as "cold-adapted" all the species strictly linked to the Alpine and Nival altitudinal belts (Table 2). In particular, concerning plants, we defined as "cold-adapted" the species with temperature index = 1 (alpine and nival) and temperature range of variation = I (temperature index variation at most ±1) in Landolt et al. (2010); concerning arthropods, we referenced to the available descriptive literature about the ecological requirement of each identified taxon (Thaler 1988, 1999; Gisin 1960; Isaia et al. 2007; Bisio 2008; Jordana 2012; Pantini and Isaia 2019; Pesarini and Monzini 2010, 2011; Potapov 2001). Hygrophilous species are those linked to high availability of water (but not aquatic): we consider hygrophilous plant species with Landolt's humidity index = 4 or 4.5; concerning arthropods, we referenced to the available descriptive literature about the ecological requirement of each identified taxon (as above). Species that are both cold-adapted and hygrophilous are defined cryophilic (Deharveng et al. 2008). All analyses were performed with PAST 4.05 software (Hammer et al. 2001).

2.3.1 Environmental variables

In order to calculate changes in mean annual temperature and snow persistence along the glacier foreland, micrometeorological data recorded on LIA moraines were used to estimate soil temperature on the whole glacier foreland, applying a standard adiabatic gradient of 0.6°C/100 m (Rolland 2003), as tested by Tampucci et al. (2015). Data recorded by datalogger placed on the supraglacial debris of Clapier were used to describe the supraglacial environment. Temperature data obtained by the dataloggers allowed us to outline the snow cover period, where temperature remain constant and close to 0°C. (Appendix 4) The shorter series of data available for the Peirabroc supraglacial environment was compared with Clapier's corresponding series in order to evaluate differences or homologies in trends between the two glaciers.

We used descriptive statistics (mean value and standard deviation for each environmental unit) to describe the distribution of soil parameters (soil pH, organic matter content, grain size distribution, total plant cover) along the investigated glacier forelands.

A non-parametric monotone correlation coefficient (Spearman's *rho*) was calculated to investigate the collinearity between the soil variables, then Principal Component Analysis (PCA) was used to evaluate the association among them in order to rule out some of the auto-correlated variables from the subsequent analyses (Hammer 1999-2021).

2.3.2 Plant and arthropod succession in relation to environmental gradients

Patterns of plant and arthropod species distribution along the glacier foreland in relation to environmental variables were described through canonical correspondence analysis (CCA; Legendre and Legendre 1998). We selected this direct gradient analysis because the response of species to the environmental variables is supposed to be unimodal due to the presence of complex ecological filtering driving the response of species occurrence and/or abundance (see Ficetola et al. 2021); furthermore, this analysis is particularly suitable for heterogeneous datasets along long ecological gradients (Hammer et al. 2001; Zeleny 2022) .

These analyses were carried out: (A) for plants, on a matrix of continuous data of plant species including 22 sampling points for 76 species on Peirabroc (20 species out of 96 were omitted since occurring in only one sampling point; 2 sampling points were omitted since no plant species was recorded in them) and 22 sampling points for 73 species on Clapier (19 species out of 92 were omitted since occurred in only one sampling point; 2 sampling points were omitted since no plant species was recorded in them); (B) for arthropods, on a binary matrix with 21 plots and 27 species on Peirabroc and 21 plots for 30 species on Clapier. Environmental variables included in all CCA analyses were slope, aspect, pH and soil organic matter; the three most correlated variables - gravel and sand, silt and clay and plant cover - were omitted, because of their ecological redundancy (Appendix 5).

For identifying typical plant and arthropod species of each environmental unit, we used Indicator Species Analysis (indicator value: IndVal; Podani & Csányi 2010), carried out on the matrix used for CCA, merging plots of the same age into the same environmental unit according to Table 1.

2.3.3 Comparative analysis of succession parameters

In order to compare the succession trend of different regions of the Alpine chain, we compared the ecological succession of the two Maritime Alps glacier foreland with one glacier from the peripheral (southern) Alps: Trobio glacier (Orobian Alps, glacier foreland above the tree line, 2350-2550 m asl, (Tampucci et al. 2015) and with two glaciers form Rhaetian (inner) Alps: Rotmoos glacier (Rhaetian Alps, glacier foreland near the potential tree line, 2280-2400 m asl, Austrian Alps; Kaufmann 2001; Marcante et al. 2009), and Cedec glacier (Rhaetian Alps, glacier foreland above the tree line, 2694-2726 m asl, Italian Alps; Gobbi et al. 2010). All these glaciers are characterized by siliceous bedrock. The terrain age for each sampled site was taken from the original publications (literature cited above).

Specifically, for each ecological succession of the glacier forelands we calculated two indices of turnover for plants, spiders, ground beetles and springtails (springtail data were available only for Peirabroc and Clapier):

(1) Whittaker species turnover index (Whittaker 1972): $\beta_W = (\gamma - \alpha)/\alpha = \gamma/\alpha - 1$ (where γ is the total species diversity and α is the mean species diversity at the habitat level);

(2) Persistence index (Vater and Matthews 2015): $PPn = 100c/a$ (where c is the number of common species of the two sites and a the number of species of the most pioneer site).

To perform a homogeneous comparison, we merged the two pioneer stages of Clapier (CLA2 and CLA3), considering the following four deglaciation stages (Tampucci et al. 2015): 1 = pioneer (1-30 years since deglaciation); 2 = early (31-100 years since deglaciation); 3 = mid (101-170 years since deglaciation); 4 = late (c. 10.000 years old, ice-free since the LG) (Table 1). Plant and arthropod data were not available for stage 1 on Peirabroc and Clapier, because this environment was not included in our sampling design being not clearly identifiable on the field: for this reason, the total persistence index was calculated from 2 to 4 for all glacier forelands.

3 Results

3.1 Environmental gradients along the glacier foreland and on the supraglacial debris

The mean annual temperature measured on the LIA moraine was 4.2°C for Clapier (at 2510 m asl) and 3.3°C for Peirabroc (at 2420 m asl). The values calculated for the uppermost areas of the glacier forelands are 4.0°C for Clapier (at 2630 m asl)) and 2.5°C for Peirabroc (at 2460 m asl). The mean annual temperature of the supraglacial debris, available only for Clapier, was -1°C.

Snow lasted on the Peirabroc LIA moraines for about 214 days and for 183 days on Clapier; on the supraglacial debris of Clapier it lasted for 295 days; considering the similarity among the thermal trends on the two glaciers we can expect similar data of snow persistence on Peirabroc glacier.

Soil parameters were not related to slope and aspect on both glaciers (Appendix 5). Soil parameters along the glacier foreland showed a progressive decrease of pH (from 7.5 to 5.5), gravel and sand fraction (from 99% to 60%) and a corresponding increase of organic matter content (from 4 to 163 g/kg), silt and clay fraction (from 1% to 40%) with increasing terrain age (Appendix 6)

PCA gave similar results for the two glaciers (Appendix 7): soil data were displaced along PCA axis 1, particularly for Peirabroc glacier, representing the main environmental gradient, while slope and aspect were related to axis 2.

3.2 Biodiversity of the southernmost alpine glacier forelands

One hundred and four plant species were found on both glacier sites; the most frequent are *Poa alpina, Festuca nigricans, Adenostyles leucophylla* (occurring respectively in 64%, 50%, 47%, of all samples), and the most abundant are *Festuca nigricans, Poa alpina* and *Carex sempervirens* (cumulative cover values are 124%, 101% and 96%, respectively). Among the observed species, 22 (21.2%) are "cold-adapted" and 13 (12.5%) are endemic to the Alps, including *Saxifraga pedemontana* ssp. *pedemontana*, stenoendemic of Maritime Alps and *Saxifraga retusa* ssp. *augustana, Adenostyles leucophylla* and *Phyteuma michelii* endemic of Western Alps. *Saxifraga retusa* ssp. *augustana* is also cold-adapted and *Adenostyles leucophylla* is also cryophilic.

Among the nine ground beetle species found on both glaciers, the most abundant are *Pterostichus morio* ssp *fenestrellanus* (80% of all individuals sampled, 117 specimens) and *Carabus pedemontanus* (10%, 14 specimens); Five of these species (56 %) are high-mountain cold-adapted species (Table 2); five species (56%) are Alpine endemic, including one species endemic of Western Alps, *Carabus pedemontanus*, two subspecies present only in Maritime Alps, *Oreonebria angusticollis* ssp. *microcephala*, *Pterostichus morio* ssp *fenestrellanus,* and *Amara carduii* ssp. *psyllocephala,* the latter present in Maritime and Ligurian Alps. All the cold-adapted species are also endemic. *Oreonebria angusticollis* ssp. *microcephala* is the only cryophilic arthropod found.

Fifteen spider species were found on both glaciers; the most abundant are *Pardosa blanda* (36%, 20 specimens) and *Coelotes pabulator* (9%, 5 specimens). Seven of them (47%) - *Coelotes osellai, Coelotes pickardi pastor, Diplocephalus helleri*, *Dysdera cribrata, Pardosa nigra, Vesubia jugorum, Xysticus desiosus* - are high mountain cold-adapted species. Five (33%) are Alpine endemic species, including *Coelotes osellai* (endemic of Maritime and Apuane Alps) and *Vesubia jugorum*, stenoendemic to Maritime Alps.

Twelve species of ground-dwelling springtails were found on both glaciers, with *Orchesella* cf. *frontimaculata* (45%, 350 specimens) and *Orchesella quinquefasciata* (25%, 195 specimens) as the most abundant. Among them only *Orchesella* cf. *frontimaculata* and *Fasciosminthurus sauteri* are high mountain and Alpine endemic species (17 %).

3.3 Plant community succession

In both Peirabroc and Clapier sites plots are arranged following two main gradients outlined by the CCA (Fig. 2): the first corresponds to soil evolution, expressed by pH value and organic matter content, that arrange plots following their chronological succession and are highly correlated with CCA axis 1 (Pearson *r* index 0.91 and -0.87 for Peirabroc and -0.71 and 0.92 for Clapier, respectively). The second gradient is related to topographic data (aspect: Pearson *r* index with CCA axis 2 0.71 and 0.65 for Peirabroc and Clapier, respectively).

The plant succession dynamic is similar along the two glacier forelands, with differences due to sporadic species occurrence. In the early successional stage of Peirabroc glacier forelands (environmental unit PEI2) we found 31 plant species (mean total plant cover for plot 32%); on Clapier this successional stage includes two different environmental units: on the young glacier foreland (CLA2) we found only six plant species (mean total plant cover for plot 2%). On the young moraine (CLA3) we found 24 species, with a mean total plant cover of 34%. According to Indval (Table 2, Appendix 8) the best indicator species of early successional stages are *Oxyria digyna, Arabis*

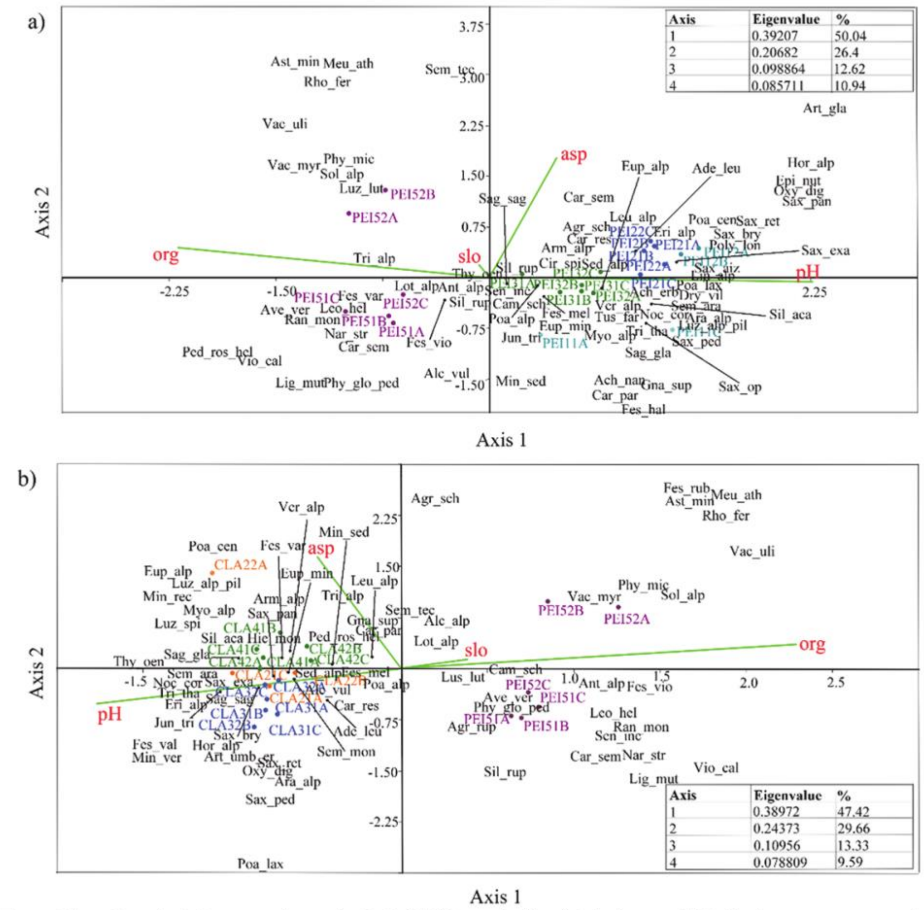

Fig. 2 Plant Canonical Correspondence Analysis (CCA) graphs for a) Peirabroc and b) Clapier. asp = aspect, slo = slope, org = organic matter, pH = soil pH.

alpina, Saxifraga aizoides, Hornungia alpina and *Linaria alpina*. In mid-successional stages on Peirabroc (PEI3, LIA moraines) eleven early colonizer species persisted, but 37 late colonizers appeared, thus reaching the highest species richness (48) with a mean total plant cover of 97%. This could be observed also in the mid-successional stage of Clapier (CLA4), with 53 species and a mean total plant cover of 115%. According to IndVal, the indicator species for this environmental unit (Table 2) are *Myosotis alpestris, Euphrasia alpina, Trifolium thalii, Luzula spicata* and *Armeria alpina*. Late successional stages (PEI5) showed slightly higher plant cover values (133%) with many exclusive late successional species such as *Carex sempervirens, Scorzoneroides helvetica, Nardus stricta* and *Ranunculus montanus*, which are the best indicator species according to IndVal (Table 2).

In general, only few species are ubiquitous along all the glacier forelands: *Leucanthemopsis alpina, Poa alpina, Luzula alpinopilosa, Saxifraga bryoides, Saxifraga exarata*. Analysing the general trend of species richness (Fig. 3), plants show an increase in species richness on the mid-successional stages and then a decrease in the late successional stages.

Among the early successional species, only

Saxifraga pedemontana ssp. *pedemontana,* the hygrophilous *Saxifraga aizoides*, the cold-adapted *Saxifraga retusa*, *Poa laxa* and the cryophilic *Adenostyles leucophylla* have been found on supraglacial debris, in Peirabroc sites (PEI1); the percentage of endemic plant species is 60% (3 species among 5) and also the percentage of cold-adapted species is 60%; 2 among 3 species are both endemic and cold-adapted. On Clapier supraglacial debris (CLA1) no plant species was found.

3.4 Arthropod community succession

Along Peirabroc glacier foreland arthropod communities are arranged primarily in relation to a soil evolution gradient (Fig. 4), with CCA axis 1 highly correlated to organic matter content (Pearson *r* index = 0.83) and soil pH (Pearson *r* index = -0.92). Axis 2 is related to aspect (Pearson *r* index= -0.42). Along Clapier glacier foreland arthropod distribution follows two main gradients: the first is that of the soil organic matter (Pearson *r* index = 0.86), arranging plots and species along the CCA axis 1 and the second is that of aspect and slope, correlated to CCA axis 2 (Pearson *r* index = -0.66, Pearson *r* index = -0.58).

IndVal analysis significantly associated to early successional stage of the young glacier foreland (CLA2) the cold-adapted and endemic springtail *Orchesella* cf. *frontimaculata* and the spider *Entelecara* sp. (Table 2, Appendix 8) with a total amount of two species of spiders and four of ground-dwelling springtails; only one species of ground beetle was sampled here, the cryophilic and endemic *Oreonebria angusticollis* ssp. *microcephala*.

In the early successional stages of young moraines (PEI2 and CLA2-3), one ground beetle species (*Nebria jockischii*), six species of spiders (four cold-adapted and three endemic) and three ground-dwelling springtail species were found. The spider *Coelotes pabulator* and the springtails *Lepidocyrtus* gr. *curvicollis* and *Orchesella alticola* resulted an indicator species of this successional stage according to IndVal (Table 2).

In the mid-successional stages (PEI3 and CLA4) we found five ground beetle species (three cold-adapted and endemic), seven spider species (four cold-adapted and three endemic; among these seven species, only *Coelotes pabulator* was found on Peirabroc) and seven ground-dwelling springtail species (one of them cold-adapted and endemic). The ground beetles IndVal analysis showed the *Carabus pedemontanus, Pterostichus morio* ssp. *fenestrellanus*, the spider *Zelotes gallicus* and the springtails *Fasciosminthurus sauteri* and *Entomobrya lanuginosa* to be indicator species for these successional stages (Table 2).

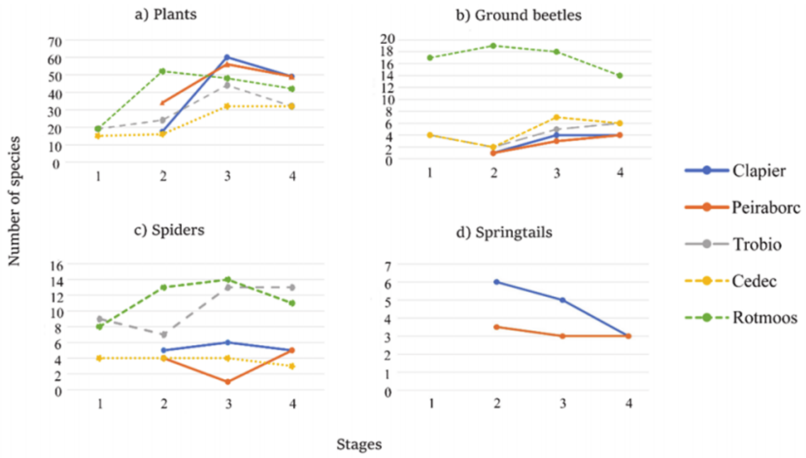

Fig. 3 Species richness for plants a), ground beetles b), spiders c) and springtails d) along the compared glacier forelands. Stages of deglaciation: 1 = pioneer stage (c. 1-30 years since deglaciation); 2 = early stage (c. 31-100 years since deglaciation); 3 = mid stage (c. 101-150 years since deglaciation, ice-free since the LIA); 4 = late stage (c. 10.000 years old, ice-free since the LG).

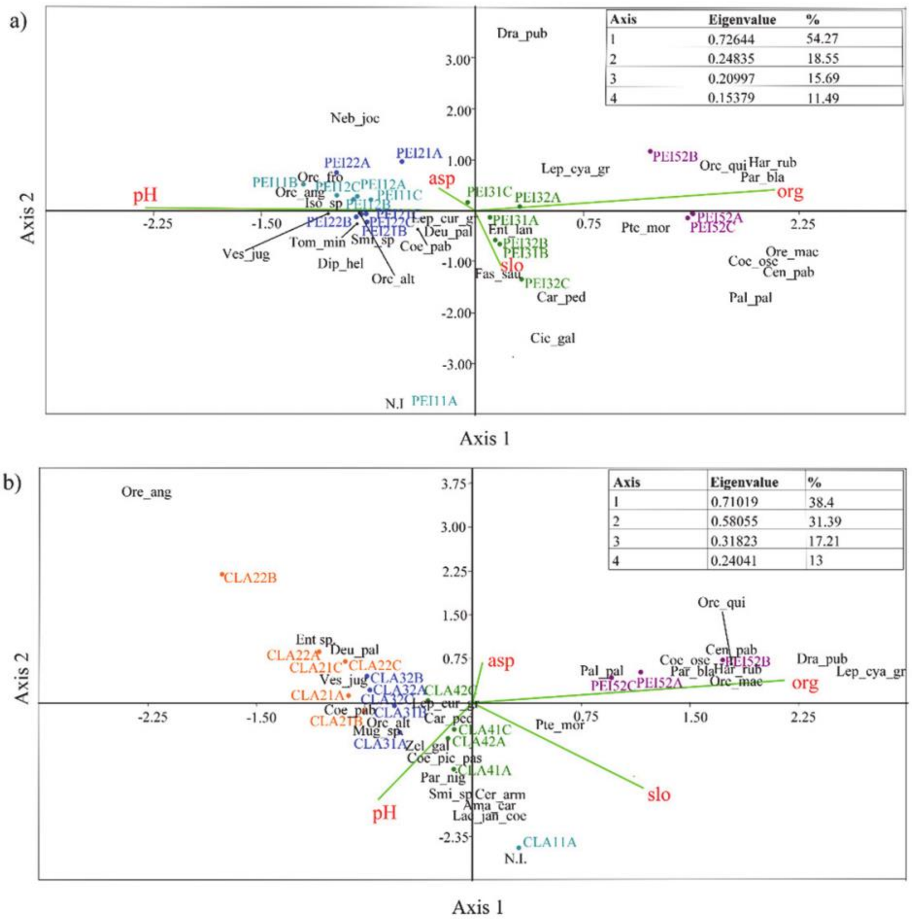

Fig. 4 Arthropod Canonical Correspondence Analysis (CCA) graphs for a) Peirabroc and b) Clapier. asp = aspect, slo = slope, org = organic matter, pH = soil reaction, pH.

The late successional stage (PEI5) hosts an arthropod community quite different from that of the previous successional stage, with four ground beetle, six spider and three ground-dwelling springtail species. According to IndVal, the indicator species linked to this successional stage are: the ground beetle *Harpalus rubripes,* the wolf spider *Pardosa blanda* and the springtail *Orchesella quinquefasciata* (Table 2).

The main difference between the two glaciers is the low number of spiders in the mid-successional stage of Peirabroc.

Analysing the general trend of species richness, arthropods and plants follow different colonization patterns, with some differences between the two glaciers (Fig. 3 b-d). Spiders show a strong decrease in total species richness in the mid-successional stages of Peirabroc but a peak on Clapier. Ground-dwelling springtails show the highest number of species in the early successional stages and then a monotonic decrease on Peirabroc. On Clapier the trend is similar but with lower initial values. Ground beetles show an increase of species during the succession until the LIA moraines, and then the number stabilizes; only along the Clapier glacier foreland there is a positive peak in the mid-successional stages.

The supraglacial debris also hosts arthropod species. Five ground-dwelling arthropod taxa were found: the cryophilic and endemic ground beetle *Oreonebria angusticollis* ssp. *microcephala* (for the indicator species for this environment; Table 2) the springtails *Orchesella* cf. *frontimaculata* (cold-adapted and endemic species), Isotomidae sp., *Deutherosminthurus pallipes, Lepidocyrtus* gr *curvicollis*. No spiders were found on this environmental unit. The percentage of endemic species among arthropods in this habitat is 40%, considering ground beetles and springtails, and 100%, considering only spiders and ground beetles. The same percentages also represent the incidence of cold-adapted species, since all species are both cold-adapted and endemic.

3.5 Comparative analysis of succession patterns

The pattern of total plant species richness along the Clapier and Peirabroc chronosequence was characterised by a mid-successional maximum in correspondence to LIA moraines. Differently, an early-successional maximum was recorded for Rotmoos (Fig. 3a). A trend similar to the plant trend, with a lower maximum, was observed for ground beetles (Fig. 3b); also for ground beetles, on Rotmoos the maximum of species richness was reached earlier than on the other glaciers. Unlike the other taxa, for spiders it is difficult to identify a general trend common among glaciers (Fig. 3c). The comparison between Peirabroc and Clapier springtail trends suggested a general decrease in species richness along the foreland (Fig. 3d).

In general, Peirabroc and Clapier are characterized by higher values of the Whittaker species turnover β_W than the other glaciers previously studied in inner and peripheral Alps. For plant succession, the highest values on Peirabroc and Clapier occurred in the transition from early to mid-successional stages (Fig. 5a), differently from other glaciers where usually the turnover lies between mid and late-successional stages. A similar trend, with different absolute values, was observed for ground beetles (Fig. 5b). For spiders, the trend is similar among glaciers, with a late peak in turnover (Fig. 5c). The comparison among Whittaker indexes in springtail succession along Peirabroc and Clapier glacier forelands suggested very different trends among the two Maritime glaciers (Fig. 5d).

The persistence index (Fig. 6a-d) showed lower values for Clapier and Peirabroc than for the previously studied glaciers, confirming an overall higher turnover. In particular, all pioneer taxa persisted to the mid-successional stage on Trobio glacier, while on Cedec and Rotmoos species persisted

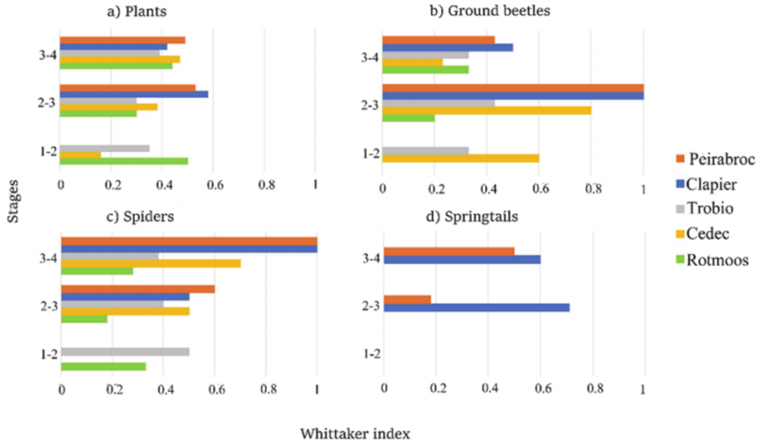

Fig. 5 Whittaker index for plants a), ground beetles b), spiders c), springtails d) along compared glacier forelands. 1-2 = from pioneer to early successional stage, 2-3 = from early to mid successional stage, 3-4 = from mid to late successional stage.

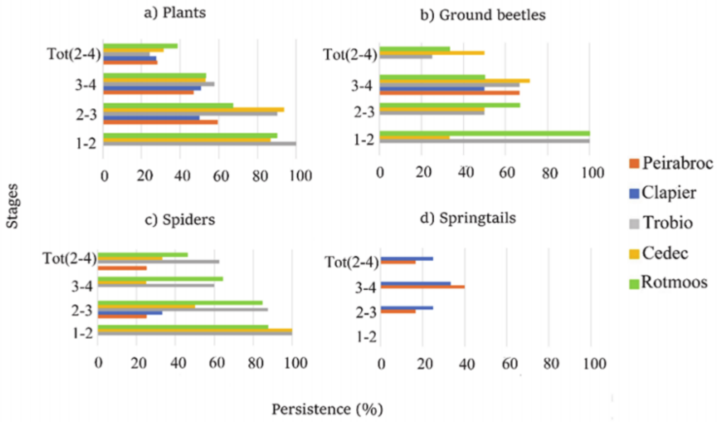

Fig. 6 Persistence index for plants a), ground beetles b), spiders c) and springtails d) along the compared glacier forelands. 1-2 = from pioneer to early successional stages, 2-3 = from early to mid successional stages, 3-4 = from mid to late successional stages. Data are not available for the passage from stage 1 to 2 on Peirabroc and Clapier: for this reason, the total persistence index was calculated from 2 to 4 for all glacier forelands.

longer through the succession. Plants (with the exception of Rotmoos) and spiders were the most persistent taxa from pioneer to mid successional stages; instead, ground beetles are persistent from mid to late successional stages. On Peirabroc and Clapier, springtail persistence index is very low in every successional stage.

4 Discussion

4.1 Thermal data

Our work is among the first to describe plant and arthropod communities colonizing the southernmost glacier forelands of the European Alps: Peirabroc and Clapier glacier forelands stand out for having remarkably higher average annual temperature (respectively 2.5° and 4.0°C) with respect to other studies in the inner (-1.8°C/-1.3°C ; Kaufmann et al. 2002a,b), and peripheral (1.7°C in Gobbi et al. 2017; from 0.5°C to 1.3°C in Tampucci et al. 2015) Central Alps, at comparable altitude. The average annual temperature recorded by our dataloggers is comparable to values reported by Federici and Pappalardo (2010) and Rapetti and Vittorini (1992) for the same area, confirming reliability of our data. The average annual temperature recorded on supraglacial debris (-1°C) is similar to those recorded on other debris-covered glaciers of the European Alps (Gobbi et al. 2017; Valle et al. 2020).

4.2 Biodiversity of the southernmost Alpine glacier forelands

The investigated glacial environments host a remarkable biodiversity, with some noteworthy peculiarities of endemic species most of which are also cold-adapted and considered to be alpine species, but there are species of the area straddling both the Southern Alps and the Northern Apennines: the ground beetle *Oreonebria macrodera*, from Maritime Alps to Northern Apennines, and the spider *Coelotes osellai*, from Maritime Alps to Apuan Alps.

The most relevant findings include the plant *Saxifraga pedemontana* ssp. *pedemontana,* the ground beetles *Carabus pedemontanus, Oreonebria angusticollis* ssp. *microcephala*, *Amara carduii* sbsp. *psyllocephala*, *Pterostichus morio* sbsp *fenestrellanus,* the spider *Vesubia jugorum,* and the springtail *Orchesella* cf. *frontimaculata*. These species have a very restricted distribution range and are strictly linked to cold environments; in particular, *Vesubia jugorum* is the only spider present in IUCN's Red List of threatened species (Mammola et al. 2016). *Vesubia jugorum* is classified as endangered because the current observed extent of occurrence (EEO 4,412 km^2) and the area of occupancy (AOO 835 km^2) are declining due to climate change (Isaia and Mammola 2018).

Supraglacial biodiversity is represented only by few species extremely specialised to cold and wet high-altitude environments. These include the springtail *Orchesella* cf. *frontimaculata* and the ground beetle *Oreonebria angusticollis;* both were found only in supraglacial habitat and in early successional stages, confirming for *Oreonebria angusticollis* its exclusivity for cold and wet habitats observed by Gobbi et al. (2011) and Bisio and Taglianti (2021).

Among springtail species, *Fasciosminthurus sauteri* is new for the Italian fauna*;* this species is an Alpine species described for Switzerland (Nayrolles and Lienhard 1990), where it was found in a scree slope vegetation and in a *Seslerio-Caricetum* grassland above 1800 m asl. Our data confirmed its presence in an open environment at high altitude; since we collected it quite far from the *locus typicus*, we can suppose that its distribution is underestimated and it may include a larger part of the Alps.

4.3 Homologies and differences among plant and arthropod successions along Peirabroc and Clapier glacier forelands

Plant and arthropod succession along Peirabroc and Clapier glacier forelands is arranged mainly in relation to soil evolution gradient driven by the time since deglaciation, as already observed in other Alpine glacier forelands (Matthews 1992; Burga 1999; Caccianiga et al. 2001; Khedim et al. 2021). However, we observed that aspect and slope also play an important role and, the latter for the arthropod communities of Clapier, suggesting that the microenvironmental variability could influence the successional pathway.

LG terrains usually host a lower number of plant species with respect to LIA moraines (Caccianiga et al. 2001; Tampucci et al. 2015); on the other hand, we cannot exclude an additional negative impact of grazing by ungulates (e.g. chamois and alpine ibex, pers. obs.) on plant species richness.

The higher values of turnover index and the lower persistence values with respects to other glacier forelands indicate that, despite some differences among taxa, plant and arthropod of Peirabroc and Clapier show the succession ‘replacement-change’ model, confirming observations by Rosero et al. (2021) and confuting our first hypothesis. In addition, Peirabroc and Clapier show some differences in their successional patterns despite their proximity: this finding stresses the hypothesis that each succession - even on a very small scale - has its own characteristics, perhaps in relation to the limited extension of these environments and the great environmental heterogeneity (Kaufmann et al. 2002b; Mori et al. 2008). Such differences between the two proglacial successions are particularly evident for spiders and springtails. We hypothesize that the high variability of spider and springtail successions could be due to their microhabitat sensitivity and mobility (Rusek 2001; Widenfalk et al. 2016) that make pitfall traps a non-fully exhaustive sampling method for these taxa. In addition, this may have been enhanced by the short duration of the sampling, for the reasons explained in Material and Method chapter.

4.4 Successional patterns on different glacier forelands: peculiarities of peripheral glaciers with Mediterranean climate

Peirabroc and Clapier markedly differ from all the other successions we have considered in their higher species turnover and, for this reason, our results disprove hypothesis (ii) because, contrary to our expectation, Peirabroc and Clapier follow a typical ‘replacement change model’, with high turnover rates, as observed along the glacier forelands crossing the tree line in the inner Alps (Gobbi et al. 2006, 2007; Tampucci et al. 2015) as well as in Norway (Matthews et al. 2018), instead of an ‘addition and persistence model’ as observed in the other peripheral glaciers (see. Tampucci et al. 2015).

The ‘replacement change model’ of colonisation has been associated with less severe environmental conditions, such as higher mean summer temperature and lower disturbance, and to a greater species pool (Holten 2003; Walker et al. 2004; D’Amico et al. 2015; Matthews et al. 2018). Tampucci et al. (2015) associated such conditions with continental climate of the inner Alpine chain, with higher tree line position and generally warmer conditions during the growing season, whereas the oceanic climate of the peripheral chains results in more severe environmental conditions during the favourable season and ultimately in a longer persistence of pioneer species. We propose that, despite of their peripheral position, the peculiar climatic traits of Maritime Alps provide mild temperatures that could promote the rapid species turnover observed along the succession, as pointed out by Ficetola et al. (2021).

Trends in species richness of plants and ground beetles seem to reflect the altitudinal distribution of the glacier with respect to the tree line. Peirabroc and Clapier glacier forelands are similar to Trobio and Cedec, being all above the tree line, while Rotmoos differs from the others.

With respect to all other analysed successions, Peirabroc and Clapier show the highest absolute values in species richness along plant succession, reflecting the biogeographic role of Maritime Alps as hotspot of biodiversity in the Mediterranean basin (Medail and Quezel 1999).

Early and mid-successional stages of the investigated glaciers are richer in species number and host the highest percentage and number of cold-adapted and/or endemic species, thus disproving our hypothesis (iii) that cold-adapted species are equally distributed along the succession, in contrast to results reported by Tampucci et al. (2015) in the Southern Alps. We propose that this is due directly to the considerably average higher temperatures of the proglacial habitat of Peirabroc and Clapier, which promotes the 'replacement change' model that disadvantages pioneer, cold-adapted species. Given the overall correspondence among cold-adapted and endemic species, the most threatened in this climate scenario (Tampucci et al. 2015; Cauvy-Fraunié and Dangles 2019), our results raise new concerns about the extinction risk of these species.

4.5 Supraglacial habitat, a threatened refugium for cryophilic and endemic species

The supraglacial habitat hosts well-defined plant and arthropod communities with cold-adapted and/or hygrophilous species. In particular, arthropod species with the combination of these characteristics, like *Oreonebria angusticollis* ssp. *microcephala*, are able to persist only on the glacier surface or on terrains very close to the ice tongue. Other arthropods, cold-adapted but not hygrophilous, seem to prefer either supraglacial or early-successional habitats. This is the case of *Orchesella* cf. *frontimaculata;* for this species the competition for food resources can be a factor limiting its presence in other environments, where other *Orchesella* species, such as *O. alticola* and *O. quinquefasciata,* occur. Other cold-adapted species - like the spiders *Coelotes pickardi pastor*, *Pardosa nigra*, *Dysdera cribrata*, or the ground beetles *Amara carduii* ssp. *psyllocephala*, *Carabus pedemontanus*, *Pterostichus morio* ssp. *fenestrellanus* and *Oreonebria macrodera* occur also on mid- and late-successional stages. Thus, hypothesis (iv), that cryophilic species are more linked to the ice, is confirmed, and it is particularly evident for arthropods.

The incidence of endemism in this supraglacial habitat is high, as predicted in hypothesis (v), especially if we compare it to the Inner Alps where no endemic species were observed (see data from Gobbi et al. 2006).

The low average annual temperatures recorded on the supraglacial debris emphasize the specific features of such habitats in comparison to the nearby glacier forelands with their relatively warmer thermal profiles; supraglacial debris climatic profile depends on microhabitat features like ice presence, debris thickness and conductivity (Mihalcea et al. 2008; Schauwecker et al. 2015; Gibson et al. 2017). Thus, supraglacial debris represents an environment decoupled from the regional climate and may have an important role as refugium for cold-adapted and hygrophilous plant and animal species, whose survival can be threatened by climate change and by a fast ecological succession in the adjacent forelands. By now, the situation in the Maritime Alps is alarming, considering the uniqueness of these glaciers and of their biodiversity in relation to the reduced surface of Peirabroc glacier, but, especially, to the observed fragmentation of Clapier glacier's tongue.

5 Conclusions

Every primary succession is mainly driven by soil evolution - a proxy for time since deglaciation. However, differences at regional but even at local scale (i.e. between two nearby glacier foreland) could be observed, suggesting that every succession responds to regional climate, local biodiversity, microhabitat heterogeneity and extension, but also to stochastic events (Matthews 1992, Erschbamer and Caccianiga 2016; Ficetola et al. 2021); this emphasizes the important role of the scale of observation, particularly when dealing with different taxa..

The Maritime Alps represent a peripheral chain with a unique combination of specific climatic features and taxonomic richness, with particular reference to endemic species. Due to their great variability and to the importance of glacial habitats as refugium for cold-adapted and endemic threatened species (Valle et al. 2021, 2022), it is important to expand the number of case studies in order to have a more complete vision of the phenomenon. Mediterranean glacial habitats, already especially threatened with disappearance for their geographical position, are further threatened by the fast species turnover, which implies that many cold adapted and endemic species, more linked to these environments, have a severe extinction risk.

Acknowledgements

The research was funded by Ente di Gestione delle Aree protette delle Alpi Marittime (Managing Body of protected areas of Maritime Alps) for the research project ”Monitoraggio della vegetazione periglaciale dei ghiacciai Clapier e Peirabroc (Alpi Marittime)", (Monitoring of proglacial vegetation of Clapier and Peirabrocn glaciers (Maritime Alps)) within the project ALCOTRA n. 1711 CClimaTT.

Electronic supplementary material: Supplementary material (Appendixes 1-8) is available in the online version of this article at https://doi.org/10.1007/s11629-022-7331-8.

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Funding note: Open access funding provided by Università degli Studi di Milano within the CRUI-CARE Agreement.

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The following Appendixes (Appendixes 1-8) is the Electronic Supplementary Material of the article entitled "Glacial biodiversity of the southernmost glaciers of the European Alps (Clapier and Peirabroc, Italy)" at https://doi.org/10.1007/s11629-022-7331-8.

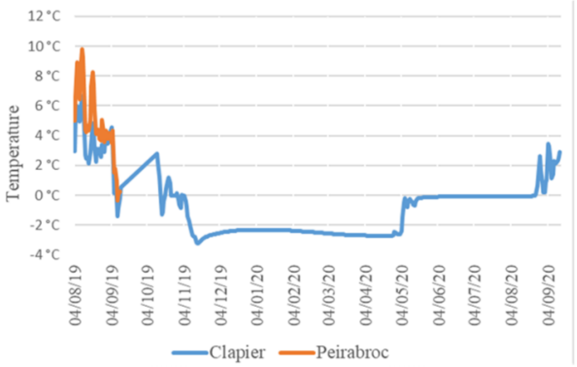
Appendix 1 A, Peirabroc glacier foreland; B, Clapier glacier foreland (younger sites); C, Supraglacial habitat (Peirabroc, PEI1); D, Young glacier foreland (Clapier, CLA2); E, young moraine (Clapier, CLA3); F, LIA moraine (Peirabroc, PEI3).

Appendix 2 Sampling point coordinates

CODE	Glacier	Landform	Age of deglaciation	Latitude (WGS8433N)	Longitude (WGS8433N)	Altitude (m asl)	Aspect (°)	Slope (°)
PEI11A	Peirabroc	Debris covered glacier	-	44.120542	7.414760	2573	5	35
PEI11B	Peirabroc	Debris covered glacier	-	44.120788	7.414786	2557	10	30
PEI11C	Peirabroc	Debris covered glacier	-	44.121437	7.414489	2519	340	20
PEI 12A	Peirabroc	Debris covered glacier	-	44.121354	7.414603	2522	350	25
PEI12B	Peirabroc	Debris covered glacier	-	44.121397	7.414534	2523	20	30
PEI12C	Peirabroc	Debris covered glacier	-	44.121395	7.414570	2564	10	15
PEI21A	Peirabroc	Moraine	1920-1980?	44.123551	7.414007	2422	40	20
PEI21B	Peirabroc	Moraine	1920-1980?	44.123609	7.413931	2421	55	15
PEI21C	Peirabroc	Moraine	1920-1980?	44.123558	7.413879	2426	80	30
PEI22A	Peirabroc	Moraine	1920-1980?	44.123620	7.414100	2429	55	15
PEI22B	Peirabroc	Moraine	1920-1980?	44.123629	7.414026	2421	60	25
PEI22C	Peirabroc	Moraine	1920-1980?	44.123760	7.413980	2431	40	20
PEI31A	Peirabroc	LIA Moraine	LIA (ca 1850)	44.124159	7.413020	2474	110	35
PEI31B	Peirabroc	LIA Moraine	LIA (ca 1850)	44.124181	7.413048	2464	100	20
PEI31C	Peirabroc	LIA Moraine	LIA (ca 1850)	44.124223	7.413088	2451	70	10
PEI32A	Peirabroc	LIA Moraine	LIA (ca 1850)	44.124125	7.412946	2476	70	15
PEI32B	Peirabroc	LIA Moraine	LIA (ca 1850)	44.124186	7.413003	2464	95	20
PEI32C	Peirabroc	LIA Moraine	LIA (ca 1850)	44.124315	7.413062	2463	110	25
PEI51A	Peirabroc-Clapier	LG Terrains	LG terrain	44.124916	7.409793	2519	100	20
PEI51B	Peirabroc-Clapier	LG Terrains	LG terrain	44.124846	7.409839	2519	70	15
PEI51C	Peirabroc-Clapier	LG Terrains	LG terrain	44.124788	7.410003	2515	70	20
PEI52A	Peirabroc-Clapier	LG Terrains	LG terrain	44.126320	7.412136	2401	40	30
PEI52B	Peirabroc-Clapier	LG Terrains	LG terrain	44.126486	7.411946	2403	40	20
PEI52C	Peirabroc-Clapier	LG Terrains	LG terrain	44.126462	7.412269	2396	70	25
CLA11A	Clapier	Debris covered glacier	-	44.113631	7.422554	2767	-	-
CLA11B	Clapier	Debris covered glacier	-	44.113733	7.422864	2813	-	-
CLA11C	Clapier	Debris covered glacier	-	44.113725	7.422903	2796	-	-
CLA12A	Clapier	Debris covered glacier	-	44.113915	7.422893	2778	-	-
CLA12B	Clapier	Debris covered glacier	-	44.114022	7.422893	2771	-	-
CLA12C	Clapier	Debris covered glacier	-	44.114060	7.422782	2764	-	-
CLA21A	Clapier	young glacier foreland	after 1980	44.117917	7.421312	2620	40	25
CLA21B	Clapier	young glacier foreland	after 1980	44.117949	7.421353	2632	25	15
CLA21C	Clapier	young glacier foreland	after 1980	44.117950	7.421266	2636	35	5
CLA22A	Clapier	young glacier foreland	after 1980	44.117997	7.421563	2620	280	<5
CLA22B	Clapier	young glacier foreland	after 1980	44.118033	7.421480	2626	350	<5
CLA22C	Clapier	young glacier foreland	after 1980	44.118056	7.421636	2646	350	10
CLA31A	Clapier	Young Moraine	1920-1980?	44.118318	7.421995	2641	300	20
CLA31B	Clapier	Young Moraine	1920-1980?	44.118304	7.421896	2636	270	35
CLA31C	Clapier	Young Moraine	1920-1980?	44.116667	7.421889		220	30
CLA32A	Clapier	Young Moraine	1920-1980?	44.118356	7.421858	2636	110	0
CLA32B	Clapier	Young Moraine	1920-1980?	44.118525	7.421872	2649	320	5
CLA32C	Clapier	Young Moraine	1920-1980?	44.118470	7.421681	2635	255	5
CLA41A	Clapier	LIA Moraine	LIA (ca 1850)	44.122222	7.418972		70	35
CLA41B	Clapier	LIA Moraine	LIA (ca 1850)	44.122582	7.419043	2539	65	40
CLA41C	Clapier	LIA Moraine	LIA (ca 1850)	44.122809	7.418921	2528	60	35
CLA42A	Clapier	LIA Moraine	LIA (ca 1850)	44.123245	7.418810	2509	345	25
CLA42B	Clapier	LIA Moraine	LIA (ca 1850)	44.123243	7.418775	2506	10	20
CLA42C	Clapier	LIA Moraine	LIA (ca 1850)	44.123327	7.418908	2494	40	10

Appendix 3 Plant species occurring in a single sampling point

Species	Plot
Androsace vitaliana (L.) Lapeyr.	PEI2
Astragalus penduliflorus Lam.	CLA4
Athamantha cretensis L.	CLA4
Avenella flexuosa (L.) Drejer	PEI5
Cerastium arvense L.	PEI3
Dianthus pavonius Tausch	PEI3
Doronicum clusii (All.) Tausch	PEI2
Festuca rubra L. subsp. *commutata* (Gaudin) Markgr.-Dann	PEI5
Galium pumilum Murray	PEI3
Hieracium pilosum Schleich. ex Froel.	PEI3
Homogyne alpina (L.) Cass.	PEI5
Luzula sylvatica Huds.) Gaudin ssp. *sieberi* (Tausch) K. Richt.	PEI5
Oreochloa seslerioides (All.) K.Richt.	CLA4
Phleum alpinum L.	PEI5
Pilosella cf. *glacialis* (Reyn. ex Lachen.) F.W. Schultz & Sch. Bip.	PEI3
Rhodiola rosea L.	PEI2
Rumex scutatus L.	PEI3
Selaginella selaginoides (L.) P. Beauv. ex Schrank & Mart.	PEI5
Sibbaldia procumbens L.	PEI5
Veronica fruticans Jacq.	CLA4

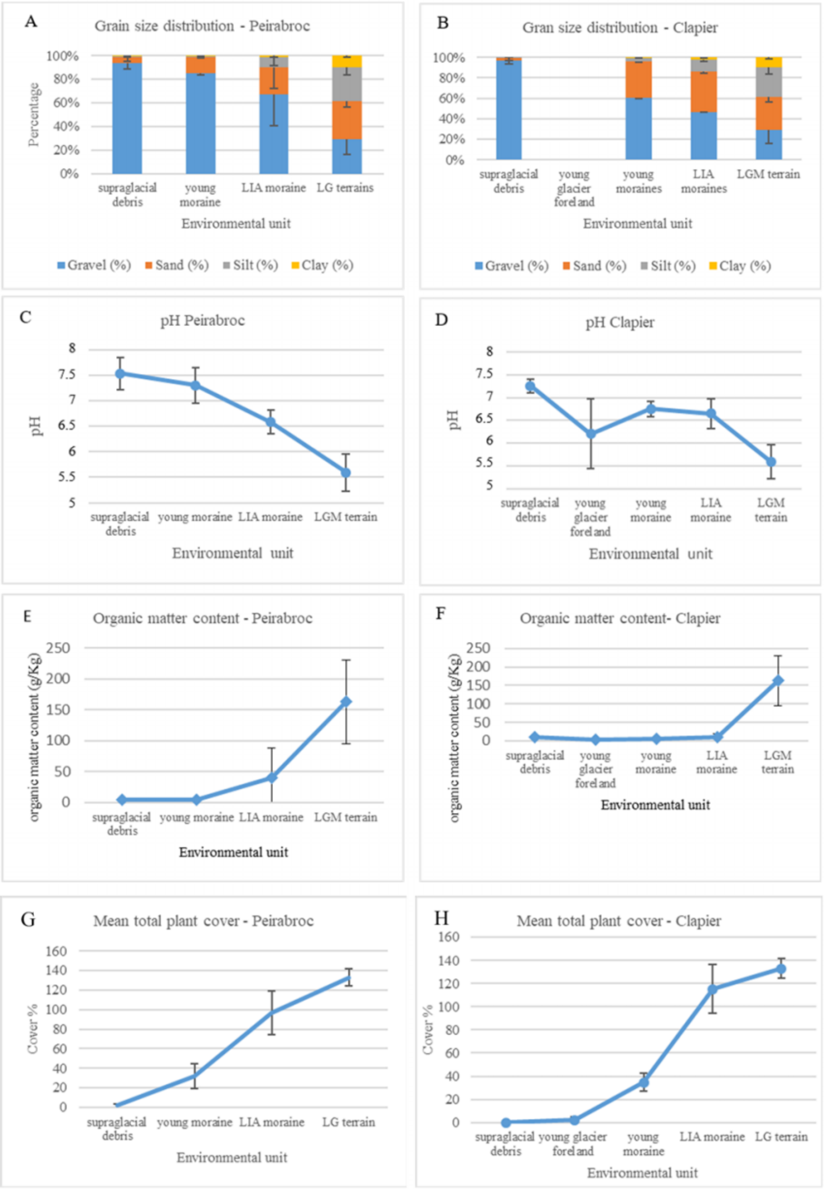


Appendix 4 Comparison between Clapier and Peirabroc supraglacial ground temperature at soil level.

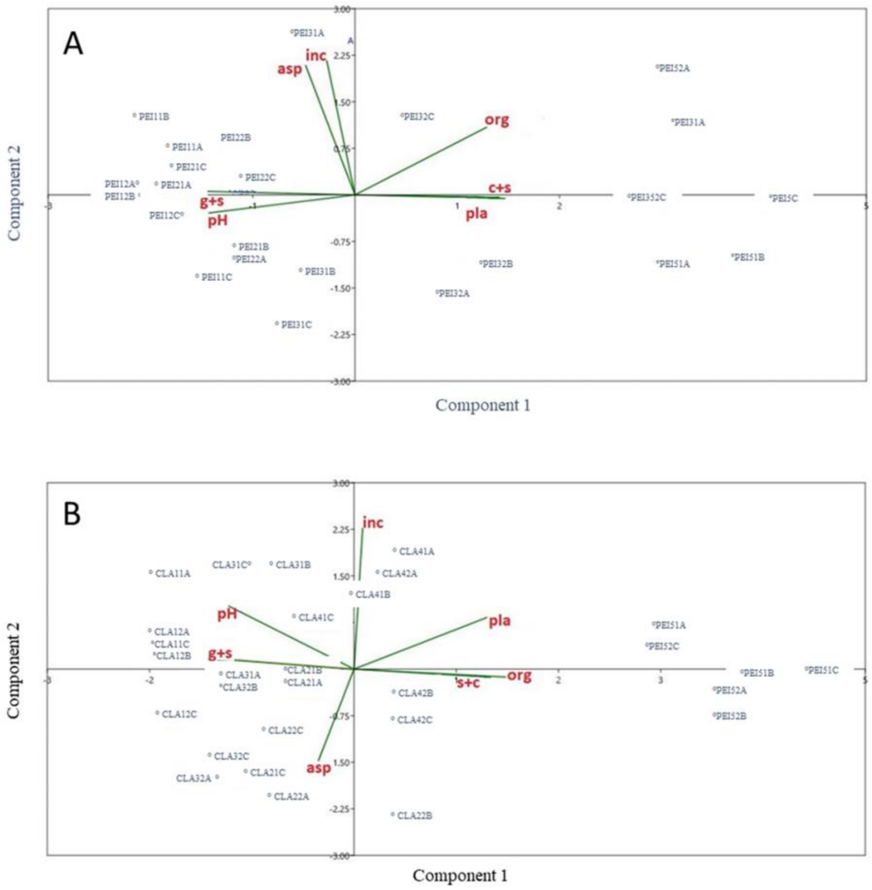
Appendix 5 Spearman correlation index among site variables and soil variables for Peirabroc (A) and Clapier (B)

A_ Rho spearman Peirabroc (from PEI1 to PEI5)	Aspect (°)	Slope (°)	Total plant cover (%)	Gravel and sand (%)	Clay and silt (%)	pH	Soil organic matter content (g/kg)
Aspect		0.3786	-0.3705	0.2064	-0.2064	0.2320	-0.0171
Slope			-0.2349	0.2404	-0.2404	0.1511	0.0675
Total plant cover (%)				-0.8808	0.8808	-0.8496	0.7502
Gravel and sand (%)					-1.0000	0.8251	-0.7723
Clay and silt (%)						-0.8251	0.7723
pH							-0.8593
Soil organic matter content (g/kg)							

B - Rho spearman CLAPIER (from CLA1 to PEI5)	Aspect	Slope	Total plant cover (%)	Gravel and sand (%)	Clay and silt (%)	pH	Soil organic matter content (g/kg)
Aspect		-0.1980	-0.2007	0.1190	0.1625	0.0529	0.0600
Slope			0.0419	0.0919	0.0755	0.2295	0.0278
Total plant cover (%)				-0.7566	-0.7504	-0.6251	0.6841
Sand and gravel (%)					0.1561	0.8538	-0.5189
Silt and clay (%)						0.2829	-0.6250
pH							-0.2784
Soil organic matter content (g/kg)							



Appendix 6 Soil parameters along the successional stages of Peirabroc and Clapier glacier foreland: grain size distribution (A-B); soil pH (C-D); organic matter content (E-F); total plant cover (G-H).



Appendix 7 Principal Component Analysis (PCA) analysis for Peirabroc (A) and Clapier (B). asp = aspect, inc= slope, org= organic matter, pH = soil pH, pla = plant cover, g+s = gravel and sand (%), s+c =silt and clay (%). Explained percentage for the first 3 axes are 63.505%, 19.791%, 9.2691% and 54.803%, 19.151%, 12.603% for Peirabroc and Clapier, respectively.

Appendix 8 Indicator Species Analysis values (indval) for Peirabroc and Clapier glacier environments

Species	Supraglacial debris		Early successional stages				Mid-successional stages		Late-successional stages	
			Young glacier foreland		Young moraine		LIA moraine		LG terrains	
	PEI1		CLA2		PIE2-CLA3		PEI3-CLA4		PEI5	
	indval %	p-row	indval %	p-row	indval %	p-row	indval %	p-row	indval %	p-row
Achillea erba-rotta	0	1	0	1	2.778	0.3410	11.110	0.1300	0	1
Achillea nana	1.905	0.7473	1.071	0.8465	8.929	0.4334	25.710	0.0260	5.714	0.5784
Adenostyles leucophylla	0	1	0	1	10.900	0.3559	30.770	0.0062	13.850	0.2503
Agrostis rupestris ssp. *rupestris*	0	1	0	1	0	1	37.180	0.0018	4.274	0.3960
Agrostis schraderiana	0	1	0	1	0	1	37.800	0.0016	4.065	0.4166
Alchemilla gr alpina	0	1	0	1	0	1	7.407	0.1973	9.259	0.2065
Alchemilla flabellata	0	1	0	1	0	1	30.330	0.0087	32.000	0.0237
Anthoxanthum nipponicum	0	1	0	1	0	1	21.540	0.0536	67.690	0.0002
Arabis alpina	0	1	0	1	51.280	0.0002	3.846	0.6435	0	1
Armeria alpina	0	1	0	1	0	1	69.440	0.0001	2.778	0.6007
Artemisia glacialis	0	1	0	1	20.830	0.0353	1.389	0.5211	0	1
Artemisia umbelliformis . *ssp.eriantha*	0	1	0	1	16.670	0.0973	0	1	0	1
Astrantia minor	0	1	0	1	0	1	0	1	33.330	0.0225
Atocion rupestre	0	1	0	1	0	1	18.940	0.0383	27.270	0.0354
Campanula scheuchzeri	0	1	0	1	0	1	34.700	0.0018	53.730	0.0003
Cardamine resedifolia	0	1	0	1	32.810	0.0036	4.688	0.7756	18.750	0.1386
Carex parviflora	0	1	0	1	0.833	0.6248	22.500	0.0286	0	1
Carex sempervirens	0	1	0	1	0	1	0.1366	0.9323	98.360	0.0001
Cherleria sedoides	0	1	0	1	0	1	31.410	0.0044	23.080	0.0520
Cirsium spinosissimus	0	1	0	1	0.641	0.7311	7.692	0.1753	7.692	0.2559
Doronicum clusii	0	1	0	1	16.670	0.1028	0	1	0	1
Dryopteris villarii	0	1	0	1	0	1	50.000	0.0004	0	1
Epilobium nutans	0	1	0	1	16.670	0.095	0	1	0	1
Erigeron alpinus	0	1	0	1	0	1	50.000	0.0002	0	1
Euphrasia alpina	0	1	0	1	0	1	83.330	0.0001	0	1
Euphrasia minima	0	1	0	1	0	1	59.520	0.0001	9.524	0.3079
Festuca halleri ssp. *halleri*	0	1	0	1	0	1	41.670	0.002	0	1
Festuca nigricans	0	1	0	1	8.276	0.8053	58.790	0.0001	19.540	0.2303
Festuca varia	0	1	0	1	0	1	46.580	0.001	15.070	0.1653
Festuca violacea ssp. *violacea*	0	1	0	1	0	1	2.778	0.41	27.780	0.0180
Helictochloa versicolor ssp. *versicolor*	0	1	0	1	0	1	3.333	0.5364	53.330	0.0027
Hornungia alpina	0	1	0	1	41.670	0.0015	0	1	0	1
Jacobaea incana	0	1	0	1	0	1	16.030	0.0723	41.030	0.0065
Leucanthemopsis alpina	0	1	2.206	0.6715	7.843	0.3974	13.480	0.1524	11.760	0.2582
Linaria alpina	0	1	0	1	41.670	0.0014	0	1	0	1
Lotus corniculatus ssp. *alpinus*	0	1	0	1	0	1	25.930	0.0156	61.110	0.0002
Luzula alpinopilosa	0	1	3.571	0.4814	1.190	0.7591	29.760	0.0075	0	1
Luzula lutea	0	1	0	1	0	1	10.710	0.1319	19.050	0.0929
Luzula spicata	0	1	0	1	0	1	66.670	0.0001	0	1
Meum athamanticum	0	1	0	1	0	1	0	1	33.330	0.0225

(-To be continued-)

Appendix 8 Indicator Species Analysis values (indval) for Peirabroc and Clapier glacier environments(-Continued-)

Species	Supraglacial debris		Early successional stages				Mid-successional stages		Late-successional stages	
			Young glacier foreland		Young moraine		LIA moraine		LG terrains	
	PEI1		CLA2		PIE2-CLA3		PEI3-CLA4		PEI5	
Minuartia recurva	0	1	0	1	0	1	41.670	0.0023	0	1
Mutellina adonidifolia	0	1	0	1	0	1	0	1	50.000	0.0033
Myosotis alpestris	0	1	0	1	0	1	91.670	0.0001	0	1
Nardus stricta	0	1	0	1	0	1	0	1	83.330	0.0001
Noccaea corymbosa	0	1	0	1	15.930	0.0896	36.030	0.0014	0	1
Omalotheca supina	0	1	0	1	0	1	33.330	0.0079	0	1
Oreojuncus trifidus	0	1	0	1	0	1	50.000	0.0006	0	1
Oxyria digyna	0	1	2.206	0.7429	83.580	0.0001	0	1	0	1
Pedicularis rostratospicata ssp. *Helvetica*	0	1	0	1	0	1	31.250	0.0053	12.500	0.1722
Phyteuma globulariifolium ssp. *pedemontanum*	0	1	0	1	0	1	25.000	0.0297	0	1
Phyteuma michelii	0	1	0	1	0	1	0	1	50.000	0.0021
Pilosella lactucella	0	1	0	1	0	1	16.670	0.1061	0	1
Poa alpina	0	1	2.174	0.9922	21.920	0.1578	36.960	0.0001	34.780	0.0018
Poa cenisia	0	1	0	1	21.880	0.0319	28.120	0.0097	0	1
Poa laxa	18.390	0.1510	0	1	17.240	0.0801	9.483	0.2871	0	1
Polystichum lonchitis	0	1	0	1	0	1	25.000	0.0304	0	1
Ranunculus montanus	0	1	0	1	0	1	0	1	83.330	0.0001
Rhododendron ferrugineum	0	1	0	1	0	1	0	1	50.000	0.0034
Sabulina verna	0	1	0	1	0	1	16.670	0.1023	0	1
Sagina glabra	0	1	0	1	1.852	0.7019	18.520	0.0412	5.556	0.3406
Sagina saginoides	0	1	0	1	0	1	41.670	0.0023	0	1
Saxifraga aizoides	8.889	0.2678	0	1	30.560	0.0064	0	1	0	1
Saxifraga bryoides	0	1	16.790	0.3542	34.200	0.0031	30.220	0.0096	0	1
Saxifraga exarata	0	1	1.103	0.9762	39.090	0.0002	52.940	0.0001	0	1
Saxifraga oppositifolia	0	1	0	1	25.000	0.0289	0	1	0	1
Saxifraga paniculata	0	1	0	1	8.929	0.1797	16.070	0.0517	0	1
Saxifraga pedemontana ssp. *pedemontana*	14.290	0.1459	0	1	38.100	0.0012	0	1	0	1
Saxifraga retusa ssp. *Augustana*	19.750	0.1304	0	1	12.350	0.1419	8.333	0.2734	0	1
Scorzoneroides helvetica	0	1	0	1	0.149	0.9633	0.446	0.9331	92.860	0.0001
Sedum alpestre	0	1	0	1	21.880	0.0680	42.010	0.0001	12.500	0.5269
Sempervivum arachnoideum	0	1	0	1	4.487	0.7112	68.380	0.0001	0	1
Sempervivum montanum	0	1	0	1	11.110	0.1256	2.778	0.3379	0	1
Sempervivum tectorum	0	1	0	1	5.128	0.3058	1.923	0.4962	7.692	0.1861
Silene acaulis	0	1	0	1	10.670	0.1912	28.330	0.0088	0	1
Soldanella alpina ssp. *alpina*	0	1	0	1	0	1	0	1	50.000	0.0021
Thymus oenipotanus	0	1	0	1	0	1	41.670	0.0022	0	1
Trifolium alpinum	0	1	0	1	0	1	17.240	0.0548	15.520	0.1038
Trifolium thalii	0	1	0	1	0	1	75.000	0.0001	0	1
Tussilago farfara	0	1	0	1	0	1	25.000	0.0283	0	1
Vaccinium myrtillus	0	1	0	1	0	1	0.439	0.7698	47.370	0.0018

(-To be continued-)

Appendix 8 Indicator Species Analysis values (indval) for Peirabroc and Clapier glacier environments(-Continued-)

Species	Supraglacial debris		Early successional stages				Mid-successional stages		Late-successional stages	
			Young glacier foreland		Young moraine		LIA moraine		LG terrains	
	PEI1		CLA2		PIE2-CLA3		PEI3-CLA4		PEI5	
Vaccinium uliginosus	0	1	0	1	0	1	0	1	50.000	0.0034
Veronica alpina	0	1	0	1	7.883	0.4319	24.320	0.0220	10.810	0.3133
Viola calcarata	0	1	0	1	0	1	0	1	33.330	0.0216
Oreonebria angusticollis ssp. *microcephala*	25.960	0.0202	5.128	0.3963	0	1	0	1	0	1
Nebria jockischii	0	1	0	1	8.333	0.3138	0	1	0	1
Cicindela gallica	0	1	0	1	0	1	10.000	0.2577	0	1
Laemostenus janthinus coeruleus	0	1	0	1	0	1	10.000	0.2607	0	1
Amara carduii ssp.*psyllocephala*	0	1	0	1	0	1	10.000	0.2607	0	1
Carabus pedemontanus	0	1	0	1	0	1	30.000	0.0029	13.330	0.1297
Pterostichus morio ssp. *fenestrellanus*	0	1	0	1	0	1	28.820	0.0071	58.820	0.0022
Harpalus rubripes	0	1	0	1	0	1	0	1	100.000	0.0002
Oreonebria macrodera	0	1	0	1	0	1	0	1	33.330	0.0751
Entelecara sp	0	1	25.640	0.0350	0	1	2.308	0.5176	0	1
Mughiphantes sp	0	1	16.670	0.1560	0	1	0	1	0	1
Diplocephalus helleri	0	1	0	1	8.333	0.3013	0	1	0	1
Vesubia jugorum	0	1	0	1	16.670	0.0858	0	1	0	1
Coelotes pabulator	0	1	0	1	25.640	0.0084	2.308	0.3890	0	1
Coelotes pickardi pastor	0	1	0	1	3.788	0.2433	5.455	0.2189	0	1
Pardosa nigra	0	1	0	1	2.451	0.2870	14.120	0.0779	0	1
Dysdera cribrata	0	1	0	1	0	1	10.000	0.2607	0	1
Xysticus desidiosus	0	1	0	1	0	1	10.000	0.2607	0	1
Zelotes gallicus	0	1	0	1	0	1	30.000	0.0124	0	1
Drassodes pubescens	0	1	0	1	1.667	0.5249	0	1	26.670	0.0510
Centromerus pabulator	0	1	0	1	0	1	0	1	33.330	0.0751
Coelotes osellai	0	1	0	1	0	1	0	1	33.330	0.0751
Palliduphantes pallidus	0	1	0	1	0	1	0	1	33.330	0.0741
Pardosa blanda	0	1	0	1	0	1	0	1	100.000	0.0002
Orchesella cf. *frontimaculata*	21.800	0.0562	38.760	0.0046	6.202	0.5726	0	1	0	1
Isotomidae sp.	5.357	0.1584	0	1	9.524	0.1536	0	1	0	1
Deutherosminthurus pallipes	6.818	0.3069	3.030	0.5309	0	1	27.270	0.0112	0	1
Lepidocyrtus gr *curvicollis*	6.670	0.6356	1.318	0.9099	32.940	0.0028	7.589	0.6113	5.270	0.4901
Orchesella alticola	0	1	13.330	0.0891	30.000	0.0043	0	1	0	1
Tomocerus minor	0	1	0	1	16.670	0.0883	0	1	0	1
Sminthurus sp.	0	1	0	1	17.860	0.0323	2.857	0.2950	0	1
Cerathophysella armata	0	1	0	1	0	1	10.000	0.2607	0	1
Fasciosminthurus sauteri	0	1	0	1	0	1	40.000	0.0019	0	1
Entomobrya lanuginosa	0	1	0	1	0	1	40.000	0.0018	0	1
Lepidocyrtus gr *cyaneus*	0	1	0	1	0	1	21.820	0.0115	15.150	0.1155
Orchesella quinquefasciata	0	1	0	1	0	1	0	1	100.000	0.0002

3.2 Biodiversity and ecology of plants and arthropods on the last preserved glacier of the Apennines mountain chain (Italy)

Research Paper

The Holocene
2022, Vol. 32(8) 853–865

DOI: 10.1177/09596836221096292
journals.sagepub.com/home/hol
SAGE

Biodiversity and ecology of plants and arthropods on the last preserved glacier of the Apennines mountain chain (Italy)

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Abstract

In the current global warming phase, relict glacial areas are one of the most threatened ecosystems in the world. They are "cold-spots" of biodiversity and of great interest both from the ecological and conservation point of view. We investigated the biological communities (plants and arthropods) hosted by one of the southernmost European glaciers: Calderone Glacier, the last preserved glacier of the Apennines mountain chain (Italy). We analyzed supraglacial debris and the nearby moraine and we found a rather diverse and peculiar biodiversity, which includes also new species. Some arthropods, such as the springtail *Desoria calderonis*, are particularly sensitive to the presence of ice at microtopographic level. Among plants, only *Arabis alpina caucasica* is able to grow on the supraglacial debris, perhaps because of factors related to the seed germination and seedling survival on this habitat type. Calderone glacier, with its particular biogeographic location, is probably currently acting as one of the last refugia for rare and endemic cryophilic species within the Mediterranean Region during the ongoing warm period.

Keywords

arthropods, cryophilic species, glacial biodiversity, global warming, plants, refugia, vanishing glaciers

Received 11 January 2022; revised manuscript accepted 15 March 2022

Introduction

Climate warming will be one of the major threats to biodiversity over the next 100 years (Román-Palacios and Wiens, 2020). In cold areas, this phenomenon directly harms several species and habitats (First, 2019; Gobbi et al., 2021; Root et al., 2003), as high altitude ecosystems are particularly threatened (Cauvy-Fraunié and Dangles, 2019; Dullinger et al., 2012; McCain and Colwell, 2011). These ecosystems, especially in peripheral mountain areas, are cold-spot of biodiversity (Cauvy-Fraunié and Dangles, 2019), having contributed to the evolution of several endemic species due their role as microrefugia during glacial and interglacial periods (Muellner-Riehl, 2019; Steinbauer et al., 2016; Zhang et al., 2020).

In the current global warming phase, alpine glaciers at global scale are experiencing a severe reduction but also an increase of supraglacial stony debris, due to freeze-thaw processes delivering large volumes of debris from the surrounding slopes to the glacier surface (Azzoni et al., 2018; Janke et al., 2015; Kirkbride, 1993; Kraaijenbrink et al., 2017; Tielidze et al., 2020). The role of glacier forelands and supraglacial debris as potential habitat and refugium for high altitude organisms, such as plants (Caccianiga et al., 2011; Fickert et al., 2022; Losapio et al., 2021; Tampucci et al., 2015) and arthropods (Gobbi, 2020a; Hågvar et al., 2020; Valle et al., 2020) is increasingly recognized. However, it is still not clear how many cryophilic species – being both cold-adapted and hygrophilous (Deharveng et al., 2008; Fjellberg, 2010; Jurekova et al., 2021) – can live in glacial habitats and how much they are directly related to the presence of ice (Stibal et al., 2020). This information is crucial for estimating possible responses, of this extremely specialized biodiversity, to global change, especially in case of the complete glacial disappearance. Previous

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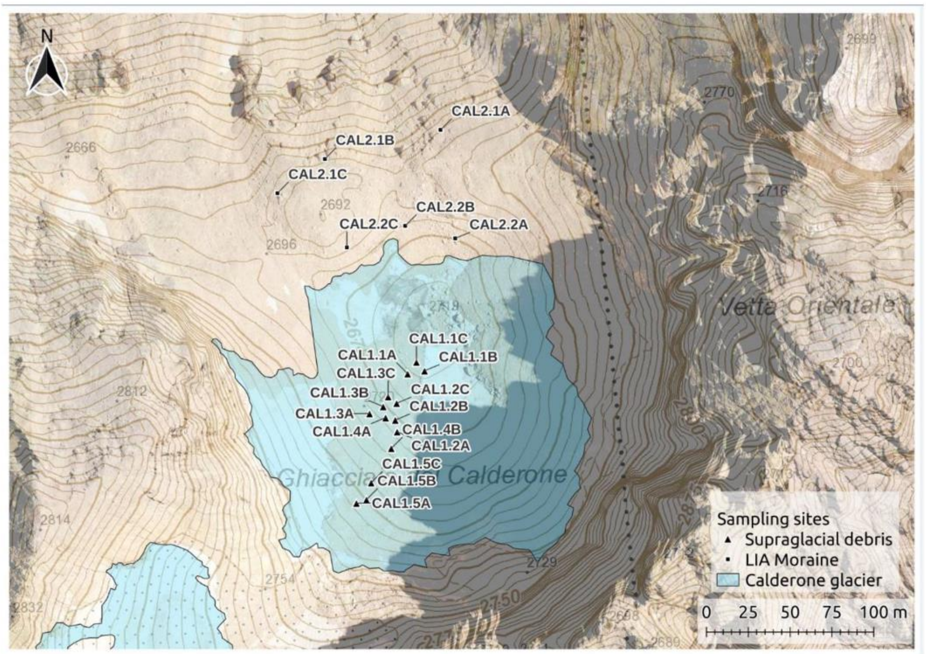


Figure 1. Calderone glacier and sampling design of the field work performed during July 2020.

studies showed that a significant fraction of plant species living on glacier forelands are considered to be at risk of local extinction following glacier retreat (Losapio et al., 2021). In addition, supraglacial stony debris may host large populations of cold-adapted and/or endemic species of vascular plants (Tampucci et al., 2017), springtails (Collembola), spiders (Arachnida: Araneae) and ground beetles (Coleoptera: Carabidae) (Bernasconi et al., 2019; Buda et al., 2020; Gobbi, 2020a; Valle et al., 2020). Species able to live in glacial or periglacial habitats have also been documented within other taxa (e.g. Coleoptera Staphylinidae (Kapp, 2007), Chilopoda (Gobbi et al., 2020b)).

In Europe, the southern and peripheral mountain areas are widely known as biodiversity hotspots with a high rate of endemic species (Branda et al., 2010; Medail and Quezel, 1999). In these areas, ice masses are very small but still persistent, owing to high winter precipitation and avalanche accumulation, particularly in association with north-facing steep and narrow valleys (Giraudi, 2002; Grunewald and Scheithauer, 2010). However, the ongoing climate change is severely threatening these small ice bodies (Smiraglia and Diolaiuti, 2015). In these areas, glacier-linked biodiversity is unique and could be particularly threatened with extinction.

Calderone glacier is one of the southernmost glaciers in Europe (Grunewald and Scheithauer, 2010; Hughes, 2009), and the only relict glacier of the Apennines. It is located in the Gran Sasso massif in Central Apennines (Abruzzo, Italy) with Corno Grande (2912 m asl) being the highest peak of the entire Apennines and dominating the glacier. This confers to Gran Sasso massif an important biogeographical position, as confirmed by its abundance of endemites together with the nearby Majella massif, compared to other Mediterranean mountain regions (Conti and Bartolucci, 2016; Tammaro, 1971; Testi et al., 1996). Calderone glacier is almost completely debris-covered and has been defined as a glacieret, that is a small glacier body with no dynamicity and erosional activity and without an accumulation and an ablation zone (Smiraglia and Diolaiuti, 2015), with a negative trend in glacier area and mass over the past two decades (Pecci et al., 2008). This unique glacial system is thus near the definitive disappearance. No detailed information is available about organisms living on Calderone glacier, although its isolated position within the Mediterranean region (following the Apennine chain, the nearest glacier is Clapier in Maritime Alps, about 530 km away) might suggest an important ecological and biogeographic role for high mountain biodiversity.

This work aims to provide an overview of plant and arthropod communities hosted by Calderone glacier, investigating the species distribution on the glacier surface and in the surrounding habitats and its alpha and beta diversity. Our goals, specifically are: (1) to identify and functionally characterize supraglacial and proglacial communities of Calderone glacier; (2) to investigate the microtopographic drivers that affect species distribution (debris thickness and soil parameters); (3) to search for species directly related to the presence of ice, currently the most threatened by global warming.

Material and methods

Study area

Calderone glacier (42°28″16.4″N 13°34″01.4″E) is located in the Gran Sasso Massif, in the Central Apennines (Italy), surrounded by steep carbonate stonewalls and overlooking the Adriatic Sea with a North-East aspect (Figure 1). It is the only glacier present on the Apennines (Smiraglia and Diolaiuti, 2015). The Little Ice Age (LIA; mid 19th century; D'Orefice et al., 2000; Rovelli, 2006) moraine borders the tongue, very close or in contact with the glacier; the distance between the moraine base and the ice cannot be assessed, the area being covered by debris.

pseudoscorpions in Gardini (2000); for spiders in Pantini and Isaia (2019), Pekár et al. (2021), Thaler (1986); for springtails in Bretfeld (1999), Gisin (1960), Mateos (2011), Pomorski and Kaprus (2007), Potapov (2001), Potapov et al. (2016), Thibaud et al. (2004); for earwigs in Costa (1882), Galvagni (1970) and Stoch (2000); for ground beetles in Brandmayr (2005), de Jong et al. (2014) and Pesarini and Monzini (2011); for rove beetles in Kapp (2007), Koch (1989) and Loebl and Loebl (2015); for snout beetles in Abbazzi and Maggini (2009). Wing morphology was detected by a stereomicroscope.

Data analysis

An principal component analysis (PCA) was performed on soil data to evaluate the association among all variables and to rule out from the subsequent analyses some of the auto-correlated variables.

Species richness was compared between the two environmental units, that is, supraglacial debris, and the LIA moraine. A T-test was used to assess the differences in species richness and functional composition between supraglacial habitats and the LIA moraine. For each functional category we estimated both the species richness and their incidence (number of species in the selected category divided by the total number of species sampled). For identifying typical plant and arthropod species of each environmental unit, we used Indicator Species Analysis (IndVal; Podani and Csanyi, 2010). To assess beta diversity for arthropod taxa we performed a permutation test of multivariate homogeneity of group dispersions (Anderson et al., 2006). The function betadisper in the 'vegan' package (Oksanen et al., 2019) was used to perform the PERMDISP analysis. This method consists in measuring the average distance from each observational unit to their group centroid and assessing variability in community structure. Average dissimilarity of sampling sites within environmental units (supraglacial debris, and the LIA moraine) was assessed using the Whittaker index (De Cáceres et al., 2013; Faith et al., 1987; Whittaker, 1952). To test for statistical differences in beta diversity between environmental units, 999 permutations were performed and tested using one-way ANOVA. We investigated the relationship between species richness and soil characteristics in the sampling point located in the supraglacial habitat using linear models (LM). The LMs were performed considering linear, quadratic and cubic terms and the model with the highest R^2 was chosen. In the same way, a Poisson generalized linear model (GLM) was used to test the relationship between arthropod abundance (see Dataset Building) and soil characteristics: debris thickness, pH, soil organic matter content (g/kg) and soil carbonate calcium content (%). The species that showed less than three occurrences in the supraglacial sampling points were excluded. The GLMs were performed both with and without quadratic terms. For each species and each soil variable, the model with the highest D^2 was chosen.

Data processing was performed with R 4.0.2 (R Core Team, 2020), using the following packages: ggplot2 (Wickham, 2016), tidyverse (Wickham et al., 2019), dplyr (Wickham et al., 2020), patchwork (Pedersen, 2020), ggpubr (Kassambara, 2020), vegan (Oksanen et al., 2019).

Results

The average annual (July 2020–July 2021) sub-surface ground temperature recorded on the supraglacial debris is 0.7°C; snow covered the glacier surface for 250 days, while average annual temperature on the LIA moraine was 1.3°C and snow cover lasted 146 days (Tables 1 and 2).

Table 1. Summary table of climatic variables recorded on Calderone glacier.

	Supraglacial debris		LIA moraine	
	Mean	SD	mean	SD
Snow cover (days)	250	17	146	/
Mean annual temperature (°C)	0.70	0.43	1.30	/
Snow-free annual temperature (°C)	3.83	0.71	4.44	/
Min annual temperature (°C)	−6.08	1.88	−9.13	/
Max annual temperature (°C)	22.31	6.42	34.83	/
Mean annual humidity (RH%)	95.7	/	88.70	/
Snow-free annual humidity (RH%)	85.9	/	84.60	/

For soil temperature and snow cover, within the supraglacial debris, we reported the mean value and standard deviation (SD) calculated for each landform. Only one data logger was on the LIA moraine, thus only the mean value is reported.

The LIA moraine (organic matter content = 3.88 g/kg and pH = 8.28) showed a higher organic content than supraglacial debris (organic matter content = 1.68 g/kg and pH = 8.62) (Table 2). The sampled supraglacial debris had a mean thickness of 23 cm with a range from 8 to 40 cm. PCA (Figure 2) highlights that organic matter content and pH are the most important variables to characterize the glacier environment.

Identification and characterization of Calderone supraglacial and proglacial communities

Forty-five species were found among the studied taxa (Table 2), 37 arthropods and eight vascular plants. Six (13%, all arthropods) are steno-endemic (species with narrow distribution range) of Majella and Gran Sasso and six (13%, one plant and five arthropods) are endemic of the Apennines (Table 2). Five species (11%, all arthropods) are cryophilic: the ground beetle *Nebria orsinii orsiniii*, the rove beetle *Aleochara meridionalis*, the pseudoscorpions *Neobisium fiscelli* and *N. osellai* and springtail *Desoria calderonis* (Table 2). Airborne arthropod fallout is reported in Supplemental Material 4, available online. Among all arthropod species, 34 were sampled with the pitfall trap method and nine with the flotation method; three species were caught only with the flotation method (the springtails *Pseudisotoma* sp. and *Protaphorura octopunctata* and the rove beetle *Liogluta roettgeni*).

Comparing the biological communities of supraglacial debris and the LIA moraine, we found a strong difference in species richness of plants and arthropods (Tables 2 and 3). On supraglacial debris, we found only *Arabis alpina caucasica* (species richness for sampling ranges from 0 to 1, mean value 0.1), while on the LIA moraine also *Cerastium thomasii*, *Hornungia alpina*, *Poa alpina*, *Saxifraga exarata*, *S. oppositifolia, Papaver alpinum alpinum*, and *Sedum atratum* were observed (species richness in each sampling ranges from 0 to 5, mean value 2.7). Arthropods species richness (considering both pitfall trap and flotation methods) was even more significantly higher on the LIA moraine (*p*-value = 0.031) and ranges from 5 to 15 (mean value 9.3) while on supraglacial debris it ranges from 2 to 9 species (mean value 4.1) (Tables 2 and 3).

Analysis of beta-diversity showed how the species assemblages of each of the considered environmental units are different (Supplemental Material 1, available online, Figure 2). According to the IndVal analysis (Supplemental Material 5, available online, Figure 5), *Desoria calderonis* is the only arthropod indicator species of supraglacial debris; conversely, indicator species of the LIA moraine are the ground beetle *Amara samnitica*, the springtails *Pseudachorutes palmiensis* and *Lepidocyrtus* spp., the spider *Pardosa cavannae*, the snout beetle *Donus oblongus* and Diplopoda. Common species of the two environmental units are the

Calderone glacier is fragmented into two ice masses, after the separation of the tongue (Lower Calderone) from the accumulation zone (Upper Calderone) occurred in 2000 (De Sisti et al., 2003; Pecci et al., 2001). In 2011 the total surface was 0.04 km^2, with a reduction of 20% from 1981–84 and of 33% from 1959–62 (Smiraglia and Diolaiuti, 2015). The thickness of the ice was 15 m at the end of the 20th century (Smiraglia and Diolaiuti, 2015). The glacier is now almost completely covered by stony debris coming from the surrounding rock walls.

Sampling design

Two environmental units were selected: the supraglacial stony debris on the Lower Calderone (Habitat 8340; Council Directive 92/43/EEC, 1992) and the LIA moraine (Habitat 8120, Council Directive 92/43/EEC, 1992). Specifically, we placed 14 sampling points on supraglacial stony debris and 6 on the LIA moraine (Figure 1). Sampling points are spaced from each other by at least 2 m. In each sampling point:

- Vegetation sampling was performed in a 2 m × 2 m plot and the plant species cover was reported as a percentage.
- Pitfall trap was set out to sample ground-dwelling arthropods. A Pitfall trap consist of a plastic glass (diameter 7 cm) filled up with a non-toxic and frost-resistant solution of water and vine winegar (2:1) with salt and soap to catch and preserve the animals during the sampling period (Gobbi, 2020a). In order not to reduce the impact on such a small and delicate habitat (Lencioni and Gobbi, 2021) we performed only two sampling session in the period of maximum activity for arthropods (Gobbi, 2020a): 7–8 July/9–10 July 2020 (2 days of trap activity) and 9–10/29 July 2020 (20 days of trap activity).
- Soil microarthropods were sampled using the flotation method (Marshall et al., 1994) on debris samples collected with a scoop at different depths (at 1, 10, 20 and 50 cm), in order to obtain a representative sample of the whole ground/soil profile, placed in a plastic glass (diameter 7 cm, height 8 cm), and screened for arthropods in a small basin filled with mineral water.
- A soil sample of 200 g was collected at the surface where to measure soil pH (in 1:2.5 soil:water), organic matter (Walkley–Black method) and carbonate calcium content (Dietrich–Fruhling calcimeter).

Sub-surface ground temperature was recorded 10 cm below the ground surface for 1 year (9 July 2020–27 July 2021) every 2 h using iButton 1922 temperature probes. Fifteen probes were placed in the study area, 14 in the supraglacial stony debris in correspondence with the sampling points and one as control, on the external side of the LIA moraine (in correspondence with the sampling point CA2.1A). Moreover, to collect relative humidity (RH%) two Tinytag plus 2 dataloggers were placed 10 cm below the soil surface, one in the supraglacial stony debris (in correspondence with the sampling point CAL1.4A) and one on the internal side of the LIA moraine (in correspondence with the sampling point CAL2.2A). In order to estimate the max and the min temperature we calculated respectively the mean value of the max temperature from the 10 hottest and coldest days.

On supraglacial debris, thickness was measured for every sampling point, digging through the debris until the underlying ice was reached.

Collected organisms were identified, when possible, to the species level by experts (See Supplementary Material 8, available online also for nomenclature references). Adult specimens were identified; juvenile specimens were identified where possible: for springtails, pseudoscorpions (Pseudoscorpiones), harvestmans (Opiliones) and earwigs (Dermaptera). The spider *Pardosa* sp. and the springtail *Sminthurides* sp. were not identifiable at species level because all the available specimens were juvenile, but *Pardosa* sp. was clearly different from *Pardosa cavannae. Deutherosminthurus* sp., *Hypogasrura* sp. and *Pseudisotoma* sp. were not identifiable at species level because of the availability of only one or few specimens.

Collected specimens are preserved in ethanol in permanent collections now stored at: Museo civico di Scienze Naturali di Bergamo (Italy) (spiders, harvestmans), MUSE – Science Museum of Trento (Italy) (ground beetles, snout beetles (Curculionidae), earwigs, springtails, other taxa not identified), Museo civico di Storia naturale di Verona (pseudoscorpions, rove beetles with the exception of *Coryphium atratum*, preserved in Zanetti, 1984).

Dataset building

Data were ordered in a matrix associating each sampling point with location data (latitude, longitude, altitude, slope, aspect), soil data (stony debris thickness, pH, soil organic matter content and soil carbonate calcium content), vegetation data (values of vegetation cover), and fauna data (number of individuals). Arthropod abundances were transformed in activity density (ratio amongst the number of collected individuals and the days of trap activity) for pitfall traps (PT) and calculated as absolute number of specimens sampled for flotation method (FM).

Ground beetles, spiders, springtails, rove beetles, harvestmen, snout beetles, earwigs, pseudoscorpions, oribatids (Oribatida) were identified at species level; millipedes and other orders of mites were analyzed only at class level. All taxa with high dispersal ability (i.e. winged species) (Supplementarl Material 4, available online), were not included in the analysis but reported as "airborne arthropod fallout (namely aeroplankton)."

We assigned a binary factor (presence/absence) to each species in relation to its geographic and altitudinal range. Specifically, we used five chorological categories: endemic of Gran Sasso and Majella, endemic of Apennines, endemic of European Alps and Apennines, occurring on Southern European mountains and species with wider distribution (also if some chorotypes are included in others, we considered this trait as mutually exclusive, assigning to every species only the more restrictive category).

Based on their altitudinal distribution, the species were divided in three main groups: alpine species occurring above the treeline (about 1800 on average on Apennines), low alpine species occurring from 1000 m asl up to the treeline, "lowland" species with a wider altitudinal distribution.

The binary factor (yes/no) was used also to identify cryophilic species: we considered as cryophilic those species that are both cold-adapted and hygrophilous (Deharveng et al., 2008; Fjellberg, 2010; Jurekova et al., 2021). Thus, snow-related species were included in this category, being adapted to cold environments characterized by high humidity.

The loss of the ability to fly is also an important trait for high altitude species, since it reduces dispersal ability; for this reason, we divided the species in winged, brachypterous and apterous (not considering taxa not winged for phylogenetic reason: e.g. springtails). We grouped the species on the basis of feeding habits: predators, saprophagous, phytophagous, spermophagous, parasitoids, microorganism consumers, detritivores; the same species can occur in more than one group due the heterogeneity of its diet.

Information about these variables were found for plants in Bartolucci et al. (2018) and Pignatti (2017); for harvestmans in Phillipson (1960), Hågvar and Flø (2015) and Hillyard (2005) (We considered *Mitopus* sp. both predator and saprophagous because, although harvestmen are scavengers, altitude ones are known as predators); for oribatid in Hajmová and Smrš (2001) for

Table 2. Species found in the two environmental units with the two sampling methods.

		Taxon		Supraglacial debris	LIA moraine
			Latitude (WGS8433N)	42.47238057	42.473505
			Longitude (WGS8433N)	13.56832701	13.568262
			Altitude (m asl)	2665	2686
			Supraglacial debris thickness (cm)	22.79	-
			Aspect (°)	85.29	237.33
			Inclination (°)	21.64	21.50
			Herbaceous cover (%)	0.01	2.60
			Moss cover (%)	0	0
			Rock cover (%)	100	100
			Soil reaction (pH)	8.62	8.28
			Soil organic matter content (g/kg)	1.68	3.88
			Soil carbonate calcium content (%)	96.11	91.41
		p	*Arabis alpina. caucasica* (Willd.) Briq.	X	X
	Ap	p	*Cerastium thomasii* Ten.		X
		p	*Hornungia alpina* (L.) O. Appel		X
		p	*Poa alpina* L.		X
		p	*Saxifraga exarata* Vill.		X
		p	*Saxifraga oppositifolia* L.		X
		p	*Papaver alpinum* L. *alpinum*		X
		p	*Sedum atratum* L.		X
*	GS-M	c	*Nebria orsinii orsinii* A. Villa & G.B. Villa, 1838	X	X
		c	*Amara morio nivum* Tschitscherin, 1900	X	
	Ap	c	*Pterostichus morio samniticus* A. Fiori, 1896		X
	Ap	c	*Amara samnitica* A. Fiori, 1899		X
*	GS-M	coll	*Desoria calderonis* Valle, 2021	X	
		coll	*Orchesella* cf. *frontimaculata* Gisin, 1946	X	X
		coll	*Lepidocyrtus* cf. *lignorum* (Fabricius, 1793)		X
		coll	*Lepidocyrtus* cf. *tellecheae* Arbea & Jordana, 1990		X
		coll	*Tomocerus vulgaris* (Tullberg, 1871)		X
		coll	*Sminthurides* sp.	X	
		coll	*Deutherosminthurus* sp.		X
		coll	*Pseudachorutes palmiensis* Borner, 1903,		X
		coll	*Pseudisotoma* sp.		X
		coll	*Hypogastrura* sp		X
		coll	*Protaphorura octopunctata* (Tullberg, 1876)		X
	GS-M	sp	*Pardosa cavannae* Simon, 1881		X
		sp	*Agyneta rurestris* (C. L. Koch, 1836)	X	X
		sp	*Oreonetides glacialis (L. Koch, 1872).*		X
		sp	*Pardosa* sp.	X	
		sp	*Entelecara* n. sp.		X
		sp	*Improphantes* cf. *improbulus* (Simon, 1929)		X
*		st	*Aleochara meridionalis* Kapp, 2007	X	X
		st	*Anotylus nitidulus* (Gravenhorst, 1802)	X	X
		st	*Atheta oblita* (Erichson, 1849)		X
		st	*Coryphium atratum* Breit, 1911	X	
		st	*Oxypoda brevicornis* (Stephens, 1832)		X
		st	*Quedius obscuripennis* Bernhauer, 1901	X	
		st	*Tachyporus nitidulus* s.l. (Fabricius, 1781)	X	X
		st	*Liogluta roettgeni* (Bernhauer, 1903)	X	
	Ap	cr	*Dichotrachelus variegatus variegatus* K. Daniel & J. Daniel, 1898		X
		cr	*Protapion trifolii* (Linnaeus, 1768)	X	
	Ap	cr	*Donus oblongus* (C.H. Boheman, 1842)		X
		op	*Mitopus* sp.	X	X
		ac	*Tectocepheus velatus velatus* (Michael, 1880).		X
		ac	Acarina (no Oribatida)	X	X
*	GS-M	ps	*Neobisium fiscelli* Callaini, 1985		X
*	GS-M	ps	*Neobisium osellai* Callaini, 1985		X
	Ap	dr	*Forficula apennina* Costa, 1881	X	X
		dp	Diplopoda		X

Mean soil parameters of the two units. For all other traits and differences among sampling methods, see Supplemental Material 7, available online.
Ap: endemic of Apennines; GS-M: stenoendemic species of Gran Sasso and Majella.
p=plants, c=ground beetles, coll= springtails, sp=spiders, st= rove beetles, cr= snout beetles, op= harvestmen, ac= mites, ps= pseudoscorpions, dr= earwigs, dp= millipedes.
*Cryophilic species.

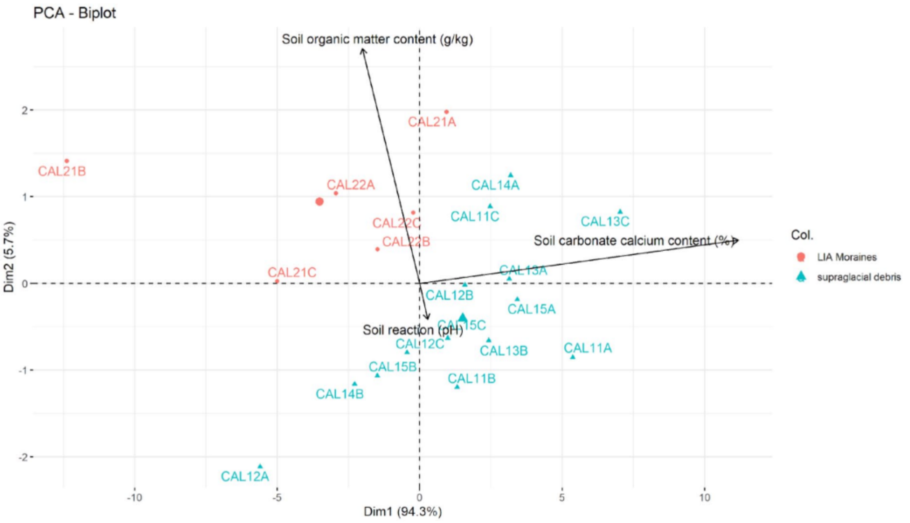


Figure 2. Principal component analysis (PCA) on soil data evaluates the association among all variables.

Table 3. Differences in species composition between the two communities (mean values of species and the mean incidence) in relation to every functional trait respectively for supraglacial debris and LIA moraine.

		Species richness			Incidence		
		Supraglacial debris mean	LIA moraine mean		Supraglacial debris mean	LIA moraine mean	
CUMULATIVE	Plant species richness	**0.143**	**2.67**	*	/	/	/
	Arthropod species richness	**4.860**	**11.800**	*	/	/	/
Altitudinal distribution	Alpine	**2.643**	**4.167**	*	65.391	47.888	
	Low alpine	**0.857**	**2.500**	*	19.898	26.197	
	Lowland	0.571	3.000		14.711	25.916	
Cryophilic	Cryophilic	1.714	1.833		**42.942**	**18.474**	***
	Non cryophilic	**2.357**	**7.667**	*	**57.058**	**78.748**	**
	Unknown	0.000	0.167		0.000	2.778	
Endemism	Apennines end.	**0.643**	**2.167**	*	15.306	22.534	
	Apennines-Alps end.	1.000	1.000		**23.469**	**12.247**	**
	GS-M end.	1.643	2.500		**41.922**	**27.057**	*
	South European orophilic	**0.214**	**1.000**	***	**4.592**	**12.247**	*
	Wider distribution	0.571	3.000		14.711	25.916	
Wings	Brachypterous	**0.643**	**1.500**	*	44.444	41.667	
	Winged	0.571	1.000		23.611	16.667	
	Apterous	**0.643**	**1.667**	*	31.944	41.667	
Diet	Detritivores	2.000	3.833		47.577	35.694	
	Microorganism consumer	2.000	3.833		47.577	35.694	
	Parassitoid	0.071	0.167		0.893	1.190	
	Phytophagous	**1.000**	**3.333**	*	22.457	29.821	
	Predator	**1.286**	**4.667**	**	**28.478**	**46.974**	*
	Saprophagus	0.143	0.333		2.806	2.153	
	Spermophagus	0.000	0.333		0.000	2.153	
	Unknown	0.929	1.833		20.247	17.331	

Bold font highlights significant values. *p-value < 0.05. **p-value < 0.01. ***p-value < 0.001***.
"end."= endemic; "GS-M end."= stenoendemic of Gran Sasso and Majella.

ground beetle *Nebria orsinii orsinii*, the springtail *Orchesella* cf. *frontimaculata*, the spider *Agyneta rurestris*, the rove beetles *Aleochara meridionalis, Anotylus nitidulus, Tachyporus nitidulus*, and the earwig *Forficula apennina*.

Stenoendemic species of Majella and Gran Sasso are the most represented on both the LIA moraine and supraglacial debris, and are dominant on supraglacial debris (incidence respectively 27% and 42% in the two communities, p-value = 0.016; Table 3, Supplemental Material 2, available online). Endemic species of the Apennines showed the highest species richness on the LIA Moraine (p-value = 0.011). The incidence of endemic species of Alps and Apennines were significantly higher in the supraglacial debris (p-value < 0.01). South European orophilic species were significantly higher on the LIA moraine both considering the species richness and their incidence (p-value < 0.001, p-value $= 0.043$, respectively).

Considering altitudinal distribution, we found that the LIA community has a significantly (or almost significantly) higher species richness of alpine and low alpine species. On supraglacial debris there is a higher incidence (65%; p-value $= 0.097$) of alpine species and a similar incidence of mountain (20%; p-value $= 0.162$) and generalist (15%; p-value $= 0.272$) species (Table3, Supplemental Material 2, available online).

The species richness of brachypterous and apterous species are higher on the LIA moraine (respectively, p-value $= 0.01$ and p-value $= 0.026$) (Table 3, Supplemental Material 2, available online).

The incidence of cryophilic species is higher on the supraglacial debris (p-value < 0.001), while non-cryophilic species are more incident on the LIA moraine (p-value $= 0.001$; Table 3, Supplemental Material 2, available online).

The feeding strategy distributions were different between LIA moraine and supraglacial debris (Table 3, Supplemental Material 3, available online): while on supraglacial debris detritivores and microorganism consumers were dominant (mean value of about 48%, corresponding to all the present springtails) and predators accounted for 28% (only *Nebria orsinii orsinii, Agyneta rurestris, Pardosa* sp. and *Tachyporus nitidulus*), the LIA moraine community was dominated by predators (mean of about 47%, p-value $= 0.021$: the ground beetles *Nebria orsinii orsinii, Pterostichus morio samniticus*, *Amara samnitica*, the spiders *Pardosa cavannae, Agyneta rurestris, Oreonetides glacialis, Entelecara* sp.n. *Improphantes* cf. *improbulus*, the rove beetle *Quedius obscuripennis*, the harvestman *Mitopus* sp. and both pseudoscorpions, *Neobisium fiscelli, Neobisium osellai*). Other feeding strategies were less represented, especially on supraglacial debris. The species richness of phytophagous was significantly higher on the LIA moraine (p-value $= 0.039$) including the snout beetles *Dichotrachelus variegatus variegatus*, and *Donus oblongus*, the springtails *Orchesella* cf. *frontimaculata*, *Lepidocyrtus* cf. *lignorum*, *Lepidocyrtus* cf. *tellecheae*, *Tomocerus vulgaris* and *Deutherosminthurus* sp. and the opportunistic oribatid *Tectocepheus velatus velatus*. On supraglacial debris the only phytophagous were the opportunistic *Orchesella* cf. *frontimaculata* and *Tectocepheus velatus velatus* and the common snout beetle *Protapion trifolii*. Saprophagus and spermophagus are not significantly different between the environmental units, since the only spermophagous was the ground beetle *Amara samnitica*, which is also a predator, on the LIA moraine. The only saprophagous was *Mitopus* sp., ubiquitous between the two environmental units. Parasitoids are represented only by the rove beetle *Aleochara meridionalis*, found in both environmental units with a single specimen.

Microtopographic drivers affecting species distributions on supraglacial debris

On supraglacial debris, the highest species richness was found in correspondence with the mean value of debris thickness, about 20 cm; Figure 3).

The springtail *Orchesella* cf. *frontimaculata* was positively related to debris thickness; this link is more notable with the pitfall trap method (PT: $R^2 = 0.5$) than with the flotation method (FM: $R^2 = 0.44$) (Figure 4). The springtail *Desoria calderonis*, on the other hand, is more abundant where the ice is closer to the surface; this result is more significant with the floatation method (FM: $R^2 = 0.64$), than with the pitfall trap method (PT: $R^2 = 0.32$). With the exception of the ground beetle *Nebria orsinii orsinii*, which seemed to slightly prefer a lower debris thickness ($R^2 = 0.12$), the abundance of other organisms considered – Acari, the spider *Agyneta rurestris* and the earwig *Forficula apennina* – showed a slight positive relation to a thicker debris.

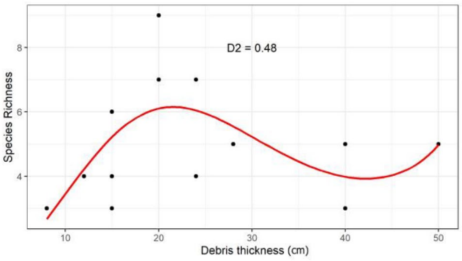


Figure 3. Generalized linear model testing the relationship between arthropod species richness (estimated with both pitfall trap and flotation method) and debris thickness (SDS) of supraglacial debris.

Only Acari abundance, excluding oribatids, ($R^2 = 0.29$) seemed positively, although weakly, related to the abundance of organic matter (Supplemental Material 6.A, available online). Acari (without oribatids) abundance was also the most negatively related to pH values ($R^2 = 0.61$) (Supplemental Material 6.B, available online). The abundance of spider *Agyneta rurestris* ($R^2 = 0.39$) and of the ground beetle *Nebria orsinii orsiniii* ($R^2 = 0.69$) are weakly negatively related to soil carbonate calcium content (Supplemental Material 6.C, available online).

Discussion

Peculiarities of supraglacial and proglacial communities

Even in such a limited space as the supraglacial and proglacial areas of Calderone glacier, biological communities are very well differentiated among the considered environmental units: the supraglacial debris and the LIA moraine (we summarize the most important features in Figure 5). The first discriminant between the two environmental units is the species richness, both plants and arthropods, which is markedly lower on supraglacial debris.

Cryophilic species – as observed in previous studies (Lamprecht et al., 2018; Valle et al., 2020) – are effective in distinguishing supraglacial debris from the LIA moraine species assemblages considering their incidence. However, their richness is similar between the two considered environmental units: we hypothesize that the moraine could be influenced directly by the proximity to the ice allowing most cryophilic species to live in this environment. Only the cryophilic springtail *Desoria calderonis* does not colonize the LIA moraine despite the proximity to the ice.

On the other hand, the LIA moraine hosts many arthropod species that are not strictly cold- or wet-loving, but characteristic of high-altitude open environments: here the trophic chain is more complex, characterized by the presence of a multiple trophic levels, including a significative incidence of herbivores. This can be explained by the differences observed in plant cover, organic matter content and stability between the LIA moraine and supraglacial debris.

Despite the potential intake of seeds from the surrounding environment (e.g. rock walls), only *Arabis alpina caucasica* grows on supraglacial debris, while on the nearby moraines eight plant species are present. This evidence suggests that not only the dispersal ability but also seed germination and seedling survival traits act as limiting factors in determining plant growth on supraglacial debris. Indeed, *Arabis alpina* shows a positive response to vernalization (i.e. the exposure of plants or seeds to

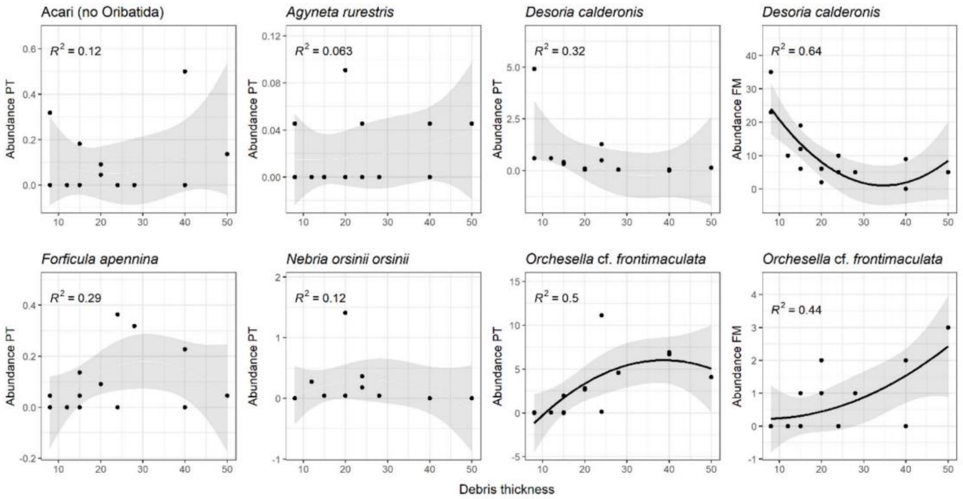
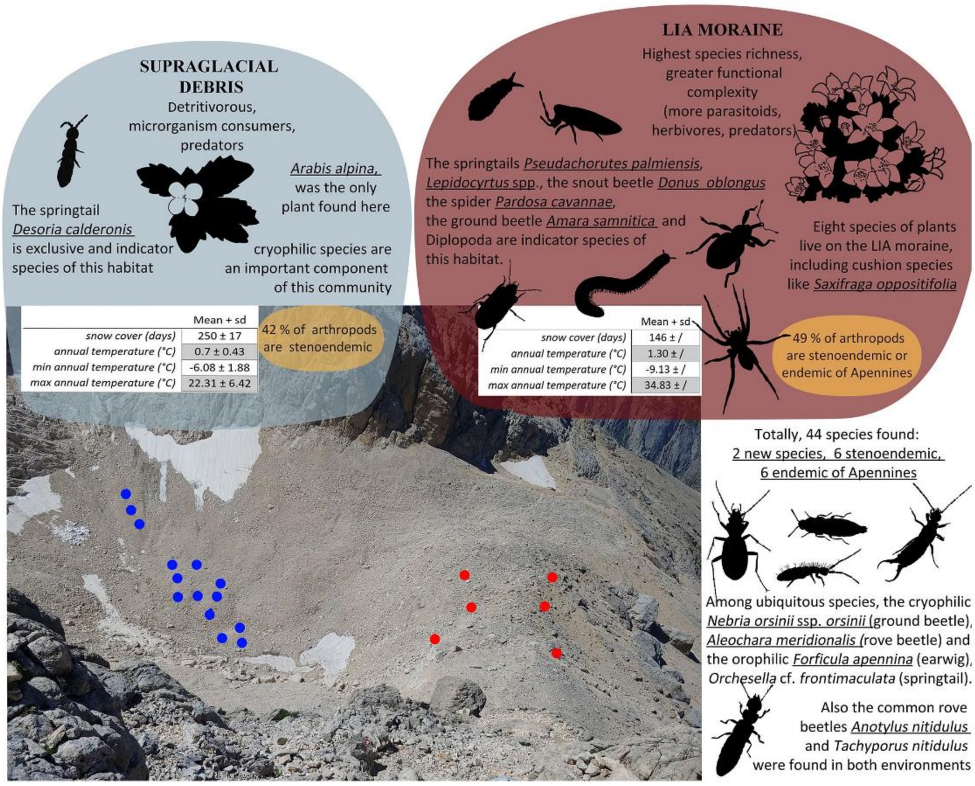


Figure 4. Linear models testing the relationship between species abundances and debris thickness (cm) on supraglacial debris. PT = samples collected with pitfall trap method and abundance calculated as activity density (AD), FM = samples collected with flotation method and abundance corresponding to absolute number of specimens collected. The standard error of the pattern is reported; the black line was reported only for significant models.



SUPRAGLACIAL DEBRIS

Detritivorous, microrganism consumers, predators

Arabis alpina, was the only plant found here

The springtail *Desoria calderonis* is exclusive and indicator species of this habitat

cryophilic species are an important component of this community

	Mean + sd
snow cover (days)	250 ± 17
annual temperature (°C)	0.7 ± 0.43
min annual temperature (°C)	-6.08 ± 1.88
max annual temperature (°C)	22.31 ± 6.42

42 % of arthropods are stenoendemic

LIA MORAINE

Highest species richness, greater functional complexity (more parasitoids, herbivores, predators)

The springtails *Pseudachorutes palmiensis*, *Lepidocyrtus* spp., the snout beetle *Donus oblongus* the spider *Pardosa cavannae*, the ground beetle *Amara samnitica* and Diplopoda are indicator species of this habitat.

Eight species of plants live on the LIA moraine, including cushion species like *Saxifraga oppositifolia*

	Mean + sd
snow cover (days)	146 ± /
annual temperature (°C)	1.30 ± /
min annual temperature (°C)	-9.13 ± /
max annual temperature (°C)	34.83 ± /

49 % of arthropods are stenoendemic or endemic of Apennines

Totally, 44 species found:
2 new species, 6 stenoendemic, 6 endemic of Apennines

Among ubiquitous species, the cryophilic *Nebria orsinii* ssp. *orsinii* (ground beetle), *Aleochara meridionalis* (rove beetle) and the orophilic *Forficula apennina* (earwig), *Orchesella* cf. *frontimaculata* (springtail).

Also the common rove beetles *Anotylus nitidulus* and *Tachyporus nitidulus* were found in both environments

Figure 5. Graphical synthesis of the characteristics of the two communities. Blue and red points represent sampling points respectively on supraglacial debris and on the LIA moraine (their position is approximate, for their actual distribution see Figure 1). Taxa represented as characteristic of the two environmental units are those found with the IndVal analysis. Organisms are not in scale. Underlined species are those represented in the figure.

low temperatures) (Wang et al., 2011). Vernalization and, more in general, seed dormancy can contribute to the maintenance of long-lived seed banks by ensuring that germination is either delayed until the onset of favorable conditions, or that the seed bank does not germinate all at once (Baskin and Baskin, 1998; Fenner and Thompson, 2005; Ooi et al., 2009). Thus, seed dormancy could be an adaptive strategy to survive in cold habitats (Schwienbacher et al., 2011). Moreover, *Arabis alpina* shows a high phenotypic plasticity (Andrello et al., 2016; de Villemereuil et al., 2018), perhaps owing to its high genetic diversity in the Mediterranean mountains (Koch et al., 2006). Indeed, as proof of its plasticity, this species is widespread over a wide altitudinal range, from 800 to 3100 m asl (Pignatti, 2017).

The comparable incidence of wing reduction or absence on moraine and supraglacial debris suggests that the reduced mobility in ground-dwelling fauna is a common and quite constant characteristic of organisms living at high altitude, specifically in glacial habitats (Gobbi et al., 2017). Reduced mobility is typical of species with a restricted distribution range, both geographical and altitudinal (Pizzolotto et al., 2014; Sattler et al., 2014): both environmental units, in fact, have an high incidence of endemic and stenoendemic species, the latter being even dominant on supraglacial debris. Concerning the altitudinal distribution range, we observed the same phenomenon: high altitude species show higher richness on the LIA moraine, but they are dominant on supraglacial debris.

Calderone glacier gives evidence of the "Collembola first principle" (Hagvar and Gobbi, 2022), being these pioneer organisms crucial for glacial habitat. They graze on biofilm (Hågvar and Pedersen, 2015) as well as on airborne organic matter (Ingimarsdóttir et al., 2014; König et al., 2011) and constitute a local source of food for all predators (Hågvar and Ohlson, 2013; Sint et al., 2019). Nevertheless airborne arthropod fallout found includes families of forestry and winged (i.e. long distance dispersers) beetles, indicating also "allochthonous" sources of preys relatively far from the glacier.

From the methodological point of view, the use of two sampling methods for arthropod was fundamental to obtain more complete data on the communities studied, whereas the communities reflected by the two methods singularly were very different. In particular, among springtails the flotation method caught the only euedaphic species found, *Protaphorura octopunctata*, well reflected the distribution of *Desoria calderonis* in the supraglacial debris and excluded a lot of strongly epiedaphic species like *Lepidocirtus* spp. and *Tomocerus vulgaris*, suggesting that this method might be very useful to study soil fauna of mineral soils (Marshall et al., 1994). Nevertheless, the pitfall trap method better reflects the general complexity of the two communities studied.

The importance of glacial refugia, "cold-spots" of biodiversity

Calderone glacier, despite its limited extension, proved to be a great coffer of exclusive biodiversity, since endemic species are a very important part of its glacial communities. We discovered two new species on Calderone glacier, the springtail *Desoria calderonis* (sampled during this field campaign and described in Valle et al., 2021) and the spider *Entelecara* sp.n. (sampled during this field campaign and currently under description by P. Pantini) taxonomically related to the species *Entelecara media* Kulczyński, 1887 Among known species, some remarkable taxonomic catches are the rare rove beetle *Coryphium atratum*, the spiders *Improphantes improbulus* – a glacial relict according to Thaler (1986) – and both pseudoscorpion species, as after the description by Callaini in 1985 for Abruzzo, there have been no more findings (Gardini, 2000).

In addition, considering the peculiarity and the isolation of Calderone glacier, the poor known springtail *Orchesella* cf. *frontimaculata*, described by Gisin (1960) on the basis of pigmentation, is probably a different and new species: pigmentation is not sufficient in distinguish this taxa and chaetotaxy could show a hidden biodiversity (Jordana and Baquero, 2005; Potapov and Kremenitsa, 2008; Smith, 2015). Similarly, *Lepidocyrtus* spp., as demonstrated by Zhang et al. (2018), could hide a great cryptic biodiversity in relation to habitat type. Thus, it would be necessary to investigate morphology, ecology and genetics of these entities in order to verify their taxonomic position (Frati et al., 2000; Porco et al., 2014; Potapov and Kremenitsa, 2008; Smith, 2015).

The richness of endemic and rare high altitude species, as well as the identification of new entities indicate how much this relict glacier is an important refugium in the current warm-stage period for high altitude biodiversity, a so called "cold-spot of biodiversity" (Cauvy-Fraunié and Dangles, 2019), with low absolute level of biodiversity, but extremely specialized and threatened. This is indicated especially by the presence of cryophilic species with endemic distribution range, as already observed for different taxa such as yeast and yeast-like organisms (Branda et al., 2010). Among such species, the best indicator of the ice presence is the springtail *Desoria calderonis*, showing a high sensitivity to the microhabitat, unlike other cryophilic organisms observed also outside, although close to the ice. We confirmed the link of *Desoria calderonis* to the ice, hypothesized in Valle et al. (2021), its narrow ecological niche and thus its role as indicator of cold thermal conditions and of the presence of sub-surface ice. The high specialization of cryophilic springtails (Collembola: Isotomidae) was already highlighted for different mountain regions, from the Rocky Mountains in North America (Fjellberg, 2010) to the Pyrenées in France (Lauga-Reyrel and Lauga, 1995; Najt, 1981), constituting a good indicator of permanent ice.

In the present global warming phase Calderone glacier is experiencing an intense phase of reduction (De Sisti et al., 2003; D'Orefice et al., 2000; Pecci, 2020) which will probably lead to its extinction if the trend of global change does not change. Giraudi (2000) outlined the past fluctuations of Calderone glacier through radiometric dating, demonstrating that it already almost disappeared during the Holocene Optimum. The resulting question is where and how these cryophilic organisms survived during such disappearance phases, a highly critical question in the present climatic phase. It is possible that residual small ice patches covered and protected by stony debris – which considerably reduced their ablation rate (Nakawo and Rana, 1999) – were persistent enough for the survival of these species. Another hypothesis, which does not exclude the first one, is that in this karstic area these organisms may have found a suitable refugium in caves or deep rock crevices where snow can accumulate and persist (Gobbi et al., 2021; Raschmanová et al., 2018). It would be important to test these hypotheses, by searching cryophilic species in proximity to subterranean habitats and performing genetic analysis at population level, in order to define where and what this past refugium was and to understand the fate of these peculiar species in the short-term climate scenario.

The small, vanishing glaciers such as Calderone glacier, located on relatively low mountain chains, could represent a reliable projection of the processes that might occur in the next future on the main glacial areas at higher latitude and altitude.

Conclusions

In two confined environmental units, located in a well studied geographic area of Europe, we found a rare and peculiar biodiversity of high altitude habitats and, even, two previously undescribed species. This biodiversity seems to be related to the biogeographic position of Calderone glacier and its role as a refugium for high-altitude species. In the current climate scenario of temperature increase, which threatens cold-adapted species (Seastedt et al., 2021), it is important to study the ecology of these environmental units in order to monitor glacial "cold-spots" of biodiversity, since an important part of this biodiversity is still taxonomically unknown, especially in peripheral mountains (Gobbi et al., 2021). Only in this way it will be possible to hypothesize also a monitoring and, possibly, a conservation strategy, as well as to forecast the global future patterns and the fate of glacial biodiversity.

Funding

The authors received no financial support for the research, authorship, and/or publication of this article.

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Supplemental material

Supplemental material for this article is available online.

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3.3 *Desoria calderonis* sp. nov., a new species of alpine cryophilic springtail (Collembola: Isotomidae) from the Apennines (Italy), with phylogenetic and ecological considerations.

European Journal of Taxonomy 787: 32–52
https://doi.org/10.5852/ejt.2021.787.1599

ISSN 2118-9773
www.europeanjournaloftaxonomy.eu
2021 · Valle B. *et al.*

Research article

urn:lsid:zoobank.org:pub:0C6C4FA5-D1D8-4C2F-825F-A3882DE02B99

Desoria calderonis sp. nov., a new species of alpine cryophilic springtail (Collembola: Isotomidae) from the Apennines (Italy), with phylogenetic and ecological considerations

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Abstract. We describe and delimit with integrative taxonomy the new springtail species *Desoria calderonis* sp. nov. (Collembola: Isotomidae). This cryophilic species is strictly linked to the supraglacial stony debris of the isolated Calderone glacier (Central Apennines, Italy), one of the southernmost glaciers of Europe. *Desoria calderonis* sp. nov. could belong to the *nivalis*-complex, a group of European mountain species included in the *violacea*-group. Genetic analysis (COI mtDNA barcoding) confirms the morphological attribution to the genus *Desoria* Nicolet in Desor, 1841, but highlights that the genus, in its current definition, is polyphyletic. We specify the peculiar micro-habitat preferences and highlight the threat of extinction for this cryophilic species in the context of the ongoing climate change and subsequent risk of complete disappearance of the glacier.

Keywords. Glacial biodiversity, glacial refugia, peripheral mountains, vanishing glaciers, unknown biodiversity.

Valle B., Cucini C., Nardi F., Caccianiga M., Gobbi M., Di Musciano M., Carapelli A., Ficetola G.F., Guerrieri A. & Fanciulli P.P. 2021. *Desoria calderonis* sp. nov., a new species of alpine cryophilic springtail (Collembola: Isotomidae) from the Apennines (Italy), with phylogenetic and ecological considerations. *European Journal of Taxonomy* 787: 32–52. https://doi.org/10.5852/ejt.2021.787.1599

Introduction

Cryophilic springtails (Hexapoda: Collembola) are cold- and moisture-requiring organisms, whose typical habitat is near or above ice or snow (Deharveng *et al.* 2008; Fjellberg 2010; Buda *et al.* 2020; Valle *et al.* 2020; Jureková *et al.* 2021). *Desoria saltans* Nicolet, 1841 (Entomobryomorpha: Isotomidae) is among the best known cryophilic springtails and is commonly known as the "glacier flea". This species was already cited by the Italian geologist Stoppani in his early essay "Il Bel Paese" (Stoppani 1876) for its showy, swarming and large assemblages on Alpine glaciers. Nowadays there are indications that "glacier fleas" include multiple taxa of cryophilic Isotomidae related to the genus *Desoria*: *Desoria* Nicolet in Desor, 1841, *Gnathisotoma* Cassagnau, 1957 and *Myopia* Christiansen & Bellinger, 1980 (Najt 1981; Fjellberg 2010). These organisms appear to be differentiated among isolated glacial areas (Deharveng 1975; Lauga-Reyrel & Lauga 1995). By comparing different European glacier forelands, Hågvar *et al.* (2020) observed how the species belonging to this group, and to a few other pioneer genera, are important not only as components of supraglacial communities (see also Gobbi *et al.* 2021), but also as early colonisers of recently-deglaciated terrains. High diversity of cryophilic Isotomidae was observed in southern Alaska and in the Canadian Rocky Mountains in North America (Fjellberg 2010). Therefore, we can assume high diversity of the genera related to *Desoria* at similar sites in Europe.

The genus *Desoria* comprises 101 described species (Bellinger *et al.* 1996–2021), mostly distributed in the Holarctic, especially at high latitudes (Potapov 2001). *Desoria* differs from the closely related genus *Isotoma* Bourlet, 1839 by the number of apical setae on tibiotarsi (11, with the exception of the *pjasini*-group), and the absence of ventroapical spine-like setae on the manubrium (Potapov 2001; Fjellberg 2007). From the ecological point of view, *Desoria* also differs from *Isotoma* by being more frequent at cold and wet sites and thus including many hygrophile and cold-adapted species (Potapov 2001). Species belonging to the genus *Desoria* overwinter in the adult stage and are often active on snow or ice, on which they feed (Hao *et al.* 2020) and migrate (Hågvar 2000; Zhang *et al.* 2017). Among these cold-adapted species, *Desoria* and taxonomically related genera like *Agrenia* Börner, 1906, *Gnathisotoma*, *Myopia* and *Kaylathalia* Stevens & D'Haese, 2016 (Najt 1981; Fjellberg 2010; Stevens & D'Haese 2017) include cryophilic species (Potapov 2001; Fjellberg 2007, 2010). Cryophilic species, in particular, are of great interest because they are particularly threatened by the current global warming and are good candidates as indicators for conservation projects aimed at investigating refugial glaciated areas (Gobbi *et al.* 2021).

Several works carried out on alpine cryophilic springtails (e.g., Deharveng 1975; Najt 1981; Lauga-Reyrel & Lauga 1995; Fjellberg 2010; Makowska *et al.* 2016; Hittorf 2017; Buda *et al.* 2020) indicated a significant knowledge gap on springtail biodiversity in glaciated areas of the World. The cryophilic collembolan fauna is still poorly described especially from Southern Europe, where it should be particularly differentiated in relation to the glacial history of the peripheral and southernmost European massifs (Deharveng 1975; Najt 1981; Lauga-Reyrel & Lauga 1995). Furthermore, the taxonomy of *Desoria* is still uncertain, as both morphological and genetic evidence indicates that this genus is polyphyletic, as it includes different subgroups (Stevens *et al.* 2006; Fjellberg 2007; Stevens & D'Haese 2017).

In this work, we present a description of a new species of *Desoria* found in one of the southernmost European relict glacial areas, the Calderone glacier (Central Apennines, Italy; Grunewald & Scheithauer 2010). This species is thus a good indicator of a "cold-spot" of the local glacial biodiversity (Cauvy-Fraunié & Dangles 2019) in the Mediterranean region. In order to provide a robust taxonomic classification for this new species, we applied both morphological and genetic approaches, to obtain a phylogenetic framework. In addition, we provide remarks on its habitat and microhabitat preferences.

Material and methods

Study area and data collection

Specimens were collected by the flotation method (Marshall *et al.* 1994) on the Calderone glacier. The Calderone glacier is located on the Gran Sasso Massif, in the Central Apennines (Italy, Abruzzo; 42°28′16.4″ N, 13°34′01.4″ E). Presently, it is classified as glacieret (total surface < 0.04 km^2; Smiraglia & Diolaiuti 2015) and it is almost totally covered by stony debris. We searched for *Desoria calderonis* sp. nov. in all glacial environments, on the supraglacial debris and on the Little Ice Age (LIA) moraines. In order to better verify its distribution, both flotation and pitfall trap methods were used for 15 sampling points on the supraglacial debris as well as 6 sampling points on LIA moraines as controls. In order to better characterize the ecology of *Desoria calderonis* sp. nov., we recorded micrometeorological (temperature and humidity) and soil data of its habitat and of the surrounding habitat where it was not found, in particular:

- temperature was recorded on supraglacial debris by 15 and on LIA moraines by 2 dataloggers (iButton 1922) for the period 9 July 2020 – 27 July 2021; using this data, we calculated the mean annual temperature, the mean temperature during the snow-free period, the minimum and the maximum temperatures and the duration of the snow-cover;
- relative humidity was recorded in both environments by a datalogger (Tinytag Plus) for the same period; with this data we calculated the mean annual value and the mean value during the snow-free period;
- soil samples were collected for 15 points on the supraglacial debris and 6 points on LIA moraines. In soil samples we measured the value of carbonate calcium content, organic matter content and pH.

All dataloggers were positioned 10 cm under the surface.

Specimen conservation and preparation

Specimens (1 holotype and 15 paratypes), preserved in 90% ethanol at -20°C, were initially cleared by a short immersion in 10% KOH solution and then mounted on slides using lactic acid or Marc André as a preservative solution. Additional specimens (five) were prepared for scanning electron microscopy: they were completely dehydrated in absolute ethanol, before critical point drying in a Balzers Union (FL-9496) apparatus and the subsequent sputter coating with gold in an Edwards Sputter Coater S150B. Morphological observations were performed with a Leica Laborlux S light microscope and a Quanta400 (FEI) scanning electron microscope.

Molecular analysis

Whole genomic DNA was extracted from 10 specimens, individually, using the Wizard®SV Genomic DNA Purification System (Promega, Madison, WI, USA). The mitochondrial marker analyzed –cytochrome *c* oxidase subunit 1, 5P fragment (*cox1*) – was amplified with a universal primer pair (Folmer *et al.* 1994). PCRs were prepared in a 25 µL reaction volume containing: 2.5 µL of whole genomic DNA, 1.25 µL of both forward and reverse primers (10 µM), 2.5 µL of $MgCl_2$ (2.5 mM), 2.5 µL of deoxynucleotides (dNTPs, 10 mM), 5 µL of Green GoTaq Flexi Buffer (Promega, Madison, WI, USA), 0.125 µL of GoTaq® G2 Flexi DNA Polymerase (Promega, Madison, WI, USA), 5 µL and 9.875 µL of ddH_2O. Amplifications were run on a GeneAmp® PCR System 2700 (Applied Biosystems, Foster City, CA, USA) thermal cycler with the following conditions for each of the 35 cycles: a denaturation step at 95°C for 1 min, an annealing step at 50°C for 1 min and an elongation step at 60°C for 90 s. An additional initial denaturation step was set at 95°C for 5 min as well as a final extension step at 72°C for 7 min. PCR products were purified with the kit Wizard®SV Gel and PCR Clean-up System (Promega, Madison, WI, USA) and sequenced on both strands using a DNA Analyzer ABI 3730 at Biofab (Rome, Italy). Sequences were then manually corrected and assembled in Sequencher ver. 4.2.2 (Gene Codes, Ann Arbor, MI, USA).

Phylogenetic analysis

Given the current uncertainties on the monophyly of the genus *Desoria* (Stevens *et al.* 2006; Stevens & D'Haese 2017) and of its closest relatives, a preliminary analysis was conducted to identify *Desoria* as well as phylogenetically related sequences in order to bypass the assumption of a monophyletic *Desoria* in the process of taxa selection. All records belonging to the family Isotomidae were downloaded from the BOLD database (Ratnasingham & Hebert 2007) with their Metadata (last download 30 June 2021). The 8483 records were filtered to retain only those including information for the COI-5P *cox1* fragment and having an assigned bin. The longest sequence for each bin was extracted using the R package 'bold' (ver. 1.2.0, written by Scott Chamberlain) and used as representative for the bin in the following analysis. For all records, metadata associated with a specific bin were revised to identify the taxonomic attribution(s), if available, of each bin, whereas bins with no taxonomic information below the family level in any sequence were discarded. Records were associated with 728 bins in BOLD, 348 of which included sequences with at least some associated taxonomic information. After the addition of the new species, *D. calderonis* sp. nov.(mean uncorrected divergence within the species is 0.4%, S.D. 0.2), the total dataset was composed of 349 sequences by 438 aligned positions (1st and 2nd positions only). The dataset was aligned with MAFFT (Katoh 2002) in order to calculate both uncorrected p-distances and phylogenetic relationships. These latter were obtained, using 1st and 2nd codon position data set, by IQ-TREE (ver. 1.6.12, default settings with 1000 fast bootstrap replicates and the model was optimized using ModelFinder; Nguyen *et al.* 2015). A reasonably supported node (bootstrap 92) was identified, including all *Desoria* sequences – with the exception of *Desoria trispinata* (3 bins, 18 sequences) and *Desoria tshernovi* (1 bin, 1 sequence, unrelated to 6 *D. tshernovi* sequences within the node) – as well as sequences from other genera. This subdataset, inclusive of related species and three outgroups (*Cryptopygus terranovus, Parisotoma notabilis* and *Folsomia quadrioculata*, grouping outside the *Desoria* cluster), accounted for 89 sequences by 438 aligned positions and was reanalyzed as above to investigate the phylogenetic position of the new species in the context of *Desoria* and related species. Once a final phylogenetic tree had been obtained, records that appeared phylogenetically related to *D. calderonis* sp. nov. were further revised in the BOLD database metadata or in the original literature to assess the existence of ecological and/or phylogeographic similarities.

Abbreviations used in the text

Abd = abdominal segment
accp-setae = accessory p-row *s*-setae
al-setae = antero-lateral *s*-setae
Ant = antennal segment
AOIII = antennal organ III
as-setae = anterosubmedial *s*-setae

bl = basolateral field (mentum)
bm = basomedian field (submentum)
ms-setae = micro *s*-setae
PAO = post antennal organ
Px = proximal field
Th = thoracic segment
Tita = tibiotarsus
VT = ventral tube

Results

Phylum Arthropoda Latreille, 1829
Class Collembola Lubbock, 1870
Order Entomobryomorpha Börner, 1913
Family Isotomidae Schäffer, 1896
Subfamily Isotominae Schäffer, 1896
Genus *Desoria* Nicolet in Desor, 1841

Desoria calderonis Valle sp. nov.

urn:lsid:zoobank.org:act:1DEC543F-66C5-4556-B5B3-6806CEB35488
Figs 1–5

Diagnosis

Desoria calderonis sp. nov. belongs to the *violacea*-group sensu Potapov, 2001, with quadridentate mucro without seta, maxillary palp bifurcate, apical folds on labrum sharp. Differences from closely related species are analysed in the section 'Taxonomic and ecological consideration'.

Etymology

The epithet of the new species reflects the name of the site from which holotype and paratypes derive, Calderone glacier (Italy, Abruzzo, Gran Sasso massif).

Material examined

Holotype

ITALY • ♀; Abruzzo (Central Italy), Gran Sasso massif, Apennines, Calderone Glacier, supraglacial stony debris; 42°28′16.2″ N, 13°34′05.8″ E; alt. 2700 m a.s.l.; 8 Jul. 2020; B. Valle and M. Di Musciano leg.; collected with flotation method; Genbank (NCBI) MZ686962-70; Collembola collection, Department of Life Sciences, University of Siena, Italy.

Paratypes

ITALY • 15 spec. (♂ and ♀); same collection data as for holotype; Collembola collection, Department of Life Sciences, University of Siena, Italy.

Description

BODY. Mean body length. 1.5 mm (standard deviation: 0.1 mm on 12 specimens, see Table 1). Colour violet-black on abdomen and antennae, lighter on furca and legs, which are brownish (Fig. 1); juveniles are much paler, bluish. Cuticle granulation fine and regularly distributed; all dorsal tergites clearly separated from each other. Abd. III and IV of approximately same width.

CHAETOTAXY. Terga plurichaetotic, consisting of micro-, meso- and macrosetae, these latter well differentiated on last abdominal tergites (Abd. IV–VI, in median position), but not well distinguished from ordinary setae on other tergites (Fig. 2A). On every segment, longer setae concentrated along the lateral and posterior edges of tergite. All setae smooth. Macrosetae on Abd. V 0.9–1 times median length of tergite and 1.8–2.4 times as long as inner edge of Claw III (Table 1). Sensory chaetotaxy constituted by *ms*-setae, *accp*-, *al*- and *as*-setae. Only Th. II and Abd. III have *ms*-setae (formula 10/001). Dorsal *s*-setae constituted by single *al*-seta on Th. II and Th. III, single *as*-seta on Abd. V and by *accp*-setae (4–7 on each tergite from Th. II to Abd. V) normally set within *p*-row (Fig. 2B). The number of *accp*-setae can be expressed as 5–6,6/5–6,5,7,6–7,4 (Fig. 2B). The number of ordinary setae between *accp*-setae may vary by 1 (rarely 2) with respect to the scheme presented in Figure 2B (after Potapov 1989).

HEAD. Antennae longer than cephalic diagonal (D/A = 0.79). Ratio among Ant. I/Ant. II/Ant. III/Ant. IV is 1/1.75/1.57/2.57. Some *s*-setae well differentiated, others thick and hardly differing from ordinary setae (hereafter 'seta-like *s*-setae'). There are often cases of asymmetry among *s*-setae between antennae of the same specimen. Ant. I has about 54 setae, 6–11 short, thick and cylindrical *s*-setae and 4 seta-like *s*-setae in ventro-lateral position; 2–3 microsetae in ventro-proximal position (Fig. 2E). Ant. II has about 90 setae, 4 *s*-setae and 2–3 seta-like *s*-setae (Fig. 2E). Ant. III has about 84 setae and a sensory field that includes 2 *s*-setae of AO III, about 8 *s*-setae and 6 seta-like *s*-setae (Figs 2E; 5C). Ant. IV plurichaetotic with more than 300 setae, with few *s*-setae and several seta-like *s*-setae; one simple small subapical, rod-shaped organite and a clearly bifurcate pin-like seta (Fig. 2D). Eye spots strongly dark pigmented with 8 + 8 ocelli (G and H usually hardly visible; Figs 2C, 5A). PAO elongated, with a weak median constriction, about 2 times as long as diameter of nearest ocellus (Fig. 2C). Prelabral setae 4. Labral formula as 5, 5, 4 and 4 sharp papillae (Fig. 4C). Maxillary palp bifurcate and maxillary outer lobe with 4 sublobal hairs (Fig. 4F). Labial palp with 5 papillae and a total of 16 guard setae (Fjellberg 1999) distributed as: A_1, B_{1-4}, C_0, D_{1-4}, E_{1-7} (Fig. 4B). Hypostomal papilla with H as long as h_1/h_2. Proximal (px), basomedian (bm) and basolateral (bl) fields of labium with 4, 4 and 5 setae, respectively (Fig. 4A).

Fig. 1. *Desoria calderonis* sp. nov., general aspect.

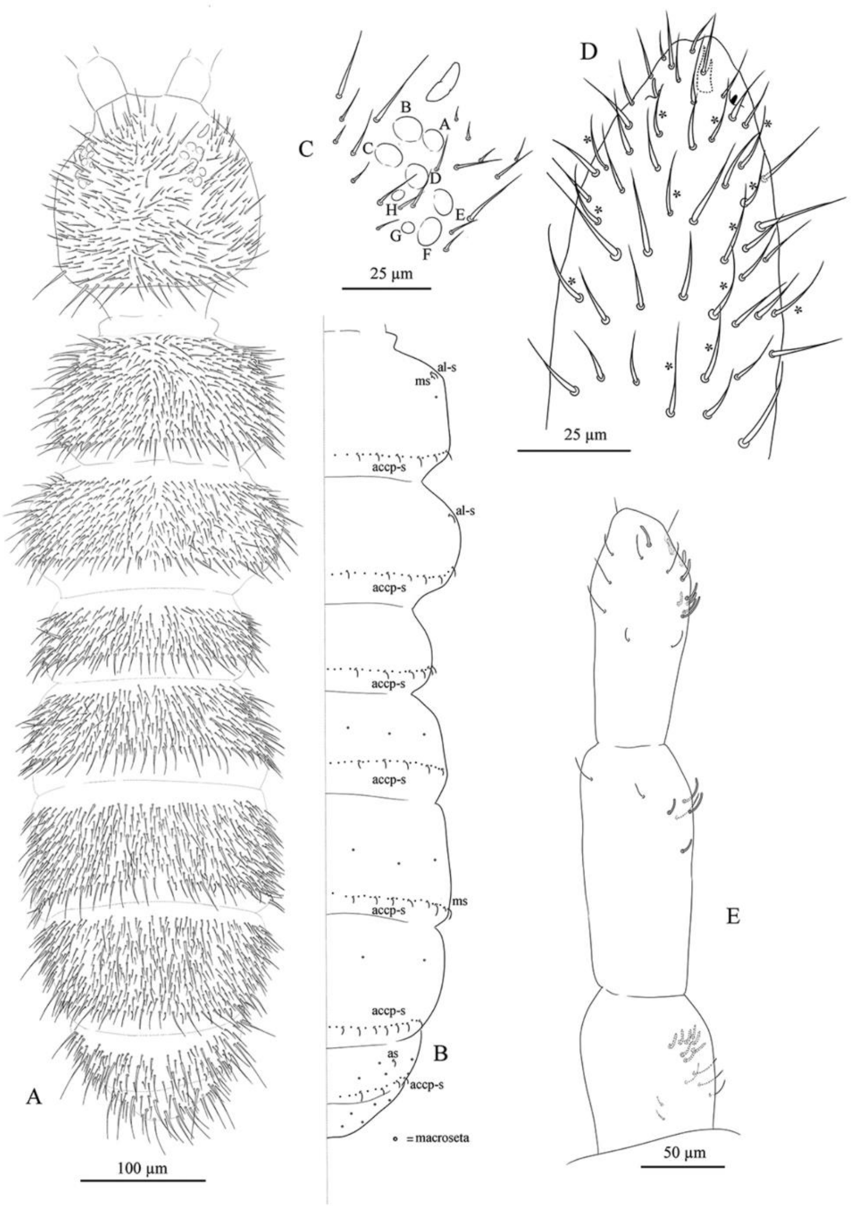

Fig. 2. *Desoria calderonis* sp. nov. **A**. Dorsal chaetotaxy. **B**. Number and distribution of dorsal *s*-setae (accp-s: *accp*-setae; al-s: *al*-setae; as: *as*-setae) and *ms*-setae (ms). **C**. Ocular plate (A–H: eyes) and PAO. **D**. Ant. IV apical dorsal part; asterisk = seta-like *s*-seta. **E**. Ant. I–III, dorsal view, with *s*-setae (double line) and seta-like *s*-setae (simple line); on ventro-proximal part of Ant. I, two isolated microsetae present.

Table 1. Body measurements of *Desoria calderonis* sp. nov.

	Length (µm)										
	Head (dorsal)	**Body**	**Ant. I**	**Ant. II**	**Ant. III**	**Ant. IV**	**Cephalic diagonal**	**Furca**	**Mac (Abd. V)**	**Abd. V**	**Inner edge of Claw3**
Mean value (µm)	311	1171	61	107	97	164	338	495	191	193	95
Standard deviation	20	82	8	11	12	15	39	43	10	13	8
Number of measurements	11	12	12	12	12	12	5	12	11	10	11

Maxilla of normal shape as in Fig. 4E, with lamellae shorter than capitulum. Ventral line of head with 9 + 9 postlabial setae (Fig. 4A). Mandible with well-developed molar plate as in Fig. 4D. VT with 2–4 + 2–4 anterior, 4 + 4 latero-distal and 4 posterior setae with 2 in apical transverse row (Fig. 4I). Retinaculum with 4 teeth and 7–8 setae (Figs 3F, 5D).

FURCA. Well-developed; ratio of mucro/dens/manubrium = 1/41/19 (Fig. 3D–E). Ventral setae on manubrium numerous (about 88) and ventro-apical setae (10–12) larger than the others (Fig. 3D), with the exception of 2 + 2 short apical setae; more than 70 dorsal setae (Fig. 3E). Dens with dorsal crenulations, about 200 ventral and 18 dorsal setae (Fig. 3D–E). Mucro quadridentate with apical tooth much smaller than subapical one (Fig. 3G).

LEGS. Upper and lower subcoxa of Leg I with 1 outer seta (Fig. 3A). Upper subcoxa of Leg II with 7, lower subcoxa with 6 outer setae (Fig. 3B). Upper subcoxa of Leg III with 10, lower subcoxa with 19 outer setae (Fig. 3C). Coxa with 5, 10, 24 setae, respectively, on leg I, II, III (Fig. 3A–C). Trochanter with 20, 21, 20 setae, respectively, on leg I, II, III. Femur with 36, 42, 74, respectively, on leg I, II, III. Tita with 45, 54,96 setae, respectively, on Leg I, II, III; tenent hair pointed (Fig. 3I). Claw of normal shape with lateral and inner teeth; empodium with a small inner tooth; pretarsus with a pair of setae (Fig. 3I).

Measurements

See Table 1.

Ecology

Desoria calderonis sp. nov. was found only on supraglacial stony debris of the Calderone glacier at 2650–2700 m a.s.l. (Appendix 1A). The supraglacial stony debris (carbonate: dolomite and limestone) is very coarse and the fine component is poorly represented (Appendix 1B). In this mineral, inorganic soil, *D. calderonis* sp. nov. was found mostly where the debris is in contact with the ice (Appendix 1B). In this environment, the vegetation cover is almost absent, with the rare exception of sporadic seedlings of *Arabis alpina* ssp. *caucasica* (Willd.) Briq. On supraglacial debris the mean annual temperature is 0.67°C (4.6°C during the snow-free period), the minimum recorded was -7.7°C and maximum 36.1°C; the snow cover persists on average for 250 days a year; the relative humidity is on average 95.7% during the whole year (85.9% during the snow-free period). Since *D. calderonis* sp. nov. was found only on supraglacial stony debris, and not in the surrounding habitats (LIA moraines: mean annual temperature = 1.3°C, mean temperature during snow-free period = 4.4°C; minimum = -9.8°C; maximum = 40.7°C; annual relative humidity = 88.7%; mean relative humidity during the snow-free period = 84.7°C; snow cover duration = 146 days), we can consider this species as cryophilic. On supraglacial debris, pH is 8.6, the organic matter content is 1.7 g/kg and carbonate calcium content is 96.2%, while on LIA moraine, pH is 8.3, organic matter content is 3.9 g/kg and carbonate calcium content is 91.4%.

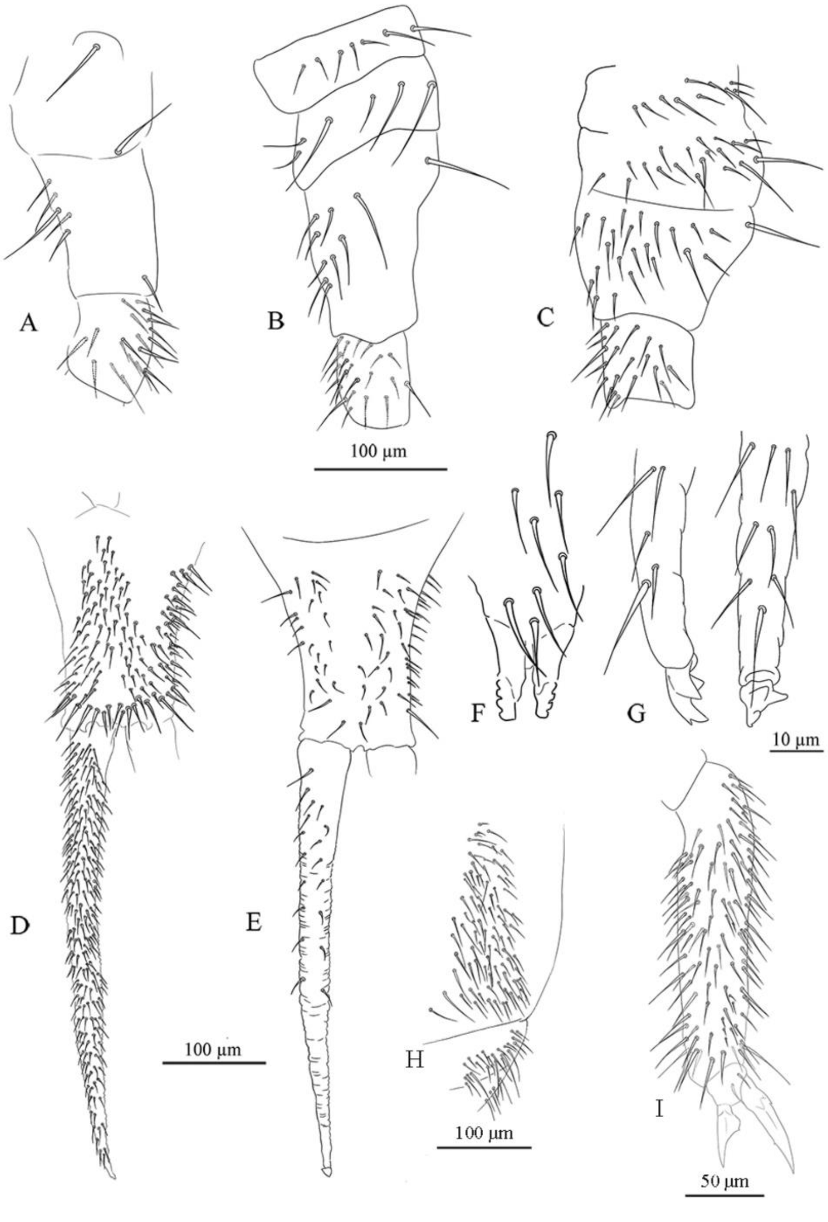

Fig. 3. *Desoria calderonis* sp. nov. **A**. Leg I, left; upper and lower subcoxa, coxa and trochanter. **B**. Leg II, left; upper and lower subcoxa, coxa and trochanter. **C**. Leg III, left; upper and lower subcoxa, coxa and trochanter. **D**. Ventral side of furca. **E**. Dorsal side of furca. **F**. Retinaculum. **G**. Mucro and apical part of dens, lateral and dorsal views. **H**. Lateral part of Abd. IV–V sternites. **I**. Tita III and Claw III.

Table 2 (continued on next page). Characters important for *Desoria* taxonomy are compared for the species of the *violacea*-group. The green colour highlights characteristics common between *D. calderonis* sp. nov. and all other known species of the group (with an inclusive criterion, in order not to overestimate differences, but, at least, to underestimate them).

Species of *violacea*-group	*D. hiemalis* (Schött, 1893)	*D. duodecemoculata* (Denis, 1927)	*D. blufusata* (Fjellberg, 1978)	*D. blekeni* (Leinaas, 1980)	*D. alaskensis* (Fjellberg, 1978)	*D. calderonis* Valle sp. nov.
Colour	dark bluish-grey or bluish-violet. With extremities paler	violet to bluish-grey	dark violet-blue	dark violet-blue	blue-red to bluish-black	violet-black on abdomen and antennae, lighter on furca and legs, which are brownish (Fig. 1); juvenile much paler, bluish
Pin-seta	bifurcate	bifurcate	bifurcate	with basal process	bifurcate	bifurcate
Short and thick sensilla on Ant I	no	no	no	no	no	x
Laterodistal setae on VT	11/23 + 11/23	4 + 4	6/13 + 6/13	5/5 + 5/6	10/26 + 10/26	4 + 4
Anterior setae on VT	10/19 + 10/19	1 + 1	5/9 + 5/9	2/4 + 2/4	–	2/4 + 2/4
Posterior setae on VT	14/22	5	6/11	6/7	12/20	4
Short apical setae on Mandible	2/3 + 2/3	2 + 2	1/2 + 1 /2	1 + 1	3 + 3 (rarely less)	2 + 2
Posterior setae on dens	9/14	8	20/40	9/11	25/45	18
Dimension of apical tooth on mucro with respect to the subapical one	equal or larger	smaller (sometimes apical one hardly visible)	equal or larger	equal or larger	larger	smaller
Basomedian setae on labium	5	4	5/6	4	5	4
Maxilla lamellae	short		short	short	short	short
PAO length with respect to the nearest OMMA diameter	0.9/1.2	1.5/2.0	1.4/1.8	0.9/1.1	1.8/2.3	2.0
Abd V–VI fused	separated or partly fused	no	x	no	x	no
Length of Abd.V macroseta with respect to median length of tergite (and of Claw3)	2.0/2.3 (3.0/4.0)	1.1 (–)	– (2/2.8)	1.1/1.5 (2.8/3.0)	– (3.0/4.0)	0.9/1.0 (1.8–2.4)
Number of characteristics in common with *D. calderonis*	5	10	4	6	3	

Table 2 (continued).

Species of *violacea*-group	*D. violacea* (Tullberg, 1876) sensu Fjellberg 1979	*D. taimyrica* (Martynova, 1974)	*D. nivea* (Schäffer, 1896)	*D. nivalis* (Carl, 1910)	*D. neglecta* (Schäffer, 1900)
Colour	dark violet blue/black.; with head, posterior part of ventral and lateral sides withish	intensively green, greyish, or dark olive green	white, eye region black	deeply black. Dens, Ant II–III and distal part of legs white	grey, greyish brown, greyish green or red
Pin-seta	bifurcate	bifurcate	simple	with basal process	simple
Short and thick sensilla on Ant I	no	no	x	no	no
Laterodistal setae on VT	7/22 + 7/22	6/13 + 6/13	7/13 + 7/13	4/5 + 4/5	7/13 + 7/13
Anterior setae on VT	3/10 + 3/10	3/8 + 3/8	4/7 + 4/7	4 + 4	7/13 + 7/13
Posterior setae on VT	4/10	5/9	4/6	4	7/14
Short apical setae on Mandible	1/3 + 1/3	2 + 2	1/3 + 1/3	2/4 + 2/4	2/3 + 2/3
Posterior setae on dens	12/19	14/19	7/11	8	15/30
Dimension of apical tooth on mucro with respect to the subapical one	equal or larger	equal or smaller	equal or larger	smaller	equal or larger
Basomedian setae on labium	5	5	5	4	5
Maxilla lamellae	short	short	long	short	short
PAO length with respect to the nearest OMMA diameter	1.2/1.5	1.2/1.5	2.0	1.5	2.0/2.4
Abd V–VI fused	no	no	no	no	no
Length of Abd.V macroseta with respect to median length of tergite (and of Claw3)	1.1/1.5 (2.3/3.1)	1.1/1.3 (2.4/2.9)	0.5/0.6 (1.1/1.2)	1.1 (–)	0.8/1.2 (2.2/2.7)
Number of characteristics in common with *D. calderonis*	8	7	6	10	6

Distribution

Desoria calderonis sp. nov. is currently known only for the type locality.

Type locality

Gran Sasso massif, Apennines, Calderone glacier (42°28′16.2″ N, 13°34′05.8″ E). Supraglacial stony debris of Calderone glacier, altitude: 2650–2700 m a.s.l.

Taxonomic and ecological considerations

Desoria calderonis sp. nov. belongs to the *violacea*-group sensu Potapov 2001, having mucro quadridentate, without seta, maxillary palp bifurcate, apical folds on labrum sharp. It differs from most species of this group (Table 2) by the reduced number of setae on VT (with the exception of *D. duodecemoculata* (Denis, 1927) and *D. nivalis* (Carl, 1910), which also have few setae, but in a different number). *Desoria calderonis* sp. nov., in addition, has a characteristic sensory field on Ant I with short, thick and cylindrical *s*-setae; this characteristic is common, for Palearctic *Desoria*, to many species of the *fennica*-group (sensu Potapov 2001) – *D.atkasukiensis* (Fjellberg, 1978), *D. fennica* (Reuter, 1895) sensu Fjellberg 1979, *D. fjellbergi* (Najt, 1981), *D. iuxta* (Dunger, 1982), *D. kaszabi* (Dunger, 1982), *D. saltans*, *D. tigrina* Nicolet, 1842 – two species of *olivacea*-group – *D. infuscata* (Murphy, 1959) and D. *olivacea* (Tullberg, 1871) sensu Fjellberg 1979 – and only one species of the *violacea*-group – *D. nivea* (Schäffer, 1896). Among species of the *violacea*-group, another peculiarity of *D. calderonis* sp. nov. is the number of dorsal setae on the dens, similar only to that in *D. neglecta* (Schäffer, 1900) sensu Fjellberg 1978, *D. taimyrica* (Martynova, 1974) and *D. violacea* (Tullberg, 1876) sensu Fjellberg 1979. In general, *D. calderonis* sp. nov. differs by a combination of at least four important characters (Table 2) from every species of the group.

Within the group, considering the number of common characteristics, *D. calderonis* sp. nov. appears most similar to *D. duodecemoculata* – present in Italy, Austria, Spain and France (Potapov 2001) – and *D. nivalis*, present in the Alps (France, Switzerland, Austria) and possibly in eastern Europe (Potapov 2001) (Table 2). Nevertheless, some features allow us to discriminate the new species from these. First, *D. duodecemoculata* and *D. nivalis* do not have short, thick and cylindrical, but only hair-like *s*-setae on Ant I. In addition, the new species differs from *D. duodecemoculata* by the chaetotaxy of VT and the number of dorsal setae on the dens; it differs from *D. nivalis* by having Ant II-III violet-black (white in *D. nivalis*), a longer PAO and by the number of dorsal setae on the dens.

Both *D. duodecemoculata* and *D. nivalis* belong to the *nivalis*-complex, a group of European mountain species included in the *violacea*-group. *Desoria nivalis*, in particular, is known to live near snow fields and other cold sites in high mountains (Handschin 1924; Franz & Serrl-Butschek 1954), while the ecology and the taxonomy of the other members of the complex need to be revised (Potapov 2001). Because of these similarities in morphology and ecology, we could ascribe our species to this *nivalis*-complex, even if we reported marked differences, in particular the presence in *D. calderonis* sp. nov. of the sensory field on Ant. I.

Phylogenetic context

The phylogenetic tree (Fig. 6), with a log-likelihood of 3077.45, is characterized by good support at recent nodes but low support at deeper nodes. It appears subdivided into three major clusters, two dominated by *Isotoma* and *Isotomurus*, respectively, and one by *Desoria*, with records representing 14 different *Desoria* species as well as others incompletely identified as *Desoria* sp. This latter cluster also included scattered sequences from the following genera: *Vertagopus*, *Pseudisotoma*, *Isotoma*, *Skadisotoma*, *Proisotoma*, *Isotomurus*, *Agrenia*, *Metisotoma*, *Axelsonia*, *Chionobora* and *Kaylathalia*. Within the *Desoria* cluster, *Desoria calderonis* sp. nov. clustered with high support (99) with one bin

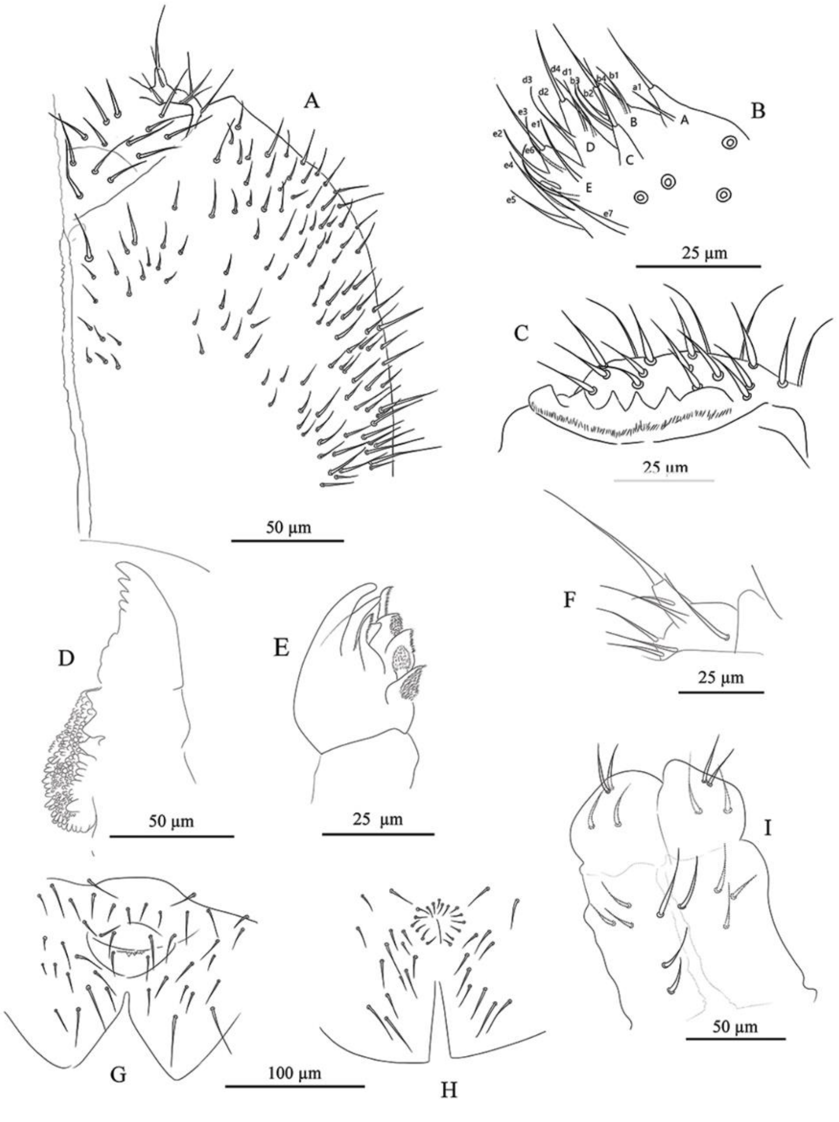

Fig. 4. *Desoria calderonis* sp. nov. **A**. Ventral chaetotaxy of head. **B**. Labial palps. **C**. Labrum. **D**. Mandible. **E**. Maxilla. **F**. Maxillary palp. **G**. Female genital opening. **H**. Male genital opening. **I**. VT in posterior view.

(AAO3603) identified as *Desoria* (with no indication on the species, 4 sequences from France) and *Vertagopus arboreus* (1 sequence from Ontario, Canada). The mean divergence between *D. calderonis* sp. nov. and this bin is 16.9% (S.D. 0.2). Both bins were associated (support 97) with one record of *D. tigrina* and this latter cluster, although with lower support, was associated with records of *D. blufusata*, *D. germanica*, *D. intermedia* and *D. violacea*.

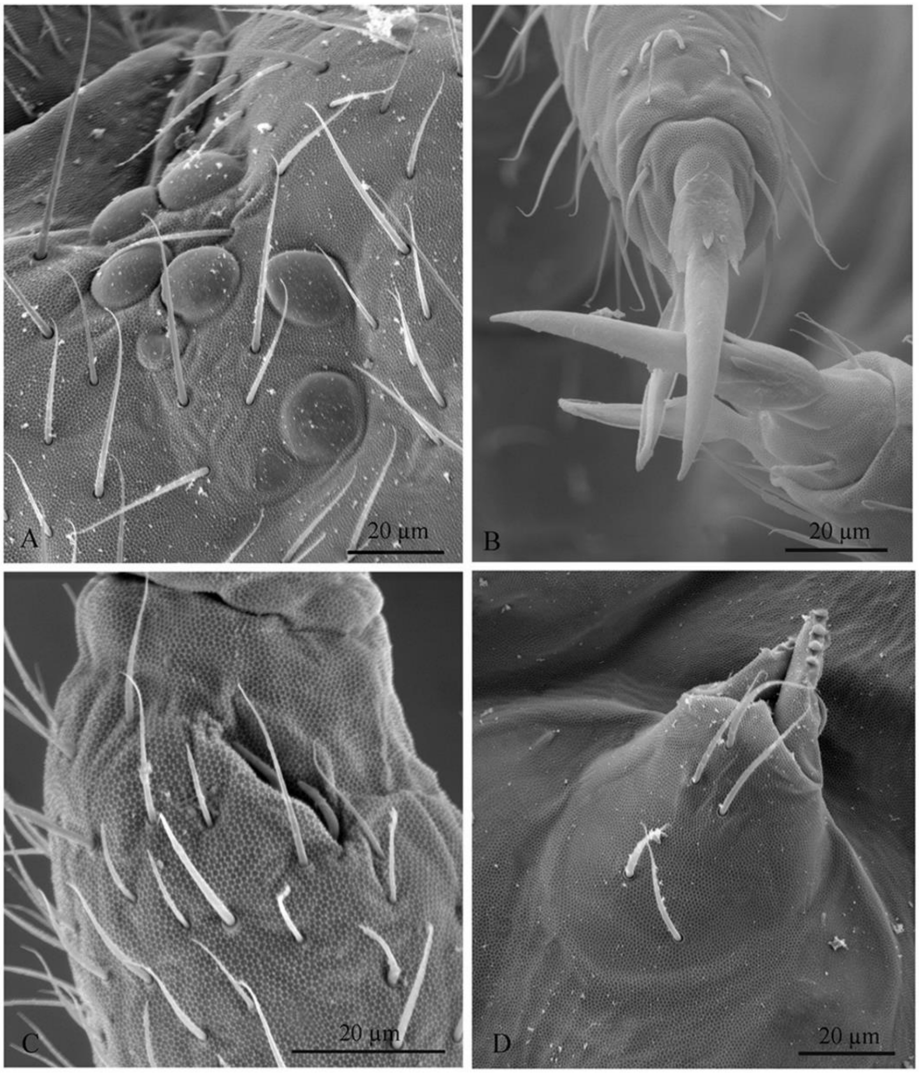

Fig. 5. *Desoria calderonis* sp. nov., scanning electron microscopy. **A**. Ocular plate. **B**. Claws. **C**. Antennal organ III. **D**. Retinaculum.

Apart from *D. violacea* (BOLD:AEA8472), *D. tigrina (*BOLD:ACS3918), *Vertagopus arboreus* (BOLD:AAO3603), and individual records mined from GenBank with no location information, all others reports come from areas characterized by a markedly cold climate, mostly in Northern Europe. Similarly to *D. calderonis* sp. nov., *D. blufusata* (BOLD:ACT9239, 3 records), *D. intermedia* (BOLD:AAI9461, 4 records) and *D. germanica* (BOLD:AAI9461, 2 records; see Stevens *et al.* 2006 for sampling information) were collected in low-temperature habitats, specifically in Norway and Sweden, with two records of *D. intermedia* explicitly associated to a snow covered setting. At variance, *Desoria* sp. (BOLD:AAO3603), for which species level identification is missing, originated from British Columbia (Canada) as well and the Ile-de-France (France).

Discussion

Our analysis supports the idea that *Desoria* is a polyphyletic group, as already observed by Stevens & D'Haese (2017). In particular, *Desoria* clustered with *Vertagopus*, *Pseudisotoma*, *Isotoma*, *Skadisotoma*, *Proisotoma*, *Isotomurus*, *Agrenia*, *Metisotoma*, *Axelsonia*, *Chionobora* and *Kaylathalia.* Most of the *Desoria* records came from areas characterized by a markedly cold climate and here cluster with other strictly cold-adapted and cryophilic organisms. In particular, *Agrenia* Börner, 1906 is a Holarctic genus living in damp and cold habitats such as banks of cold-water streams and the shores of lakes in tundra and mountain zones (Fjellberg 1988), on or near snow (Fjellberg 1976, 1986, 1994) and polar deserts (Chernov *et al.* 1977). Hågvar (2010) reported *A. bidenticulata*, *Desoria olivacea* and *D. infuscata* as the most pioneer species of the proglacial succession along Midtdalsbreen glacier (Norway). *Skadisotoma* Greenslade & Fjellberg, 2015 is a mountain endemic Australian genus linked to snow patches (Greenslade & Fjellberg 2015) and taxonomically related to *Desoria*. *Chionobora* Greenslade & Potapov, 2015 is an endemic hygrophilous Tasmanian genus, living around the lakes of the Central Plateau, the largest area of high ground in Tasmania. *Kaylathalia* is an Antarctic isotomid and was regarded as belonging to *Desoria* until Stevens & D'Haese (2017). *Isotoma* and *Isotomurus* are present in this cluster with a few sparse sequences identified at the genus level, but most of the sequences belonging to these genera were grouped in two alternative well defined groups outside the *Desoria* cluster. Thus, we hypothesize that the sparse *Isotoma* and *Isotomurus* sequences clustering with *Desoria* could be phylogenetically misplaced or not properly identified specimens. Therefore, we suppose that the genera more strictly related to *Desoria* are *Vertagopus, Skadisotoma*, *Agrenia, Metisotoma, Axelsonia, Chionobora* and *Kaylathalia.*

The position of the new species in a cluster composed entirely of *Desoria* sequences (with the exception of a single sequence of *Vertagopus*) supports its morphological identification as belonging to the genus. *Desoria calderonis* sp. nov. is dissimilar (17.8% genetic variability) to all other sequences present in the BOLD database. Morphologically, *D. calderonis* sp. nov. is more similar to *D. nivalis* and *D. duodecemoculata* of the mountain and cold-adapted *nivalis*-complex (*violacea*-group). However, this affinity was not testable phylogenetically with the available dataset, since no sequences from this complex are present.

In terms of subgeneric relationships, *D. calderonis* sp. nov. appears to be related to species belonging to both the *fennica*- (*D. tigrina*: bin BOLD:ACS3918; *D. germanica* and *D. intermedia*: bin BOLD:AAI9461) and *violacea*-group (*D. blufusata*: bin BOLD:ACT9239 and *D. violacea*: BOLD:AEA8472), leaving the question of its morphological assignment to the *violacea*-group untestable. In general, our phylogenetic results do not support the morphological groups reported by Potapov (2001) as natural assemblages.

From a methodological standpoint, the *Desoria* phylogeny presented here is difficult to interpret due to the possibility that some key groups are polyphyletic, the lack of sequence data for crucial elements and the uncertainty in the attribution of some sequences. In fact, building robust phylogenetic trees would require the combination of data from a large number of genes, integrating nuclear and mitochondrial

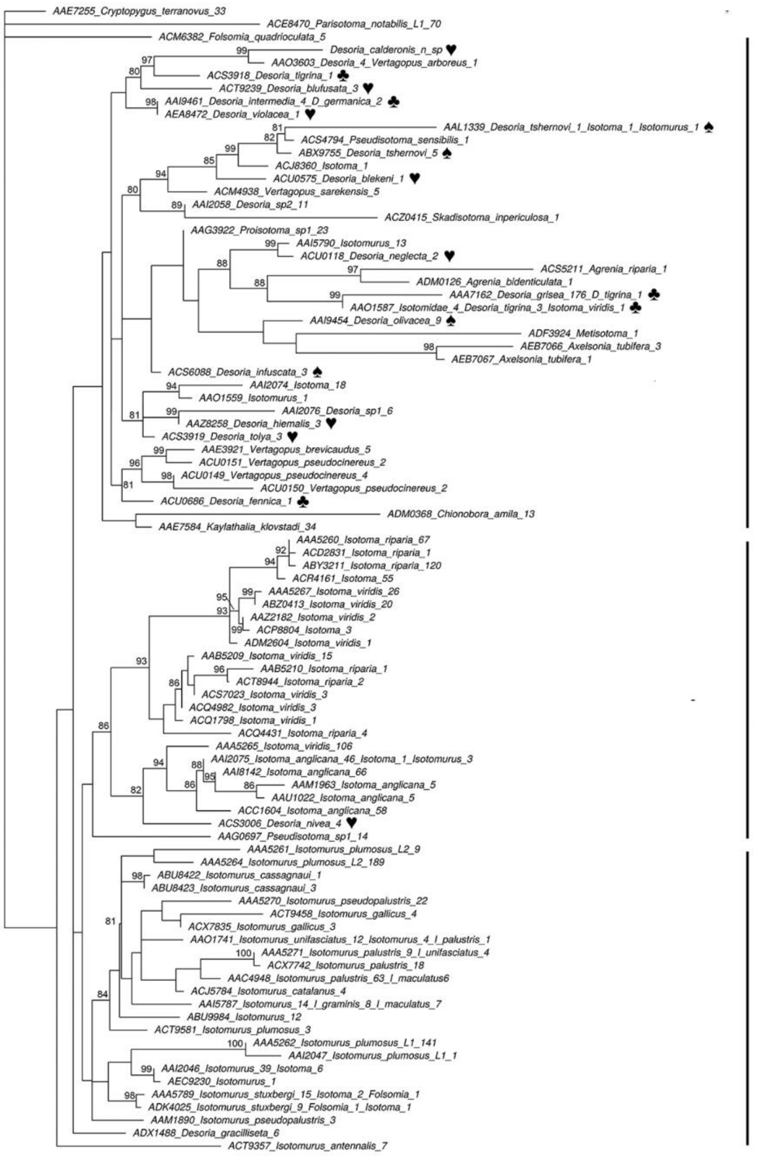

Fig. 6. Phylogenetic tree of *Desoria calderonis* sp. nov. and related species, on the basis of the *cox1* gene. Names include the BOLD bin number, as well as the taxonomic attribution and number of sequences included in the bin. Genera were abbreviated where unambiguous within the bin. When records of the same bin had multiple taxonomic attributions, the one at the lowest level was retained if all were compatible. Alternatively, all were listed separately. Bootstrap support is indicated if > 80. ♠: *olivacea*-group; ♣: *fennica*-group; ♥: *violacea*-group of *Desoria*.

information, and the *cox1* barcoding fragment is suboptimal in terms of resolution, especially at deeper nodes. Nevertheless, a great advantage of *cox1* is the availability of a large number of sequences in the BOLD database, including sequences from rare or difficult to sample species. Thus, the use of this gene allows for preliminary considerations on the phylogenetic context of the new species even in the absence of a consolidated taxonomy of the group, which would require more complete phylogenetic analyses.

Desoria species, with few exceptions (e.g., *D. violacea*, xerophilic, *D. blekeni,* mesophilic; Fjellberg 1975, 1988; Leinaas 1980), are cold and wet adapted organisms (Potapov 2001). Cold and wet environments are more common in northern Europe also in mountain forests, ponds and rivers. In Mediterranean regions, these environments are extremely fragmented and there is evidence that cryophilic springtails could find suitable habitat – ice – only in isolated refugial areas, like caves (Raschmanová *et al.* 2018) or alpine glaciers, glacierets, the banks of glacial streams and permanent snowfields (Lauga-Reyrel & Lauga 1995; Fjellberg 2010). This fragmentation of suitable habitats is compatible with the notion of a great undescribed cryophilic endemic biodiversity, largely constituted by springtails taxonomically related to the *Desoria* genus (Deharveng 1975; Najt 1981; Lauga-Reyrel & Lauga 1995; Fjellberg 2010; Hittorf 2017).

Desoria calderonis sp. nov. was described for the Calderone glacier, a relict, isolated glacier of the Apennines, a peripheral mountain chain without other existing glaciers. This is in line with the hypothesis of an undescribed fragmented glacial springtail biodiversity in refugial areas. It is noteworth that, these glacial areas are highly threatened by climate change (Grunewald & Scheithauer 2010). We do not know the fate of the cold adapted and cryophilic collembolan fauna in these areas, but extinction seems to be a likely scenario (Greenslade & Fjellberg 2015). This underlines the importance of studying these unique environments and preserving their biodiversity in order to know it before its definitive disappearance.

Acknowledgments

The authors thank L'ubomír Kováč and the anonymous reviewer who provided helpful comments that improved the manuscript, and Georgine Faulkner and Giorgio Valle for the linguistic revision. We also wish to thank the staff of the Rifugio Franchetti that gave us an important logistic support during the field work. B.V. also thanks her dad for having inspired the work. This work was partially funded by the European Research Council under the European Community's Horizon 2020 Programme, Grant Agreement no. 772284 (IceCommunities) (G.F. Ficetola).

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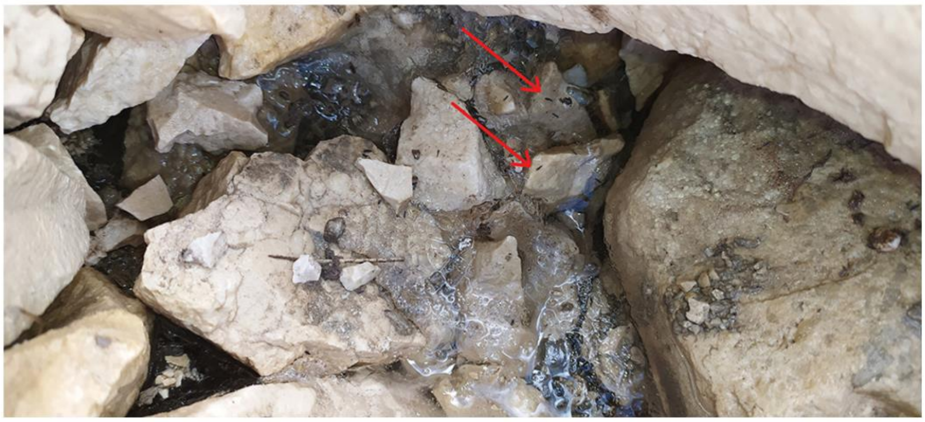
Manuscript received: 13 August 2021
Manuscript accepted: 22 October 2021
Published on: 29 December 2021
Topic editor: Tony Robillard
Desk editor: Fariza Sissi

Appendix 1A. Calderone glacier, lower tongue mostly covered by stony debris. Photo taken on 8 Jul. 2020, when there was still a high snow cover. Red arrows indicate the sampling points where *Desoria calderonis* sp. nov. was sampled with the flotation method.

Appendix 1B. Supraglacial debris where *D. calderonis* sp. nov. was discovered. This is a coarse mineral soil in contact with the ice of the Calderone glacier: *D. calderonis* sp. nov. lives at the ice-stony debris interface. Red arrows indicate *D. calderonis* sp. nov. specimens moving on the ice and cold debris.



3.4 Ecology of the cold adapted species *Nebria germarii* (Coleoptera: Carabidae): the role of supraglacial stony debris as refugium during the current interglacial period.

Acta Zoologica Academiae Scientiarum Hungaricae 66(Suppl.), pp. 199–220, 2020
DOI: 10.17109/AZH.66.Suppl.199.2020

ECOLOGY OF THE COLD-ADAPTED SPECIES *NEBRIA GERMARI* (COLEOPTERA: CARABIDAE): THE ROLE OF SUPRAGLACIAL STONY DEBRIS AS REFUGIUM DURING THE CURRENT INTERGLACIAL PERIOD

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In the current scenario of climate change, cold-adapted insects are among the most threatened organisms in high-altitude habitats of the Alps. Upslope shifts and changes in phenology are two of the most investigated responses to climate change, but there is an increasing interest in evaluating the presence of high-altitude landforms acting as refugia.

Nebria germari Heer, 1837 (Coleoptera: Carabidae) is a hygrophilic and cold-adapted species that still exhibits large populations on supraglacial debris of the Eastern Alps.

This work aims at describing the ecology and phenology of the populations living on supraglacial debris. To this end, we analysed the populations from three Dolomitic glaciers whose surfaces are partially covered by stony debris.

We found that supraglacial debris is characterised by more stable colder and wetter conditions than the surrounding debris slopes and by a shorter snow-free period. The populations found on supraglacial debris were spring breeders, differently from those documented in the 1980s on Dolomitic high alpine grasslands, which were reported as autumn breeders. Currently, *Nebria germari* seems, therefore, to find a suitable habitat on supraglacial debris, where micrometeorological conditions are appropriate for its life-cycle and competition and predation are reduced.

Keywords: Coleoptera, Carabidae, climate change, cold-adapted species, warm-stage refugia, glacier retreat.

INTRODUCTION

In the current scenario of global warming, high altitude habitats are among the most threatened (Cauvy-Fraunié & Dangles 2019, Fattorini *et al.* 2020). Some of the most visible effects of climate change are the reduction in glaciers mass and surface and the increase of debris cover on their surface, because of the reduction of the pressure of the ice volume on the glacier headwalls and the amplification of frost and heat weathering that increases erosion. This phenomenon is transforming many Alpine glaciers into debris-covered glaciers (Citterio *et al.* 2007, Paul *et al.* 2007, Kraaijenbrink *et al.* 2017, Tielidze *et al.* 2020). The debris cover has a strong impact on the dynamic of glaciers: when the debris is thicker than 3–5 cm, it reduces the rate of ice ablation, with critical thickness depending on the lithological nature of the debris and the climatic regime (Nakawo & Rana 1999).

Under the current climate change scenario, debris-covered glaciers are assuming a key biological role in high-altitude environments because they can host cold-adapted arthropod and plant species (Caccianiga *et al.* 2011, Gobbi *et al.* 2011, Hågvar *et al.* 2020). In fact, cold-adapted species may react to rising temperatures by finding *refugium* areas in glacial and periglacial landforms, as suggested for the Alps by Gobbi *et al.* (2011, 2014, 2018). These landforms are defined "cold spots" of biodiversity, because glaciers host few species, which are, however, extremely specialised and exclusive (including many endemics), but currently threatened of extinction (Cauvy-Fraunié & Dangles 2019, Gobbi & Lencioni 2020). Together with the study of habitats acting as potential refugia for cold-adapted species, the knowledge of the ecological needs of climate-sensitive species in these cold habitats is fundamental to understand how climate change will affect Alpine biodiversity.

The ground beetle *Nebria germari* Heer, 1837 (Coleoptera: Carabidae) is a cold-adapted and hygrophilic species (Brandmayr & Zetto Brandmayr 1988, Gereben 1995, Kaufmann & Juen 2001). It can be defined as a climate-sensitive species because it is currently restricted to high altitude habitats of the Eastern Alps, from Tessin, Switzerland, to the Prokletije Massif, Albania (Ledoux & Roux 2005). This species also exhibits a fragmented distribution pattern (Ledoux & Roux 2005), suggesting refugial occurrence, and local scale extinctions were already documented (Pizzolotto *et al.* 2014). Moreover, *N. germari* is a brachypterous species with low dispersal ability and nocturnal foraging behaviour. High humidity and low temperatures are known to be the main environmental features affecting its distribution and abundance (Brandmayr & Zetto Brandmayr 1988, Kaufmann & Juen 2001, Pizzolotto *et al.* 2014). It prefers open grounds with low vegetation cover, and substrates with a high percentage of gravel (Brandmayr & Zetto Brandmayr 1988, Kaufmann & Juen 2001). It lives on scree slopes, along glacier forelands, on rock glaciers and debris-covered glaciers (Kaufmann & Juen 2001, Gereben *et al.* 2011, Gobbi *et al.* 2014, 2017). In these habitats, *N. germari* co-occurs with other ground-dwelling arthropods; the most common on debris-covered glaciers being spiders (Arachnida: Araneae), springtails (Hexapoda**,** Collembola), and less frequently centipedes (Myriapoda: Chilopoda). Springtails are at the base of *Nebria germari* diet (Sint *et al.* 2019). Intraguild predation was demonstrated in arthropods living near the glacier fronts (König *et al.* 2011, Raso *et al.* 2014, Sint *et al.* 2019). Thus, we can hypothesise that the co-existence (*sensu* Staples *et al.* 2016) with spiders might affect the size of *N. germari* populations, particularly in glacier and near-glacier habitats. For instance, spiders may compete with *N. germari* in hunting activity: even if *N. germari* is primarily nocturnal and spiders are mainly diurnal, in this harsh environment *N. germari* activity was also documented during the day (Gereben 1995). Other competitors are centipedes, predators that in few cases were found in the same habitat of *N. germari* (unpublished data).

In this study, we aimed at describing the phenology and the current population dynamic of *N. germari* on supraglacial debris concerning both biotic (competitors and prey availability) and abiotic factors (micrometeorological conditions and soil gravel fraction). Besides, in order to investigate how global warming might affect this species, we compared our data on the present distribution of this species with those found in the literature to highlight possible ecological changes that have occurred in the last 60 year. Specifically, we focused on past and present altitudinal distribution of this species, which seems to respond to climate warming (Pizzolotto *et al.* 2014), and its past and current phenology. Indeed, the timing of life-history events is crucial for insect species living in high altitude habitats, where the favourable season for the development, growth and reproduction lasts a few weeks (Sota 1996). We expect an upward shift in the distribution, and earlier phenology of this species in the present compared to past studies.

MATERIAL AND METHODS

Study area

We investigated three populations of *Nebria germari* located on three glaciers of the Dolomites (Italy): Western Sorapiss and Central Sorapiss Glaciers (46°30′43.34′′–12°12′ 25.12′′ and 46°30′43.55′–12°13′ 20.75′′ Ampezzo Dolomites) and Vedretta d'Agola Glacier (46°9′6.29′′–10°51′29.01′′ Brenta Dolomites) (Fig. 1). In these sites, *N. germari* occurs almost exclusively on supraglacial debris, characterised by a vegetation cover always < 5% and consisting of sparse young individuals of pioneer plant species typical of carbonatic substrata of the alliance *Thlaspion rotundifolii* Jenny-Lips 1930, with only a very sporadic occurrence on the nearby moraines (Bernasconi *et al.* 2019, Valle 2019).

All these glaciers of the Dolomites are characterised by relatively low altitude and small surface (Table 1). Climatic features of the investigated areas were extrapolated from closely located weather stations (see micrometeorological analysis paragraph); average annual and monthly temperatures and average annual precipitations are reported in Tables 2 and 3.

During the fieldwork (2017–2018), data on the minimum altitude of glacier systems were collected, and the extent of the glaciers and the percentage of debris-covered surface were calculated using aerial photographs from 2015 (Table 1). Besides, debris thickness was estimated with different methods (Table 1). On Western and Central Sorapiss Glaciers debris thickness was measured digging the debris up to the ice along a regular grid

Table 1. Altitude and surface characteristics of three glacial sites. Measurements at Agola were made in 2018, at Sorapiss in 2017. The extent of the glaciers and the degree of debris-covered surface were calculated using aerial photographs from 2015 and field data collected in 2017–2018.

Glacier	Type of glacier	Min altitude (m asl)	Max altitude (m asl)	Sampling altitude (m asl)	Surface (km^2)	Surface covered by debris, %	Estimated debris thickness
Agola	Active mountain glacier	2601	2873	2596–2603	0.17	1.2	10–15 cm
Western Sorapiss	Active mountain glacier	2254	2756	2382–2419	0.134	32	>50 cm at 50% of measurement points
Central Sorapiss	Inactive glacier – glacieret	2213	2621	2210–2264	0.08	57.9	>50 cm at 80% of measurement points

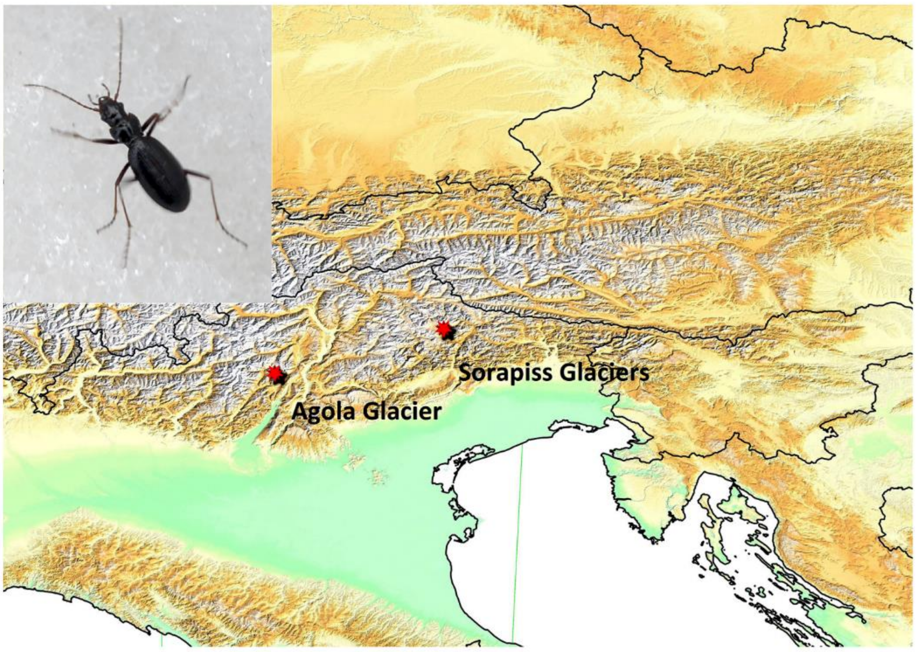

Fig. 1. Map with the position of the two sampling sites (Agola and Sorapiss). At the top left, a picture of *N. germari* taken on Sorapiss. (Photo by D. Dalpiaz and F. Pupin/ Archive MUSE)

of points spaced 20 m to one another (29 points for Wester Sorapiss and 51 for Central Sorapiss, due to different size of the sampling areas). On Agola we measured the thickness around the traps because the use of a regular grid was impossible due to the small extent of the debris-covered part of the Glacier.

Field procedures

Sampling was carried out during the snow-free period of 2017 (Western and Central Sorapiss Glaciers) and of 2018 (Agola Glacier) by pitfall traps put on the supraglacial debris. Specifically, two plots were selected on Agola, two on Western Sorapiss and four on Central Sorapiss (two on the glacier and two on a dead-ice area separated from the glacier). Each plot was characterised by similar conditions in grain size distribution and vegetation cover (see the sampling plan in Appendix 1). Each plot consisted of three pitfall traps – spaced from each other by at least 10 meters. Pitfall traps consisted of a plastic glass (diameter 7 cm) filled up with a non-toxic and frost-resistant solution to catch and preserve the animals during the activity period of the trap. The solution was made by one litre of water, ½ litre of wine-vinegar, one tablespoon of salt and two-three drops of soap. This solution is slightly different from those used in similar studies (e.g. Gobbi *et al.* 2017) and was used to reduce its attractive smell toward marmots (*Marmota marmota*) and alpine ibexes (*Capra ibex*), which are the most common vertebrates that damage the traps. Three sampling sessions were performed on Agola (6 August 2018 – 27 August 2018 – 18 September 2018), four on Western Sorapiss (5 July 2017 – 27 July 2017 – 17 August 2017 – 07 September 2017), three on Central Sorapiss (28 July 2017 – 18 August 2017 – 07 September 2017). Sampled specimens of *N. germari* were analysed at the stereomicroscope in order to distinguish them in three developmental stages: larva, teneral (i.e. newly hatched adults) and adult.

A sample of approximately 2 kg of soil was taken from each plot and used to estimate the grain size distributions by dry, wet sieving and aerometry.

Temperature and humidity (micro-meteorological variables hereafter), were recorded every 60 minutes on the supraglacial debris of each glacier by a datalogger (Tinytag plus 2), positioned 10 cm below the surface close to the plots (see Appendix 1). One datalogger was also placed on the recent moraine of 1908 (Agola) or 1920 (on Western and Central Sorapiss), respectively 500 and 200 m from the glacier front, to record the same variables on ice-free debris. Datalogger recording periods started from the beginning of the sampling period and were: 17 June 2018 – 02 June 2019 on Agola, 22 June 2017 – 21 August 2018 on Western Sorapiss, and 07 July 2017 – 22 August 2018 on Central Sorapiss.

Analysis of micrometeorological data

Day and night values were analysed separately because *Nebria germari* is known to be mainly a nocturnal predator (Gereben 1995). The average sunrise and sunset times for each month was used to assess day and night measures. The average annual temperature, the average day and the night summer temperature (mean of all daily day and night averages collected from the beginning of sampling period to the end of the snow-free season) were considered. Humidity was not recorded on Central Sorapiss because the humidity sensor was not available. Although we are aware that conditions can vary according to debris depth and grain size, we are confident that the data we collected are representative of the conditions of the sampling sites.

Table 2. Monthly vertical thermal gradient for Agola site. Data are the means calculated from weather station records during 2011–2018 (Alimonta= 2577 m asl, Val d'Ambiez = 1888 m asl, Giustino = 877 m asl).

Altitude (m asl)	Mean temperature (°C) in												Annual average	
	J	F	M	A	M	J	J	A	S	O	N	D	temperature (°C)	precipitations (mm)
877	0.7	4.1	8.3	11.1	15.4	17.7	18.7	15.2	11.1	6.9	2.1	0.9	9.4	–
1888	–4.2	–2.0	1.2	4.1	8.2	11.5	12.9	10.2	6.2	3.8	–1.1	–2.3	4.0	–
2577	–6.0	–3.1	–0.1	2.7	6.5	8.3	8.4	4.9	2.5	–2.4	–5.5	–5.7	0.9	1000
Vertical gradient Δt/100 m	–0.20	–0.21	–0.25	–0.26	–0.26	–0.28	–0.30	–0.30	–0.25	–0.27	–0.22	–0.19	–0.25	

Table 3. The monthly vertical thermal gradient at the Sorapiss site. Data are the means calculated from weather station records during 1994–2018 (Cortina d'Ampezzo = 2235 m asl, Faloria = 1271 m asl).

Altitude (m asl)	Mean temperature (°C) in												Annual average	
	J	F	M	A	M	J	J	A	S	O	N	D	temperature (°C)	precipitations (mm)
1271	–1.8	–0.9	2.4	5.8	10.3	13.8	15.8	15.4	11.2	7.3	2.4	–1.0	8.0	–
2235	–5.2	–5.5	–3.1	–0.5	4.2	8.1	10.2	10.0	6.1	3.2	–1.4	–4.3	1.8	1100
Vertical gradient Δt/100 m	–0.54	–0.48	–0.32	–0.65	–0.63	–0.59	–0.58	–0.56	–0.53	–0.43	–0.39	–0.34	–0.50	

Supraglacial temperatures of each glacier were compared with values detected on the moraines of 1908/1920 and with atmospheric values calculated on the base of the data from the nearest weather stations with complete available data (Val d'Ambiez weather station for Agola Glacier, 1888 m asl, Trento Province, 3 km apart from the sampling site; Faloria weather station for Sorapiss Glaciers, 1743 m asl, Belluno Province, 4 km apart from the sampling site). In order to correctly compare datalogger and weather station values, which were recorded at different altitudes, we applied to weather station values a correction factor equal to the average vertical thermal gradient for each site and month (Tables 2, 3). These correction factors were calculated for each site and month by linear interpolation of the data from weather stations located at different altitudes. For Agola Glacier, we used data from Meteotrentino weather stations of Alimonta refuge (2577 m asl, Trento Province), Val d'Ambiez (see above) and Giustino (877 m asl, Trento Province). Available data spanned 2011–2018. For Sorapiss, we used data from ARPA Veneto weather stations of Cortina d'Ampezzo (2335 m asl, Belluno Province) and Faloria (see above). Available data spanned the period 1994–2018.

Ecological and phenological data analysis

We considered the following information collected at each trap: days of trap activity, the absolute abundance of *N. germari* larvae, tenerals and adults, the absolute abundance of centipedes, springtails, adult spiders (sum of all Araneae taxa found: *Acantholycosa* spp., families Lyniphiidae and Thomisidae) and gravel percentage. We then used Generalised Linear Models (GLMs) assuming a Poisson data distribution to model the abundance of different *N. germari* developmental stages according to a set of predictors selected in agreement with the literature (see introduction), namely: day of the year (1 January = 1), gravel percentage, the abundance of centipedes and springtails (potential prey of *N. germari*), and abundance of spiders (potential predators/competitors of *N. germari*). A three-level factor indicating the glacier was also entered in the models together with the log10-transformed number of days for which a trap was active; the latter variable was entered as an offset to account for the difference in sampling effort. With this parameterisation, the GLM modelled the average number of individuals collected per day of trap activity. We also accounted for possible data overdispersion, which may inflate type-I error rate of the model, by using the family = quasipoisson option in R. Analyses were performed with R 3.6.2 (R Core Team 2019).

RESULTS

A total of 138 individuals of *Nebria germari* were collected on Agola Glacier (51 larvae, 81 tenerals, 6 adults), 257 on Western Sorapiss Glacier (51 larvae, 9 tenerals, 197 adults) and 444 on Central Sorapiss Glacier (104 larvae, 82 tenerals, 258 adults). The average activity density (AD: number of collected individuals per day of trap activity) of all *N. germari* (larvae, adults and tenerals) recorded on each glacier during the whole sampling periods was higher on Sorapiss glaciers (0.64±0.64 on Western Sorapiss and 0.64±0.41 on Central Sorapiss) than on Agola glacier (0.38±0.45).

Table 4. Mean annual temperatures (±S.D.), mean temperatures (±S.D.) during the snow-free period and length of the snow-free period on the supraglacial debris. Period 2017–2018.

Location	Mean annual temperature (°C)	Mean temperature during snow-free period (°C)		Snow-free period (days)
		Daytime	Nighttime	
Western Sorapiss	–0.2±2.8	2.8±2.7	2.9±2.7	130
Central Sorapiss	–0.8±1.4	1.1±1.6	0.8±1.2	105

Temperature and humidity

We estimated the duration of the snow cover from the daily trend of day and night temperatures (see Appendix 2). The beginning of snow cover is indicated by a monotonous decreasing trend of daily temperatures. This occurred on October 28th on Agola Glacier and on November 6th on Sorapiss Glaciers. The long spring plateau at 0 °C indicates that melting was occurring. The end of this plateau indicates the beginning of the snow-free period. On Western Sorapiss snow completely melted by June 30th, on Central Sorapiss by July 25th. The datalogger on Agola Glacier did not record data from 3 July 2019 to 16 June 2019. To estimate the beginning of snow-free season at this site. We, therefore, used data collected by the datalogger placed on the 1908 moraine to estimate the beginning of the snow-free period. On the moraine snow melted on June 30th. Thus, on supraglacial debris this happened between 30 June 2019 and 16 June 2019 (the end of missing data period). We used these data to calculate thermal conditions linked to our sampling period, reported in Table 4; for Agola Glacier it was not possible due to missing data for June and July.

Day temperature during the snow-free period was almost equal to (on Sorapiss) night temperature (Table 4).

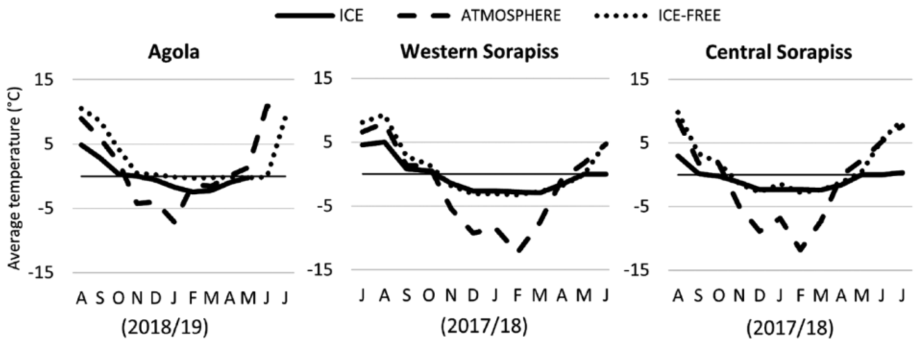

Fig. 2. Monthly temperatures on supraglacial debris, ice-free debris and atmosphere.

In Figure 2, monthly temperature trends on supraglacial debris, on ice-free debris and in the atmosphere, are reported for each glacier (values are reported in Appendix 3). Supraglacial habitat showed colder condition than the atmosphere and the ice-free debris during summer and warmer conditions than the atmosphere during winter. The annual average temperature of supraglacial debris is always lower than that of ice-free debris and atmosphere. However, each datalogger showed different values, probably because of the different thickness and porosity of the supraglacial debris.

Maximum recorded values were: 16 °C on Agola (23/VII/2018), 10.2 °C on Western Sorapiss (07/VII/2017) and 6.9 °C Central Sorapiss (20/VII/2017). All daily values of day and night humidity are reported in Appendix 4. Missing data are due to the reset of the sensor when it remains saturated of water for a long time. On the glacier, air under the surface showed high levels of relative humidity, with an average daily humidity of 94% with almost no difference between the day and night values.

Ecological and phenological data analysis with GLM

The abundance of the different developmental stages at each sampling session and glacier is shown in Figure 3. Abundance of both larvae and subadults increased with day-of-year (larvae: coef. = 0.03±0.01 SE, $F_{1,64} = 9.10$, $P = 0.004$; subadults: coef. = 0.04±0.01 SE, $F_{1,64} = 10.13$, $P = 0.002$), while that of adults decreased along the season (coef. = –0.04±0.01 SE, $F_{1,64} = 43.90$, $P < 0.001$).

Abundance of larvae did not differ among glaciers ($F_{2,64} = 0.66$, $P = 0.528$), There was a tendency toward differences in overall abundances of subadults among glaciers ($F_{2,64} = 3.54$, $P = 0.035$); however, Tukey post-hoc tests failed in

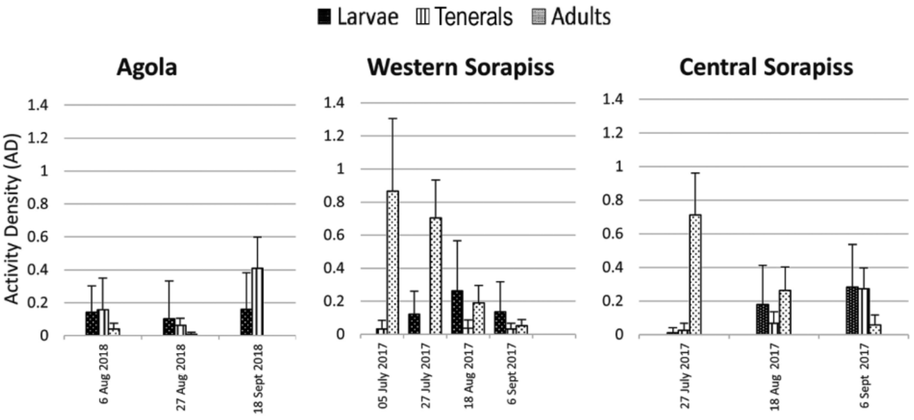

Fig. 3. Sampling data are expressed as average Activity Density (AD: number of individuals per day of trap activity). Whiskers represent standard deviation

detecting any pairwise difference between glaciers ($|z| \leq 2.04$, $P \geq 0.095$). In contrast, abundance of adults was significantly lower on Agola glacier than on both Sorapiss glaciers ($F_{2,64} = 9.62$, $P < 0.001$, post-hoc tests: $|z| \geq 2.71$, $P \leq 0.016$), which did not differ to one another ($z = 0.73$, $P = 0.728$).

Abundance of the different life-stages was also affected by different ecological variables of sampling sites. As shown by the GLM analysis, larvae abundance increased with increasing abundance of centipedes (coef: 0.06±0.02 SE, $F_{1,64} = 8.15$, $P = 0.006$), teneral abundance decreased with increasing number of spiders (coef: –0.57±0.27 SE, $F_{1,64} = 6.14$, $P = 0.016$), adult abundance decreased at increasing gravel percentages (coef. = –5.10±1.44 SE, $F_{1,64} = 13.22$, $P < 0.001$. All the other effects were not significant ($F_{1,64} \leq 2.54$, $P \geq 0.115$).

DISCUSSION

Data collected on the investigated glaciers of the Dolomites provided the first evidence about the micrometeorological features of the supraglacial habitats inhabited by *N. germari*. Besides, they allowed us to describe population patterns in time and in relation to potential competitors and prey availability.

Micrometeorological conditions

Micrometeorological data gave detailed information about the cold conditions characterising supraglacial debris where *N. germari* currently lives. The recorded annual average temperatures always spanned between –1 °C and 0 °C. These data is in agreement with those recorded on the debris cover of Amola Glacier (Presanella Group, Central-Eastern Alps; Gobbi *et al.* 2017) suggesting similar thermal properties notwithstanding different lithology (tonalite, an igneous intrusive rock) of the debris of this latter glacier. Average temperatures recorded in the supraglacial habitat were similar or slightly lower than those on the adjacent ice-free debris, but always higher than those estimated for the atmosphere during winter, as an effect of the snow cover, and lower than both them during summer, probably as a direct effect of the presence of ice. Temperatures were almost identical during day and night, but this also occurred on the glacier forelands. Thus, temperature homogeneity between day and night is not due to the presence of ice, since it is not an exclusive feature of supraglacial environment, but probably to the thermal inertia of stony debris. Other essential features recorded on supraglacial debris are the low annual temperature excursions and the quite constant high level of humidity, an important condition for a species like *N. germari* that lives where the soil is drenched of water, as observed by Brandmayr and Zetto Brandmayr (1988). Thus, the micrometeorological conditions in the extreme environment of the debris cover of glacier are more stable than those of the close ice-free debris, and therefore probably more suitable for this species.

Literature data reported that *N. germari* lives only in drenched soils, but little is known about the influence of temperature on its activity. Indeed, a study performed on the Rocky Mountains by Slatyer and Schoville (2016) demonstrated that cold and heat tolerances vary little among *Nebria* species along an elevation gradient, and these variations are not generally associated with species turnover; in particular, heat tolerance of adults spans between 32.2 °C and 37.0 °C. Even if our dataloggers registered maximum hourly peak of 16 °C on Agola, 10.2 °C on Western Sorapiss and 6.9 °C on Central Sorapiss, Gobbi *et al.* (2017) found that temperatures in other sites where *N. germari* lives (Amola glacier) can reach up to 30 °C. This information suggests that *N. germari* adults might survive at higher temperatures like those found by Slatyer and Schoville (2016). As suggested by Hågvar *et al.* (2017) for Norwegian alpine ground beetles, the ecology of larvae and their temperature preferences could be the key element determining alpine *Nebria* survival and habitat choice (Thiele 1972). Personal observations on Alpine glaciers highlighted that occurrence of *N. germari* larvae is higher at the ice-debris interface, where debris pressure melts the ice, which is the place where their prey (springtails) occur at high density. Therefore, we hypothesised that larvae might represent the stage of *Nebria* development that is more linked to the presence of ice. Low temperatures of supraglacial debris could also influence biotic factors related to interspecific interactions (Slatyer & Schoville 2016), for example reducing the predation pressure on larvae due to the absence of other predators, as proposed by Currie *et al.* (1996). However, heat tolerance of *N. germari*'s adults and larvae still needs to be assessed in the laboratory to confirm these hypotheses.

Phenology

Our results show that *N. germari* adults are abundant at the beginning of the snow-free period, and then progressively decrease during summer. Larvae found during the snowmelt period (early July) develop during summer (July–September), resulting in the increase of tenerals observed in late season (August–September). During our first sampling session on Agola Glacier, we collected a low number of adults and proportionally more larvae than on the other glaciers, suggesting that on that glacier, larvae development had started already; the lack of early adults, which are the most abundant developmental stage on Sorapiss Glaciers, may explain the generally lower numbers on Agola Glacier. Our data suggest that *N. germari* can be considered a spring breeder: the reproduction seems to start at the very beginning of the snow-free period (end of June – early July), and larvae develop during the following months, from July to September at least (the date of our last sampling). These observations differ from those of Brandmayr and Zetto Brandmayr (1988), who reported that *N. germari* was an autumn breeder, at least for the populations found in high alpine carbonate discontinuous grasslands. However, our observations are consistent with Kaufmann and Juen's (2001) observations on a pioneer habitat on an Austrian glacier. Previous studies, therefore, support evidence of differences in breeding time on alpine grasslands concerning glacier forelands and glaciers surface. We stress, however, that species inhabiting alpine habitats usually reproduce during the short snow-free period. Therefore the dichotomy between spring and autumn breeder may have little ecological relevance since breeding period only spam from July to September (Sota 1996).

Our dataloggers allowed estimating a very short snow-free period (121 days on Agola, 130 days on Western Sorapiss, 105 days on Central Sorapiss). A long persistence of the snow cover is a constant of *N germari*'s habitat (Brandmayr & Zetto Brandmayr 1988, Gereben, 1995). Overwintering larvae and a biennial life-cycle are key adaptive features to high alpine environments characterised by a very short snow-free season (Sota 1996, Andersen 1984). Both these features are already known for *N. germari* (De Zordo 1979, Brandmayr & Zetto Brandmayr 1988, Kaufmann & Juen 2001) and are consistent with our observations. Indeed, both the large number of larvae and tenerals found at the end of the snow-free season and the abundance of adults immediately after snowmelt (also reported by Gereben, 1995) suggest that also supraglacial populations have overwintering larvae and probably a biennial life-cycle. However, it is still unknown if *N. germari* larvae enter diapause or remain active during winter. Indeed, even winter could potentially be a favourable growing season for *N. germari*, because environmental conditions are stable under the snow cover, and food may be available, due to cold-hardiness of Collembola. These features may allow either winter activity or dormancy (Vanin & Turchetto 2007, Block & Zettel 1980, Sømme 1981, Woude & Verhoef 1988). Which overwintering strategy is actually used by *N. germari* should therefore be tested in laboratory conditions.

Responses to ecological factors

GLM analysis supports the evidence that different life-stages respond to different predictors; this is reasonable if we consider that larvae have lower mobility (Hågvar *et al.* 2017) and a different vertical distribution than adults and tenerals (Kaufmann & Juen 2001). Besides, larvae and tenerals may be more vulnerable to predation than adults because of the less sclerotised exoskeleton.

Adults density on the supraglacial debris was significantly related to grain size distribution; in particular, the gravel fraction was negatively related to *N. germari* adult abundance probably because of a lower detection probability where grain size is greater as suggested by Tenan *et al.* (2016).

Teneral abundance was negatively related to spider abundance, maybe because of intraguild predation of spiders on teneral ground beetles. Differently from larvae that live deep in the debris, and adults that have a thicker exoskeleton, tenerals have a soft exoskeleton and inhabit the surface, probably experiencing a higher predatory pressure. Alternatively, this association may be spurious and related to independent temporal trends of *N. germari* tenerals and spiders. The very similar temperatures during day and night allow hypothesising that *N. germari* could be active even during the day in the supraglacial habitat, thus being huntable by the spiders. The abundance of larvae was positively related to that of centipedes even if they are both predators, probably because they co-occur in the same site where food is abundant. Indeed, they share similar edaphic needs and they probably live at the same depth. However, it should be considered that centipedes are very few (only 5 specimens on Agola and 4 on Central Sorapiss). In order to fully understand the interactions of *Nebria germari* with other predators, direct observations in the field and gut content analysis are therefore necessary (Raso *et al.* 2014, Sint *et al.* 2019).

Contrary to our expectations, we found no significant relation between *N. germari* density and springtail abundance. Springtails were often very abundant in our samples, particularly those belonging to the genus *Orchesella* that can represent an ideal prey for *N. germari*. We hypothesised that the lack of relation could be due to a generally large abundance of surface-active springtails on the supraglacial debris, which therefore does not constitute a limiting factor for *N. germar*i.

Changes in altitudinal distribution

N. germari seems to have moved to the higher altitude, probably as a consequence of climate change. Indeed, previous works (Marcuzzi 1956, Brandmayr & Zetto Brandmayr 1988, Pizzolotto *et al.* 2014) reported that, until the second half of the last century, the lower altitudinal limit of *N. germari* in the Dolomites was around 2000 m asl. Specifically, the species was found in discontinuous alpine grasslands on carbonate substrata dominated by *Carex firma*. Field data collected in the last thirty years on the Paneveggio-Pale di San Martino Dolomites (Pizzolotto *et al.* 2014) demonstrated the current extinction in this grassland type of the Southern Alps and an altitudinal shift of 300 meters about 30 years (1980–2008/09), with a consequent contraction of the distribution range. Our observations confirm the absence of this species from alpine grassland and the migration to more pioneer communities. In particular, we observed *N. germari* only on the supraglacial debris (excluding sporadic catches on the nearby glacier foreland; Bernasconi *et al*. 2019, Valle 2019).

The minimum altitude in which this species occurs in the studied areas is currently 2598 m asl on Agola (Brenta Dolomites), 2264 m asl on Western Sorapiss, 2168 m asl on Central Sorapiss (Ampezzo Dolomites). In order to calculate the altitudinal shifts, we compared our data with historical work of Marcuzzi (1956) and with Marcuzzi's Collections preserved at Natural History Museum of Genova (10 specimens; sampling year: 1972) for Ampezzo Dolomites and with MUSE – Science Museum's collections (15 specimens; sampling years: from 1935 to 1942) for Brenta Dolomites. The average altitudinal shift occurred in cc. 60 years was of cc. 210 m in Ampezzo Dolomites (1956–2017; cc. 260 m in Western Sorapiss and 170 m in Central Sorapiss) and of cc. 500 m in about 80 years in Brenta Dolomites (1939–2018).

Alpine refugia

In the last decades, the key biological role of debris-covered glaciers has been recognised. Indeed, this habitat is hosting cold-adapted arthropod species during the current interglacial period (Gobbi *et al.* 2011, 2018, Hågvar *et al.* 2020). The Dolomites are particularly sensitive to the effects of climate change because of their relatively low altitude and the small size of their glaciers, which are undergoing a shrinking of surface size and an increase in debris cover that could partially reduce melting rate (Nakawo & Rana 1999). Here, *N. germari*, currently finds a suitable habitat only on the supraglacial debris, that persists at different altitudes depending on the glacier morphology and the degree of debris cover (Pelfini *et al.* 2012): on Central Sorapiss the debris cover 70% of the glacier surface and protect the ice from melting even at an altitude as low as 2213 m asl. Here we observed the minimum altitudinal shift in *N. germari* distribution.

We found that glacier debris cover (of both active and inactive glaciers, like Central Sorapiss) has peculiar micrometeorological features that make this habitat a perfect *refugium* for a cold-adapted hygrophile species like *N. germari* during the current interglacial period. However, depending on the climatic regime, different landforms can assume the same role (Tampucci 2017): in more continental and cold climates rock glaciers can persist at lower altitudes than debris-covered glacier, and can provide an ideal refuge also for subterranean species, because they are characterised by a thickness of the debris that can exceed 6 m with a considerable fissure network among boulders, which can include human-sized caves (Gobbi *et al.* 2014).

The first satellite mapping of supraglacial debris of glacial and periglacial landform was provided by Scherler *et al.* (2018) and allowed estimating that the extent of *N. germari* potential habitat in Eastern Alps is 555 km^2, but extremely discontinuous and fragmented. This habitat is currently expanding, providing refuge to cold-adapted species. However, we do not know how long these landforms will last if the climate continues to warm. The risk of a complete loss of suitable habitats for this species is exacerbated by the fact that *N. germari* is present in Dolomites with the steno-endemic subspecies *simony* Ganglbauer, 1892; thus, its extinction in the Alps will cause an essential loss for this "cold spot" of biodiversity.

*

Acknowledgements – We thank Michael Bernasconi, Marina Serena Borgatti and Marta Tognetti for the key support during sampling sessions. We also thank Ampezzo Dolomites Natural Park and the Adamello-Brenta Natural Park for permission for carrying out this research.

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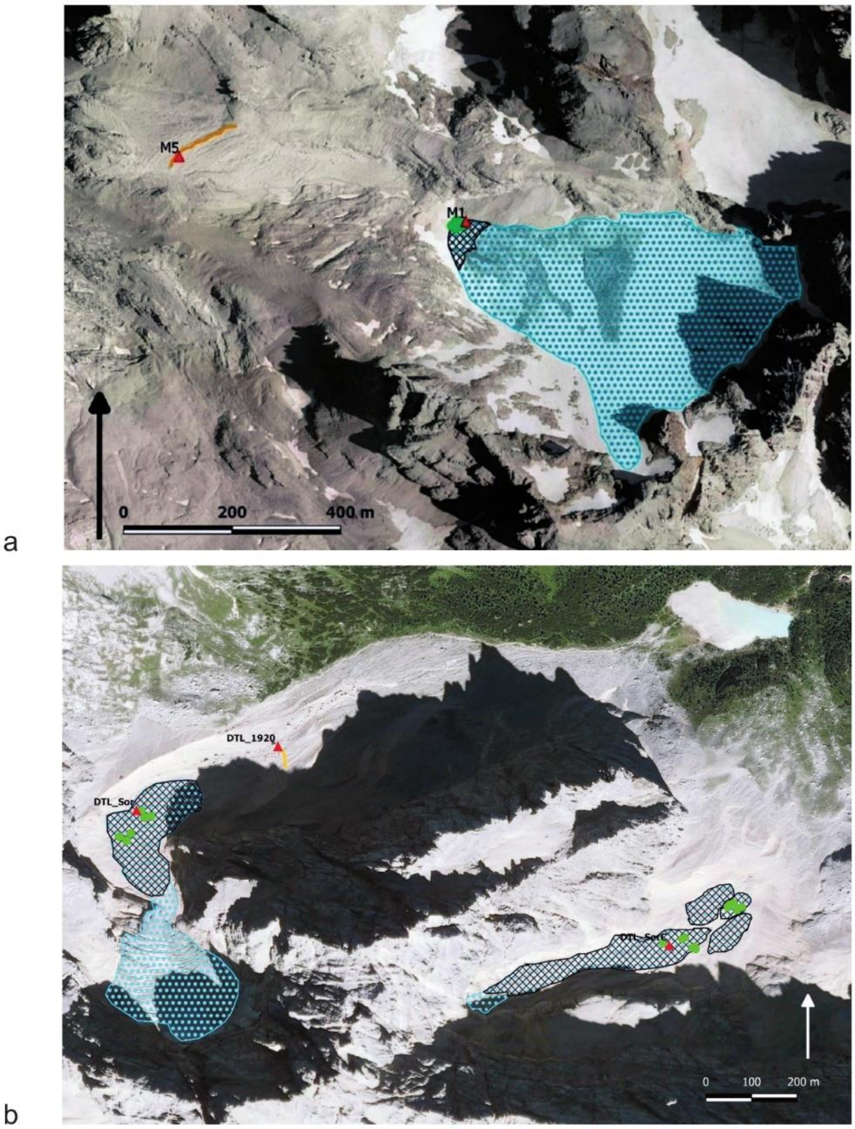
Received August 12, 2020, accepted November 21, 2020, published December 28, 2020

SUPPLEMENTARY MATERIALS

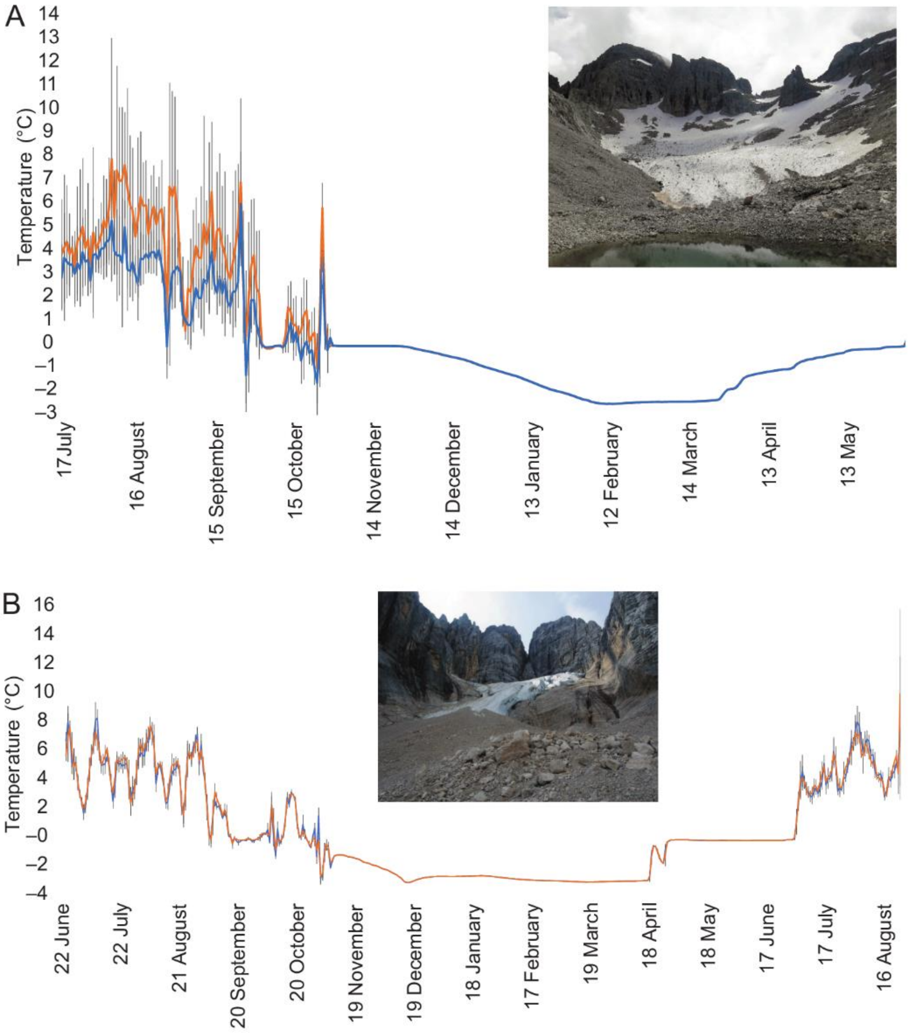


Appendix 1. The sampling plan map of Agola (a) and Sorapiss (b) glaciers. Light-blue pointed polygons: permanent ice; reticulated polygons: supraglacial debris; green points: pitfall traps; red triangles: datalogger positions. M1 = supraglacial datalogger on Agola, M5 = datalogger on 1908 moraines of Agola; DTLSor = supraglacial datalogger on Western Sorapiss; DTLSorC = supraglacial datalogger on Central Sorapiss; DTL 1920 = datalogger on the 1920 moraines of Sorapiss.

Appendix 2. Average monthly temperatures, average annual temperature and annual excursion on supraglacial debris (SGD), ice-free debris (IFD) and atmosphere (Atm) of Agola, Central and Western Sorapiss glaciers. Monthly temperature is the average of daily temperatures per month. Measurements at Agola were made in the 2018/19 season, those at Sorapiss in 2017/18.

Site	Average monthly temperature (°C)													Annual excursion (°C)	Annual average (°C)
	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul		
Agola (altitude: 2600 m)															
SGD	ND*	4.8	2.8	0.3	0.0	–0.6	–1.7	–2.4	–2.2	–1.0	–0.2	ND	ND	7.2	ND
Atm	ND	9.0	5.9	2.2	–4.3	–4.1	–7.1	–1.3	–1.6	0.0	1.3	10.9	10.7	18.0	1.8
IFD	ND	10.6	8.6	4.2	0.5	0.3	–0.1	–0.3	–0.2	–0.2	–0.2	–0.1	9.2	10.9	2.7
Western Sorapiss (altitude: 2360 m)															
SGD	5	5.1	0.8	0.5	–1.4	–2.6	–2.6	–2.8	–2.9	–1.6	0	0	ND	8.0	–0.3
Atm	6.6	8.0	1.3	1.4	–5.4	–9.2	–8.4	–12.3	–7.6	–0.7	1.7	4.8	ND	20.3	–1.7
IFD	8.1	9.3	2.8	1.5	–1.8	–3.1	–3.1	–3.2	–2.7	–1.8	–0.1	5	ND	12.4	1.0
Central Sorapiss (altitude: 2360 m)															
SGD	ND	3	0.2	–0.2	–1.2	–2.3	–2.3	–2.3	–2.4	–1.6	0	0	0.3	5.4	–0.8
Atm	ND	8.5	1.8	1.8	–5.0	–8.9	–6.9	–11.8	–7.3	–0.1	2.3	5.3	7.7	20.3	–1.0
IFD	ND	9.8	3.3	1.9	–1.4	–2.8	–1.4	–2.8	–2.4	–1.2	0.5	5.6	8.6	12.6	1.5

*ND= no data



Appendix 3. Temperatures recorded on supraglacial debris at Agola (A) during 2018–2019, Western (B) and Central Sorapiss (C) during 2017–2018. Orange lines indicate average daytime values, blue lines are the average nighttime values. Grey bars indicate ±S.D. of the daily values.

3.5 *Sex*-ratio and body size plasticity in two cold-adapted ground beetles (Coleoptera: Carabidae) co-occurring in a periglacial area of the European Alps.

PAPER SUBMITTED

Journal: Fragmenta Entomologica

Title: *Sex-ratio* and body size plasticity in two cold-adapted ground beetles (Coleoptera: Carabidae) co-occurring in a periglacial area of the European Alps

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Abstract

Differences in the sex-ratio and morphometric parameters in cold-adapted ground beetles were analysed to investigate environmental heterogeneity at small scale in a periglacial contest of the European Alps. Four hundred and thirty specimens of two cold-adapted ground beetles - *Nebria germarii* (Heer, 1837) and *Nebria castanea* (Bonelli 1810) - were analysed in order to test the presence of variation in *sex-ratio,* sexual dimorphism and morphometric parameters in relation to the occurrence of ice, and other environmental variables. Specifically, the populations found on an ice-related landform (active rock glacier) were compared with those on ice-free landforms (a fossil rock glacier and a scree slope). Both species experience sex-dependent morphometric plasticity. In addition, *sex-ratio* is female-biased, supporting female pioneering tendency in all the studied landforms.

With the exception of head length, all considered morphometric variables resulted autocorrelated in the population of the two species. Two sensitive parameters are indirectly affected by the presence/absence of ice in the terrain: the head width decreases, while elytra length increases passing from ice-free to ice-related landform. Both these morphometric differences may be related to the increase of intra/interspecific competition and to the lower trophic availability.

This study highlights that even if these high altitude cold-adapted species are able to survive on ice-free landforms, they find more favourable conditions on ice-related landforms. Since the two species show different sensitivity to the ice-presence, it is not always possible to detect this preference through abundances variability, but it necessary to use more detailed functional analysis. Head width and elytra length are good candidates as response traits of interstitial ice occurrence in stony terrains.

Key-words: co-occurence, ice, morphometric parameters, *Nebria germarii*, *Nebria castanea*, permafrost, rock glacier, plasticity.

INTRODUCTION

The occurrence of high geomorphological heterogeneity in the Alpine environment is one of the most important variables determining high biodiversity in Alpine ground beetle assemblages and their maintenance over time (Gobbi et al., 2021a). Some examples of these heterogeneous environments are represented by glaciers, proglacial plains, debris-covered glaciers, active rock glaciers and scree slopes. In particular, rock glaciers are the best expression of permafrost (i.e. soil, rock or sediment that is frozen for more than two consecutive years (Haeberli et al., 2006)) occurrence on the European Alps. They consist of coarse surface debris that insulates an ice-core or ice-debris mixture. In the European Alps they represent a fragmentary habitat, linked to discontinuous and azonal permafrost that locally determines existence of micro-thermal environments (Seppi, 2006). Also among/within rock glaciers a further heterogeneity is given by the different debris size: when it consist of large blocks, a negative thermal anomaly originates which determines a colder microclimate on the surface (Juliussen & Humlum, 2008).

Active rock glaciers, like debris-covered glaciers, allow cold-adapted species (i.e. animal and plant species closely related to alpine and nival belt) to survive, by acting as refuge areas in the current warm-stage period (Tampucci et al. 2017; Brighenti et al., 2020; Valle et al., 2020; Gobbi et al., 2021b; Valle et al. 2021).

On Alpine rock glaciers, springtails (Collembola), ground beetles (Coleoptera: Carabidae), spiders (Araneae) and centipedes (Chilopoda) are among the most abundant taxa, in terms of species richness and abundance of individuals (Gobbi, 2020; Gobbi et al., 2020; Gobbi & Lencioni, 2020; Gobbi et al., 2011). Specifically, ground beetles are the most studied from the ecological point of view, due to their sensitivity to local-scale climate change, large percentage of endemic species, low dispersal capacity and ability to respond clearly to different environmental conditions (Brandmayr at al., 2003; Gobbi et al., 2011; Gobbi, 2020; Pizzolotto et al., 2016). In addition, an increasing number of papers that used a species-trait approach highlighted the existence, in several species, of a certain morphological plasticity, linked to different factors such as temperature, trophic availability, intra and interspecific competition (Kingsolver & Huey, 2008; Talarico et al., 2020; Sukhodolskaya et al., 2021). Previous studies on ground beetles proved the existence of morphometric variability at different scales, reflecting the response to different environmental conditions: at large scale along latitudinal or altitudinal gradient (Sukhodolskaya, 2016; Sukhodolskaya & Ananina, 2017; Cvetkovska-Gjorgjievska et al. 2017), or at smaller spatial scale, like along glacier forelands (Gobbi et al. 2010).

The present study focuses on two cold-adapted ground beetle species, *Nebria germarii* (Heer, 1837) and *Nebria castanea* (Bonelli 1810), co-occurring on a periglacial area of the European Alps. The goal of this article is to evaluate at small scale (i.e. comparing neighboring landforms) the variations in *sex-ratio* and morphological parameters within the populations of these two species living on ice-related (active rock glacier), and ice-free (fossil rock glacier and scree slope) landforms. In particular, in this paper we aim to test if: i) *sex-ratio* and sexual dimorphism of the two cryophilic species change in relation to the landforms analysed, ii) the presence of ice indirectly influences the morphological parameters of the investigated populations.

MATERIALS AND METHODS

Study area

The study was performed in the glacial cirque Lazaunkar (Val Senales, Trentino-Alto Adige, Italian Alps, 46°44′49″ N, 10°45′20″ E.). Three landforms were analysed: an active rock glacier, a fossil rock glacier and a scree slope (Fig.1).

The selected ice-related landform is an active rock glacier classified as a "tongue-shape rock glacier" (Whalley & Martin, 1987); it occupies an area of 0.12 Km^2 and it develops for 660 m with a NE aspect, covering the altitudinal range between 2700 m and 2480 m a.s.l. (2005 data from Krainer et al., 2015). Being active it has an ice-core that determine its dynamicity and morphology: flow velocities are low along edges and increase towards the central part of the rock glacier (mean velocity from 2 to 6 mm/day), where the transverse ridges and the furrows are well developed (Fey & Krainer, 2020).

The selected ice-free landforms are a fossil rock glacier and a scree slope that do not have permafrost. The fossil rock glacier is a former rock glacier that lost its ice core and is located about 400 m North from the active rock glacier and occupies an area of 0.05 km^2 (calculated in QGIS 3.26.2). The scree slope is located upstream the fossil rock glacier and occupies an area of about 0.05 km^2 (calculated in QGIS).

The surface of the three geomorphological landforms is characterized by coarse-grained debris characterized the presence of large boulders (> 1 m), with the exception of sparse isles of fine debris. Herbaceous plants are present on the active rock glacier, specifically on fine stony debris islands. On the other hand, on fossil rock glacier and scree slope fine debris islands with small shrubs (*Vaccinium* spp., *Juniperus communis* and *Rhododendron ferrugineum*) are also present.

Sampling design

The sampling design (Fig. 1) consisted of six plots located on the surface of the active rock glacier (Laz1, Laz2, Laz3, Laz4, Laz5, Laz6), while two plots on the surface of the fossil rock glacier (Laz7 and Laz8) and two plots on the surface of the scree slope (Laz 9 and Laz 10) were selected due to the limited extent of these landforms. Each plot was represented by three pitfall traps (Gobbi, 2020; Gobbi & Lencioni, 2020) distanced each other about 10 m. Each pitfall trap consisted of a plastic vessel (diameter 7 cm, height 10 cm) baited with a mixture of wine-vinegar, salt and few drops of soap (Gobbi, 2020). All traps were active over the entire snow-free period, specifically from the 14th of July to the 04th of September 2020 and collected and reset every ca. 20 days (Tab.1 Suppl. Files). In proximity of each traps a sample of about 200 g was taken to measure substrate pH (in 1:2.5 substrate:water) and organic matter content. Coordinates, altitude and vegetation cover (percentage coverage estimate) were also recorded in correspondence of each trap.

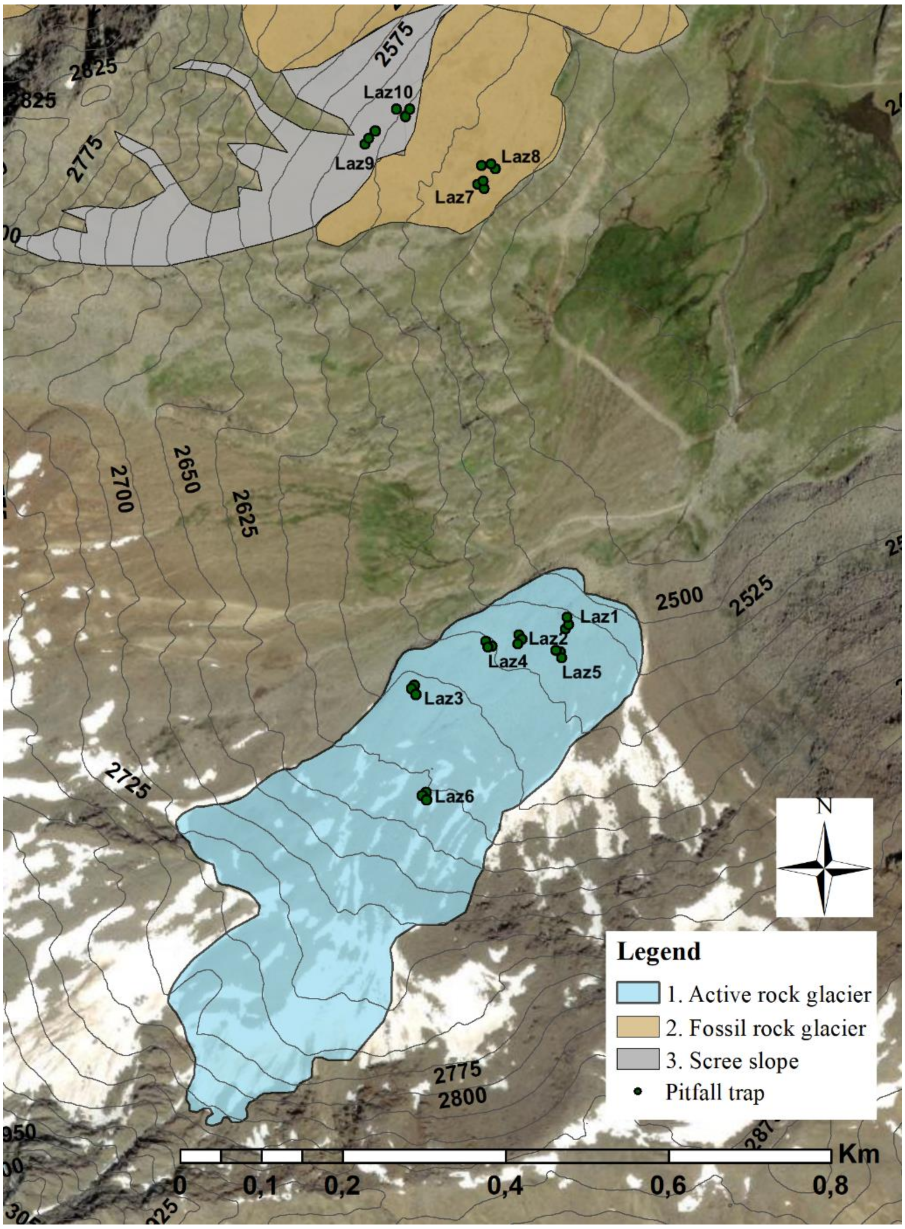

Figure 1 *– Sampling plan: distribution of pitfall trap at the Lazaunkar site*

Morphometric parameters

All the sampled arthropods were counted and sorted. Ground beetles were identified to the species level using a stereomicroscope and dichotomous keys reported in Ledoux & Roux (2005) and Pesarini & Monzini (2010, 2011). In addition to species identification, vital stage and sex of each specimen were also annotated through the analysis of the genital organs and/or secondary sexual characteristics. Species identification of the larval stage was not carried out; thus larvae are excluded from the analysis. Finally, morphometric data of the ground beetles belonging to *Nebria germarii* (215 specimens) and *Nebria castanea* (215 specimens) were measured. A stereomicroscope equipped with a micrometric objective was used for the measurements. Following Sukhodolskaya et al. (2020) six morphometric parameters were recorded (Fig.2):

A. Elytra length as distance between posterior end of scutellum and terminus of right elytron (in absence case of intact right elytron, left one is acceptable).

B. Elytra width as distance between anterior-distal corners of elytra.

C. Pronotum length measured along of central furrow pronotum.

D. Pronotum width as distance between posterior corners of pronotum.

E. Head length as distance between clypeus and juncture of occiput and postgena.

F. Head width as distance between proximal innermost sides of eyes.

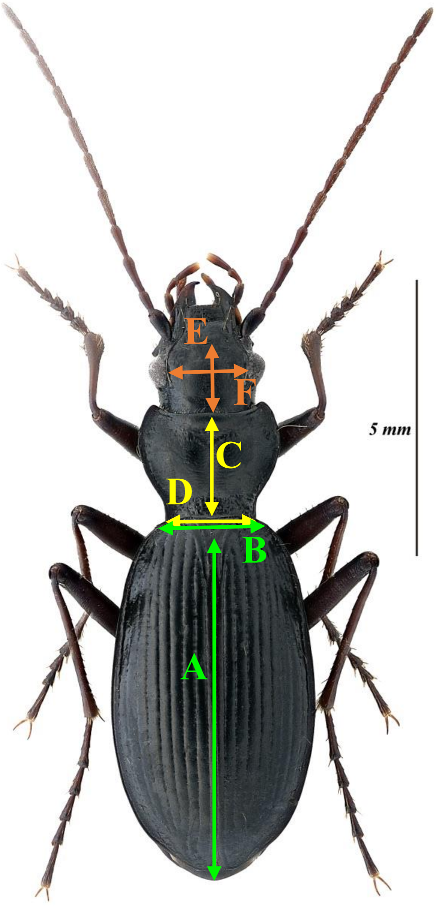

Figure 2 - *Dorsal view of* Nebria germarii *and representation of the measured body prameters. For the meaning of the letters see the text. Photo by A. Carlin*

Data analyses

Each analysis was performed at pitfall trap level, thus considering each trap separately.

An analysis of variance (ANOVA, because of the normal distribution - assessed by the Shapiro-Wilk test - of the male and female abundance data) was performed to test the differences of the *sex ratio* in *N. germarii* and *N. castanea* among each landform type and each plot. A total of 118 females and 97 males for *N. germarii* and a total of 127 females and 88 males for *N. castanea* were analysed.

Then, an analysis of variance was performed using the Kruskal-Wallis test (because of the non-normal distribution of the data assessed by the Shapiro-Wilk test) to verify the existence of sexual dimorphism in *N. germarii* and *N. castanea* on the whole study site. When the model is significant, the Dunn test with Benjamini-Hochberg correction (Benjamini & Hochberg, 1995) was performed, to define which landforms or plots have significant differences.

A principal component analysis (PCA) was carried out to identify the main variation gradients of the morphometric parameters and their relationship with the analysed landforms.

A morphometric analysis was performed using the Kruskal-Wallis test in order to evaluate the presence of significant differences in body size between landforms for *N. castanea* and *N. germarii*. The analysis was carried out by comparing the specimens of the landform with ice (active rock glacier) with those of the landforms without ice (fossil rock glacier and scree slope). For the morphometric analysis, body measurements of 426 ground beetles were used, instead of 430, because of four damaged specimens (one *N. castanea* and three *N. germarii*). The analyses were performed considering only one sex at a time to avoid differences related to sexual dimorphism.

For females of *N. castanea*, a correlation analysis (using Pearson coefficient) was carried out, to evaluate which environmental variables (between pH, vegetation cover, altitude, springtails (Collembola) abundance and spiders (Arachnida: Araneae) abundance determine the significant differences found in the morphometric analysis. Through preliminary analysis (with Pearson test) a high autocorrelation between organic matter and pH was observed (Correlation coefficient = -0.8). Therefore, only pH was used in the correlation analysis as soils variable. This correlation analysis was not performed for *N. germarii*, due to the small number of specimens sampled on fossil rock glacier and scree slope.

ANOVA test and Kruskal-Wallis tests were performed with R software (version 4.1.1) (R Core Team, 2020), while the PCA and the correlation analysis were performed with PAST software (version 4.03) (Hammer et al., 2001).

RESULTS

Abundances of ground beetle species in the considered landforms

A total of four ground beetle species (432 individuals) were collected in the study area: *Nebria germarii*, *Nebria castanea*, *Pterostichus unctulatus* (Duftschmid, 1812) and *Cychrus attenuatus* (Fabricius, 1792). *Nebria germarii* and *Nebria castanea* resulted the most abundant species.

Specifically, two-hundred and one *Nebria germarii* specimens were sampled on landform with ice (sampling with 18 traps divided into six plots; 11.2 specimens/trap on average) and 14 specimens on ice-free landforms (sampling with 12 traps divided into four plots; 1.2 specimens/trap on average). As regards *Nebria castanea*, 123 specimens were sampled on the landform with ice (sampling with 18 traps divided into six plots; 6.8 specimens/trap on average) and 92 specimens on the ice-free landforms (sampling with 12 traps divided into four plots; 7.7 specimens/trap on average). The sampling revealed the presence of *Nebria germarii* in almost ten times higher abundances on landforms with ice than those present on ice-free landforms (11.2 specimens/trap vs 1.2 specimens/trap). As regards *Nebria castanea*, the abundances present in the two landforms are similar (6.8 specimens/trap vs 7.7 specimens/trap). Ground beetle community detected includes also two *Pterostichus unctulatus* sampled on fossil rock glacier and one specimen of *Cychrus attenuatus* sampled on scree slope. Therefore, both these two species were collected only on ice-free landforms.

Sex-ratio in Nebria germarii *and* Nebria castanea

For both species no significant differences in sex-ratio were observed as a function of landforms and plots. A total of 118 females and 97 males of *Nebria germarii* were sampled. The average *sex-ratio* in the whole study area is slightly female-biased (percentage of females = 55%; χ^2 = 14,475; p <0.01). About *Nebria castanea*, 127 females and 88 males specimens were sampled. Similarly to *N. germarii*, also for this species the populations are slightly female-biased (percentage of the females = 59%; χ^2 = 16,999; p <0.01).

Sexual dimorphism in Nebria germarii *and in* Nebria castanea

For both species the existence of sexual dimorphism was assessed, with significant differences for all body measurements (Tab.1; Tab.2), specifically female specimens resulted bigger than male specimens (Fig.3; Fig.4).

Kruskal-Wallis test	**p-value**
Elytra length ~ Sex	< 2.2E-16*
Elytra width ~ Sex	7.33E-09*
Pronotum length ~ Sex	5.59E-11*
Pronotum width ~ Sex	6.67E-07*
Head length ~ Sex	2.66E-07*
Head width ~ Sex	2.68E-08*
Body length ~ Sex	< 2.2E-16*

Table 1 *- p-value of the Kruskal-Wallis tests for* N. germarii *body size as a function of sex. Asterisk highlight significant values.*

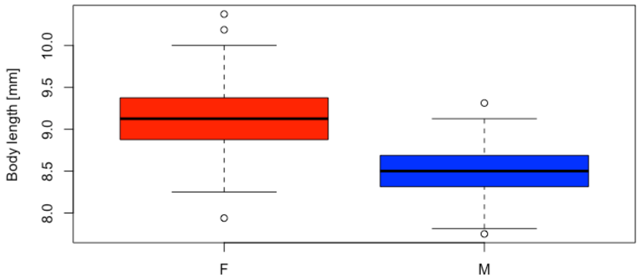

Figure 3 *– Boxplot of* N. germarii *body length as a function of sex (F=female; M=male)*

Kruskal-Wallis test	**p-value**
Elytra length ~ Sex	1.17E-14*
Elytra width ~ Sex	1.90E-09*
Pronotum length ~ Sex	5.70E-07*
Pronotum width ~ Sex	1.74E-11*
Head length ~ Sex	4.98E-04*
Head width ~ Sex	2.26E-10*
Body length ~ Sex	5.27E-14*

***Table 2** - p-value of the Kruskal-Wallis tests for* N. castanea *body size as a function of sex. Asterisk highlight significant values.*

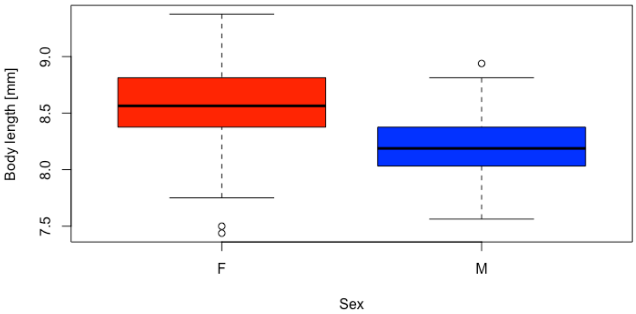

***Figure 4** – Boxplot of* N. castanea *body length as a function of sex (F=female; M=male)*

Main gradients of morphometrc variables for Nebria germarii *and* Nebria castanea

For both species it was observed that the morphometric parameters analysed vary along the same gradient, expressed by axis 1, with the exception of the head length which is associated with the second main component. Through this analysis, no clear distinction was observed between the specimens of the analysed landforms (Fig.5).

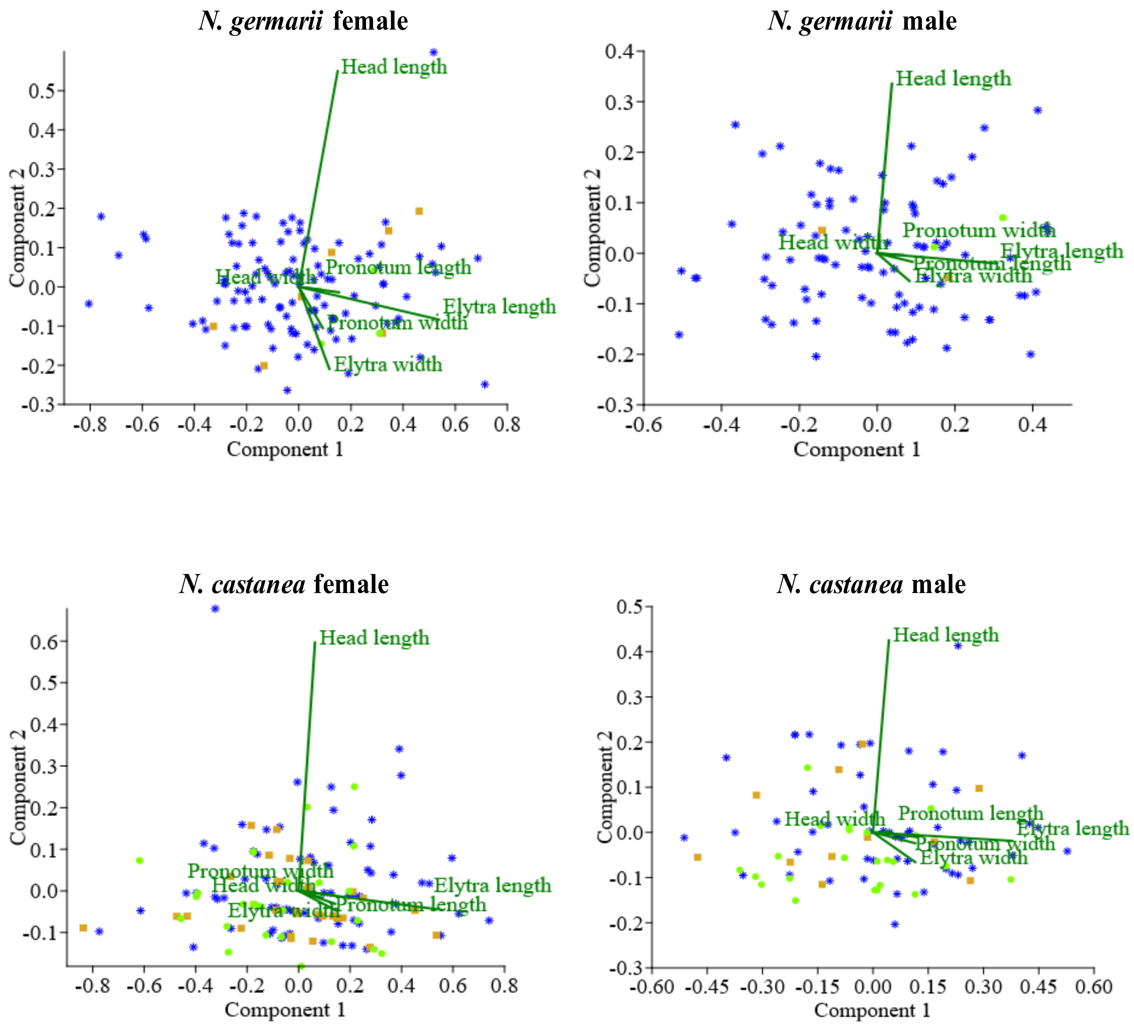

***Figure 5** – PCA analysis graphs. Blue stars=active rock glacier specimens; Gold squares=fossil rock glacier specimens; Green dot=scree slope specimens*

Morphometric analysis of Nebria germarii

By comparing the morphology of the specimens sampled on the active rock glacier (landform with ice) with the specimens collected on both the fossil rock glacier and scree slope (landforms without ice), a significant effect of the landform type in relation to the ice-presence on the width of the head was found (p-value = 0.026) (Tab.3). In particular, the head of specimens found on the active rock glacier resulted significantly narrower with respect to the head of the specimens on the landforms without ice (Fig.6).

Nebria germarii	**Females**	**Males**
Elytra length	0.052	0.136
Elytra width	0.082	0.772
Pronotum length	0.158	0.664
Pronotum width	0.170	0.618
Head length	0.791	0.447
Head width	0.026*	0.643

Table 3 *– p-value of* N. germarii *morphometric analysis with Kruskal-Wallis test, that evaluate the presence of significant differences in body size between landforms with ice (active rock glacier) and without ice (fossil rock glacier and scree slope). Asterisk highlight significant values.*

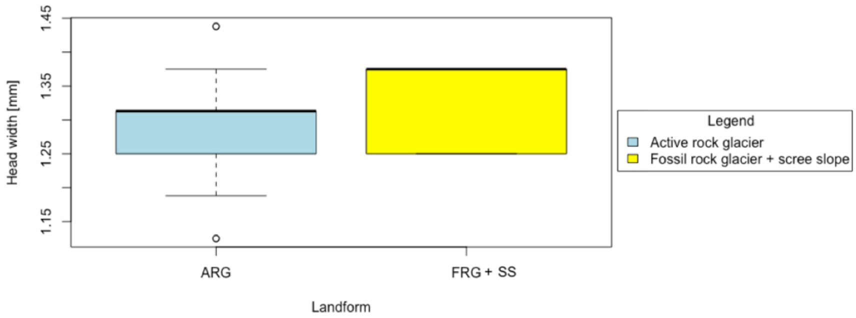

Figure 6 *– Boxplot of head width of* N. germarii *females as a function of landform*

Morphometric analysis of Nebria castanea

Significant differences were found in the female specimens' elytra width as a function of landform type (p-value = 0.007) (Tab. 4); in particular the elytra of the active rock glacier specimens are significantly wider than the elytra of the specimens on the landforms without ice (Fig.7).

Significant differences were found in the females' head length (p-value = 0.022) and in the males' head length (p-value = 0.007) as a function of landform (Tab.4); in particular the head of the active rock glacier specimens of both sexes is significantly longer than the head of the specimens on the landforms without ice (Fig.7).

Nebria castanea	Females	Males
Elytra length	0.122	0.093
Elytra width	0.007*	0.897
Pronotum length	0.889	0.372
Pronotum width	0.786	0.745
Head length	0.022*	0.007*
Head width	0.156	0.232

Table 4 *– p-value of* N. castanea *morphometric analysis with Kruskal-Wallis test, that evaluate the presence of significant differences in body size between landforms with ice (active rock glacier) and without ice (fossil rock glacier and scree slope). Asterisk highlight significant values.*

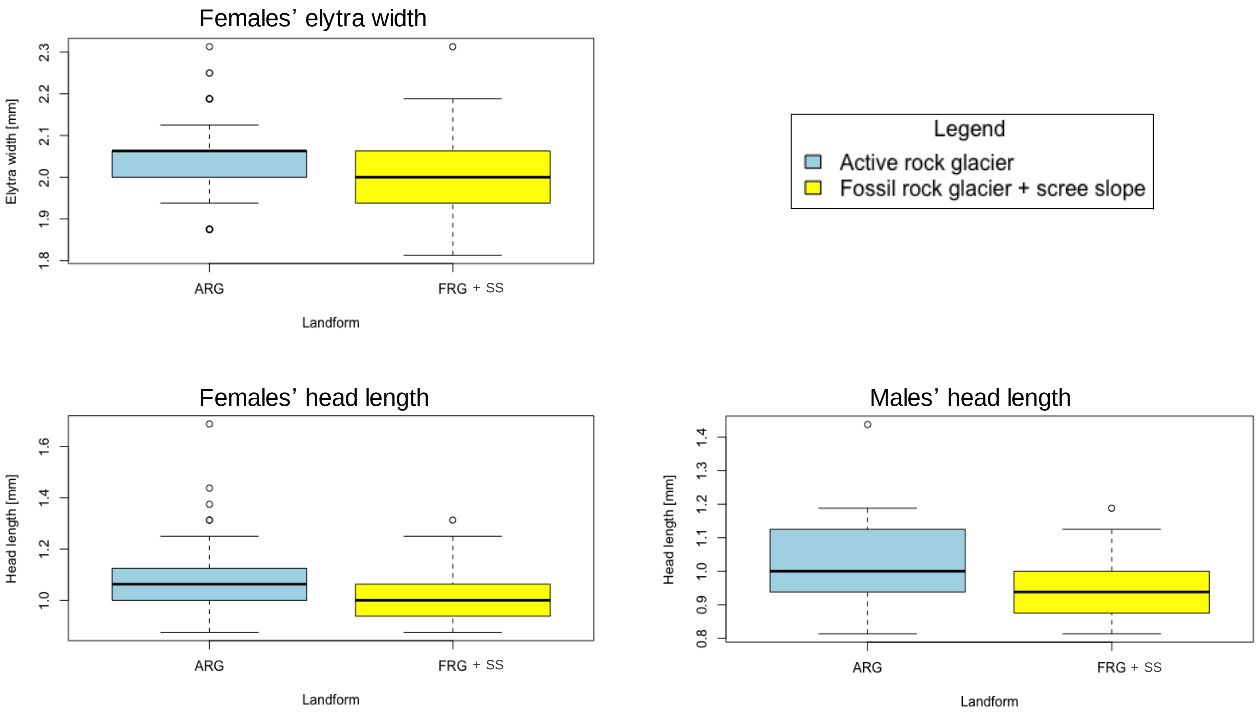

Figure 7 *– Boxplots of the significant morphometric analysis of* Nebria castanea

Correlation analysis for Nebria castanea

The morphometric parameter which showed the greatest significant variation in relation to the landform type is the elytra width in female specimens of *N. castanea*. The analysis showed a weak, but positive and significant correlation between elytra width and soil pH (p-value = 0.026) and springtail abundance (p-value = 0.005) (Tab.5, Fig.8, Fig.9). The analysis was not performed for males because no significant differences were found in males' analysis.

Correlation test (plot)	Correlation coeff.	p-value
Elytra width ~ altitude	0.110	0.310
Elytra width ~ pH	0.239	0.026*
Elytra width ~ vegetation cover	0.159	0.141
Elytra width ~ springtails abundance	0.298	0.005*
Elytra width ~ spiders abundance	-0.108	0.318

Table 5 *- Correlation coefficients and p-value of the correlation analysis between elytra width of the* N. castanea *females, of the significant plots specimens, and the environmental variables. Asterisk highlight significant values.*

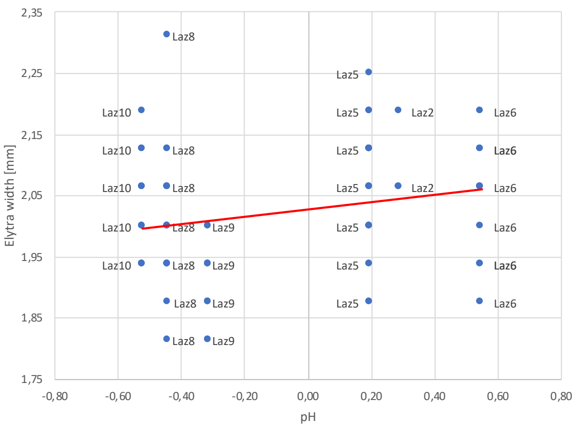

Figure 8 *– Linear regression graph between elytra width of* N. castanea *females and the soil pH*

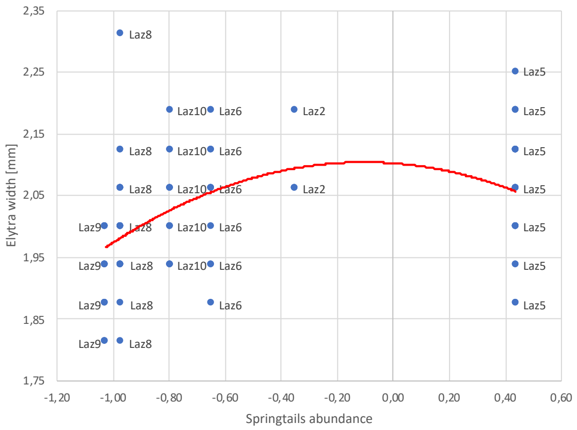

Figure 9 *– Polynomial regression graph between elytra width of* N. castanea *females and the springtails abundance*

DISCUSSION

Sex-ratio and sexual dimorphism in Nebria germarii *and* Nebria castanea *populations*

On Alpine debris-covered glacier and along its proglacial area it has been observed for the species *Nebria germarii* and *Nebria castanea* the tendency to have female-biased populations (Tenan et al. 2016). Specifically, it has been observed that the presence of female-biased populations is linked to the greater propensity of females to disperse with respect to males, useful for colonizing pioneering environments with less interspecific competition (Tenan et al., 2016; Hågvar et al., 2020). In our case the populations of *Nebria germarii* and *Nebria castanea* sampled in the study area resulted only slightly female-biased. Therefore, the presence or absence of ice in the investigated landforms does not affect the *sex-ratio* in *Nebria* populations suggesting the presence of almost stable and close populations.

In general, for *N. germarii* and *N. castanea* sexual dimorphism has been assessed, in which females are significantly bigger than males; this is a common pattern already documented in carabid's populations and the ecological significance concerns the greater accumulation of biomass by the females useful for the production of a great number of eggs (Marshall et al., 2013). On the other hand, large sizes imply an increase in the duration of development of larval stages, a greater food needs/consumption, and a significant risk of mortality due to the higher exposure to predators (Nylin & Gotthard, 1998; Sukhodolskaya et al., 2021).

Variation in Nebria germarii *and* Nebria castanea *abundance in relation to the ice presence*

Differently to *Nebria castanea* that occurred both on ice-free and ice-related landforms, *N. germarii* showed a marked preference for the considered ice-related landform (active rock glacier). This preference can be explained by *N. germarii* occurrences on terrains with high humidity and low average annual temperatures as highlighted in other researches (Kaufmann & Juen, 2001; Pizzolotto et al., 2014; Valle et al., 2020).

Morphometric variations of Nebria germarii *and* Nebria castanea *in relation to the ice presence*

With the exception of head length, all the considered morphometric variables vary along the same gradient in the population of *N. germarii* and *N. castanea*. The different trend in the head length is in contrast with the literature, reporting that the head length tends to vary along the same gradient as the other morphometric parameters (Brygadyrenko & Reshetniak, 2014; Brygadyrenko & Korolev, 2015; Sukhodolskaya et al., 2020). This discrepancy can be explained by a problem encountered during the measurement phase. In fact, in this phase, only some specimens presented a head extended with respect to the pronotum in the same way, as a result of the specimens' permanence in vinegar and alcohol which probably lead to a head evagination: it was therefore not possible to define a unique reference for all the specimens, which probably generated a bias that could have compromised the outcome of the statistical analysis. Thus, we preferred to avoid any ecological interpretation about this parameter.

Interestingly, head width and elytra length resulted to most sensitive parameter in relation to the landform type, specifically this variation is sex-related. More in details, female specimens of *Nebria germarii* with a wider head resulted on the ice-free landforms (fossil rock glacier and scree slope), compared to the specimens of the ice-related landform (active rock glacier). This was also observed for *N. castanea*, for both males and females. Springtails represent the main trophic resource for ground beetles in glacial habitat (Raso et al. 2014; Valle et al., 2020); our data on springtails showed that their average abundance for trap is lower on ice-free landforms (10.3±2.5 individuals on the ice-related landform vs 40.8±5.4 on ice-free landforms). It is known that trophic availability is a factor determining greater or lesser intra and interspecific competition among alpine ground beetles (Tenan et al., 2016). Thus, we can suppose that, in the ice-free landforms only the most competitive *Nebria* specimens, thus those with larger head size, are better adapted to live in habitats with limited trophic resources (springtails) and great intra and interspecific/inter-taxa competition or greater intra and inter-guild competition. About the inter-taxa competition it is also important to highlight that in these high-altitude environments, spiders represent the direct competitors of ground beetles (Gobbi et al., 2017; Sint et al.

2019) The wider head could allow a more efficient ingestion in larger quantities of food with respect to other competitors (Forsythe 1982), like for instance, spiders, and could also allow a more efficient intra guild predation (e.g. spiders vs ground beetles), in particular in landforms, like the ice-free, with low availability of preys (collembola).

In *Nebria castanea* significant morphometric variations were found also for the female elytra width between the analysed landforms; this difference was confirmed by the correlation analysis: a positive relationship was observed between springtails abundance and females' elytra size of *N. castanea*. The greater size of the elytra of the specimens on active rock glacier may be linked (as suggested also by head morphometric variations) to greater abundance of springtails present on ice-related landform. In fact, the greater abundance of springtails determines a greater trophic availability, therefore a greater biomass accumulation (Raso et al., 2014). Morphological plasticity has already been documented for other ground beetle species (Talarico et al., 2020; Sukhodolskaya et al., 2021) and specifically in *Nebria castanea* (Gobbi et al. 2010); in this species it is considered an adaptive capacity that allows this species to survive even in extreme conditions such as those of glacial and periglacial areas. Individuals of those populations have different body size, related to the environment stability in which they live. A stable environment allows a longer larval development, and a high trophic availability allows high foraging rates; the action of these two effects determines the presence of larger specimens (Blake et al., 1994; Gobbi et al. 2010).

The positive relationship between the female elytra width of *N. castanea* and soil pH can be a proxy of soil degree of evolution. Specifically, on micaschists – the bedrock type of the study area - higher pH and lower organic matter values in soils on the ice-related landforms respect to soils on ice-free landforms could indicates the presence of a more immature substrate (Ji et al., 2014). The presence of environment on the landform with ice with less competition and more trophic availability causes the presence of larger ground beetle specimens, compared to the specimens present on ice-free landforms (fossil rock glacier and scree slope).

In summary, elytra width and head length are two morphometric parameters varying in synchronous in relation to the landform type.

Ice-related landforms support optimal microclimatic conditions for cold-adapted arthropod species (Brighenti et al., 2020; Gobbi, 2020; Valle et al., 2021). The result obtained by our study allowed to advance the hypothesis that ice-related landforms, respect to ice-free landforms, host less inter- and intra-specific competition for cold-adapted species. Thus, even if some cold-adapted *Nebria* species manage to survive also on neighbour ice-free landforms, they probably find more favourable conditions on landforms with ice, and this preference is detectable thought morphometric analysis.

This is an important step ahead on the knowledge about the relationship between species traits plasticity in climate-depend species in relation to their environment.

CONCLUSIONS

This work represents the first study that analyses morphometric parameters in high altitude ground beetles and shows how the morphology is influenced by environmental factors, in particular the ice presence. Furthermore, it allowed to increase the knowledge regarding the cryophilic species *N. germarii* and *N. castanea* in their pioneering characteristics in colonizing ice-related landform (i.e. with female-biased populations). However, we highlighted different sensitivity to ice presence in these two cryophilic species. For some organisms, morphometric analysis result fundamental to detect with a high sensitivity cold-adapted species' response to ice presence, thus suggesting the effectiveness of this method for investigating in detail the ecology of this endangered habitat.

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3.6 Checklist ragionata della flora e degli artropodi (Coleoptera: Carabidae e Arachnida: dei ghiacciai Centrale e Occidentale del Sorapiss (Dolomiti d’Ampezzo).

Frammenti CONOSCERE E TUTELARE LA NATURA BELLUNESE N. 9 49-65 2019

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CHECKLIST RAGIONATA DELLA FLORA E DEGLI ARTROPODI (COLEOPTERA: CARABIDAE E ARACHNIDA: ARANEAE) DEI GHIACCIAI CENTRALE E OCCIDENTALE DEL SORAPISS (DOLOMITI D'AMPEZZO)

Riassunto - Il detrito roccioso posto sulla superficie dei ghiacciai è in grado di ospitare una biodiversità, sia animale che vegetale, che include specie microterme a rischio di estinzione nello scenario attuale di riscaldamento climatico globale. Gli ambienti glaciali delle Alpi Orientali, dominati da substrato carbonatico, non sono mai stati studiati sotto questo aspetto. Con questo lavoro si è descritta la distribuzione delle specie lungo le piane proglaciali e sul detrito epiglaciale del ghiacciaio Occidentale e del ghiacciaio Centrale del Gruppo del Sorapiss (Parco Naturale delle Dolomiti d'Ampezzo), al fine di poterne studiare il ruolo ecologico e biogeografico di rifugio per specie microterme e/o endemiche. Per perseguire questi obiettivi sono stati quindi effettuati dei rilevamenti vegetali e dei campionamenti di artropodi (coleotteri carabidi e ragni) nelle varie unità ambientali, differenziate in base all'età di deglaciazione. Le *checklist* ottenute annoverano 122 specie di piante vascolari, 19 di coleotteri carabidi, 28 di ragni. Dal paragone con dati di letteratura, lo studio ha rivelato la risalita altitudinale del carabide *Nebria germari* di circa 300 metri nel corso degli ultimi 70 anni.

Parole chiave: coleotteri, Dolomiti, flora, ghiacciai neri, ragni.

Abstract - In this paper we present the list of species of plants and arthropods found on the surface and along the glacier forefields of two debris-covered glaciers. These data allow to assess the changes in plant and arthropod community as a function of time since deglaciation. The total amount of species found sums up to 122 vascular plants species, 19 ground beetles and 28 spider species. The obtained results showed the altitudinal shift of the ground beetle *Nebria germari* as high as 300 meters of altitude in the past 70 years pointing out the reduction of this species distribution due to climate change.

Keywords: beetles, debris-covered glaciers, Dolomites, flora, spiders.

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Introduzione

Fin dalla fine della Piccola Età Glaciale (PEG: secoli XIV-XIX) le Alpi sono state interessate da una fase di ritiro glaciale, interrotta o rallentata solo durante alcuni brevi periodi del secolo scorso (anni '20 e '80). Negli ultimi decenni la regressione glaciale si è fatta più intensa (Citterio et al., 2007) e questo sta determinando la liberazione di sempre più ampie aree vergini che nel tempo vengono progressivamente colonizzate dalle biocenosi. Un'altra tendenza sempre più osservabile negli ambienti glaciali alpini è legata all'aumento della copertura detritica rocciosa sulla superficie della maggior parte dei ghiacciai che, da ghiacciai bianchi (*debris free*), stanno diventando ghiacciai neri (*debris-covered glacier*) (Citterio et al., 2007; Paul et al., 2007). La copertura detritica, che si accumula come conseguenza degli intensificati cicli di termoclastismo e crioclastismo sulle pareti circostanti la massa glaciale, può cambiare notevolmente le dinamiche del ghiacciaio sottostante. Se lo strato detritico supera i 3-5 cm, si osserva infatti una riduzione logaritmica del tasso di ablazione, che limita le variazioni frontali (Nakawo & Rana, 1999) e che consente ad alcuni ghiacciai di persistere anche a quote relativamente basse (Pelfini et al., 2012; Citterio, 2016).

Recenti studi hanno dimostrato come i ghiacciai neri, e le loro piane proglaciali, non solo possano essere colonizzati da vari organismi, come ad esempio piante e artropodi, ma siano anche gli habitat ideali per lo studio dei tempi che le biocenosi impiegano per colonizzare tali substrati.

La distribuzione delle piante sul detrito epiglaciale è guidata dalla profondità e dalla stabilità del substrato (Caccianiga et al., 2011), dal disturbo presente (a causa dell'acqua di fusione o di eventi gravitativi), dalla concentrazione di sostanza organica, dalla granulometria (Tenan et al., 2016) e dal microclima, influenzato dalla profondità a cui si trova il ghiaccio. In questo contesto le piante dominanti sono pioniere microterme, dall'apparato radicale superficiale e dagli adattamenti volti alla riduzione dell'evapotraspirazione e all'ottimizzazione delle sostanze organiche presenti. Lungo la piana proglaciale il fattore determinante nel descrivere la distribuzione delle specie è l'età di deglaciazione; man mano che questa aumenta, anche la stabilità del substrato, la copertura vegetale e la concentrazione di sostanza organica aumentano. Allontanandosi dal ghiacciaio si osserva quindi l'ingresso di specie più esigenti, fino ad arrivare ai substrati mai rimaneggiati dalle avanzate glaciali oloceniche, con specie tipiche di ambienti maturi.

Fig. 1. Collembolo appartenente all'ordine degli Entomobryomorpha che si muove tra il detrito epiglaciale. Le sue dimensioni sono di circa 2-3 mm.

Anche l'artropodofauna segue i parametri imposti dal tempo di deglaciazione. In prossimità del ghiacciaio, e sul detrito epiglaciale, si notano specie pioniere, detritivore (Hexapoda: Collembola; Acarina) e predatrici (Coleoptera: Carabidae; Arachnida: Araneae). Sul ghiacciaio è inoltre ben rappresentata la componente alloctona (principalmente acari, collemboli e ditteri), portata in loco da correnti ascensionali (Kaufmann et al., 2001; Gobbi et al., 2011, Valle, 2019), la quale spesso costituisce la base della catena alimentare (Raso et al., 2014). I predatori qui presenti, posti all'apice della catena alimentare, sono coleotteri carabidi e ragni.

Lungo la piana proglaciale, man mano che la distanza dal ghiacciaio aumenta, e con essa la maturità del substrato e la copertura vegetale, si insediano anche specie tipiche di ambienti più maturi (Gobbi et al., 2010). I taxa qui più rappresentativi sono collemboli (Fig. 1), acari, coleotteri carabidi, ragni e opilioni (Arachnida: Opiliones).

I rapidi cambiamenti osservabili negli ambienti glaciali e proglaciali stanno determinando una progressiva riduzione degli habitat disponibili per le specie microterme e una risalita altitudinale di specie più termofile provenienti da quote inferiori. In questo contesto di riscaldamento climatico globale i ghiacciai neri assumono una rilevanza ecologica fondamentale, in quanto non solo sono in grado di ospitare varie specie di piante e artropodi microtermi, ma, grazie all'elevata inerzia termica che li contraddistingue, possono assumere un ruolo di rifugio per tali specie (Caccianiga et al., 2011; Gobbi et al., 2011; Citterio, 2016).

Al fine di comprendere al meglio le dinamiche ecologiche di piante e artropodi che colonizzano i ghiacciai neri e le piane proglaciali ad essi antistanti il MUSE - Museo delle Scienze di Trento e l'Università degli Studi di Milano, in collaborazione col Parco Naturale delle Dolomiti d'Ampezzo, hanno svolto un progetto pluriennale volto allo studio della flora e dell'artropodofauna caratteristiche degli ambienti legati ai ghiacciai Occidentale e Centrale del Gruppo del Sorapiss, un massiccio carbonatico appartenente al Gruppo delle Dolomiti Ampezzane. Obiettivo del lavoro è quello di presentare la *checklist* delle specie vegetali e di artropodi, nello specifico di ragni e coleotteri carabidi. Gli studi ad oggi presenti sull'ecologia di piante e artropodi dei ghiacciai neri sono per lo più concentrati nelle Alpi Occidentali e Centrali, su substrati cristallini (Tampucci et al., 2017; Caccianiga et al., 2011; Gobbi et al., 2011; Pelfini et al., 2012; Fickert et al., 2007; Citterio, 2016, Caccianiga et al., 2001); gli affioramenti dolomitici e calcarei presenti sul Sorapiss costituiscono quindi un campo di studio finora poco esplorato.

Area di studio

La peculiarità dei ghiacciai del Sorapiss è legata alla loro collocazione geografica e alla natura litologica del substrato su cui poggiano. Essi infatti sono collocati nelle Dolomiti, un settore alpino dove è stato possibile osservare forti tassi di ritiro glaciale; le maggiori perdite riscontrate in Veneto dagli anni '60 ad oggi sono state rilevate in particolare nel Gruppo del Sorapiss (-36%) (Smiraglia e Diolaiuti, 2015).

Nello specifico, i due ghiacciai presi in esame sono caratterizzati da dimensioni molto ridotte. Il Ghiacciaio Occidentale ha esposizione media di 359°, un'altitudine massima di 2756 m s.l.m. e la minima di 2254 m s.l.m. (dati riferiti al 2017; Borgatti, 2018); nel 2009 aveva un'estensione di 0,19 km^2 (Smiraglia e Diolaiuti, 2015), mentre i rilevamenti effettuati nel 2017 nell'ambito di questo progetto ne hanno rilevato un'area di 0,134 km^2, rendendo possibile stimare una riduzione areale negli ultimi 8 anni del 36% (Borgatti, 2018). La superficie coperta da detrito, nel 2017, risultava essere di 0,043 km^2, corrispondente al 32% dell'apparato glaciale (Borgatti, 2018). Il bacino d'accumulo appare tuttavia libero; per questo motivo il ghiacciaio è riconosciuto come ghiacciaio montano.

Il Ghiacciaio Centrale ha esposizione media di 52°, un'altitudine massima di 2621 m s.l.m. e una minima di 2213 m s.l.m. (dati riferiti al 2017; Borgatti, 2018). Una copertura detritica di 0,047 km^2 interessa gran parte della superficie glaciale (Borgatti, 2018). Dal confronto tra la superficie del ghiacciaio nel 2009, stimata intorno a 0,14 km^2 (Smiraglia e Diolaiuti, 2015), e quella relativa all'anno 2017 si osserva una riduzione areale del 42%.

Le due piane proglaciali presentano dei complessi apparati morenici (Fig. 3) che sono stati oggetto di studio nell'ambito di questo progetto di ricerca (Borgatti, 2018): attraverso dati e fotografie storiche è stato possibile datare le morene.

In corrispondenza di ciascuna morena sono state individuate delle unità ambientali omo-

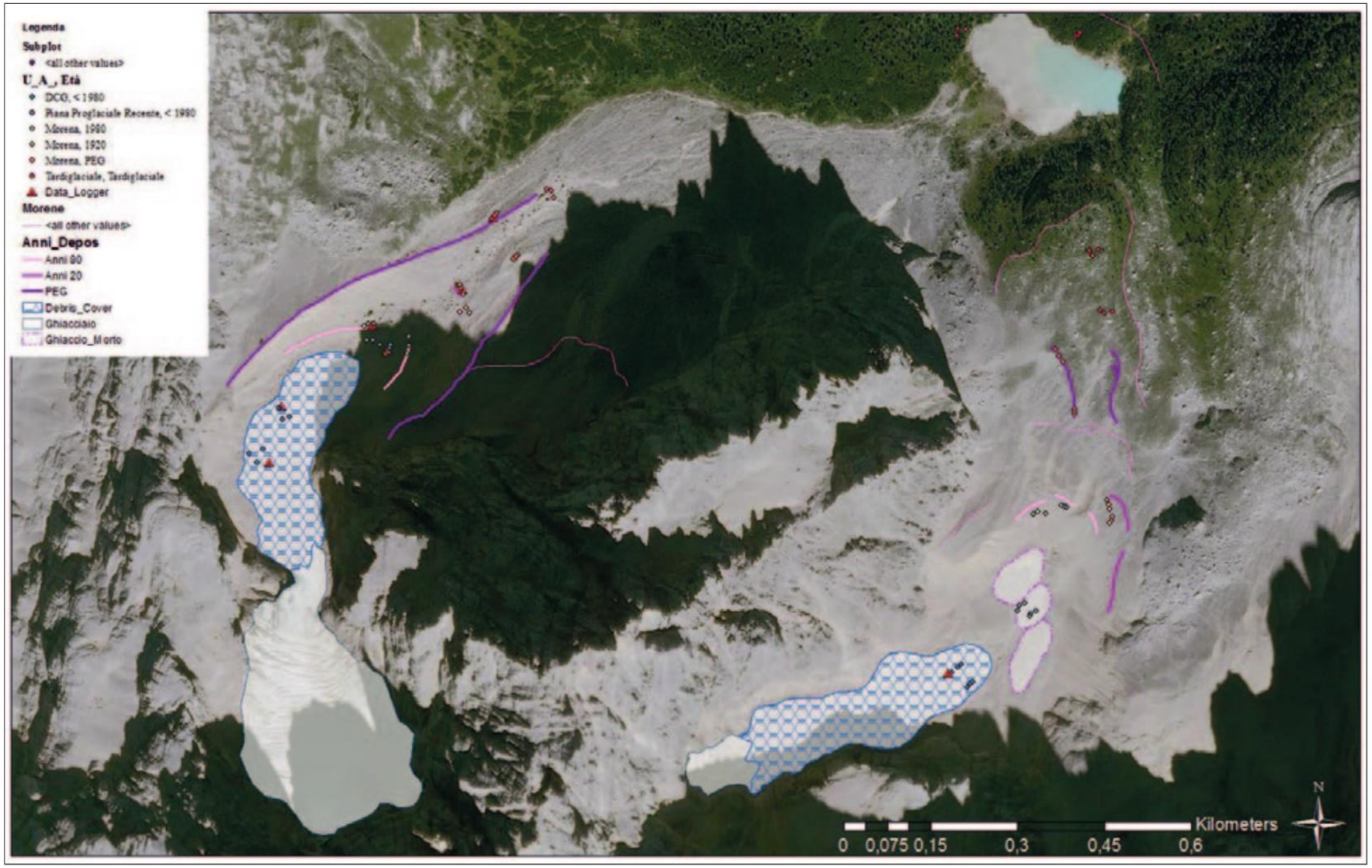

Fig. 2. Unità ambientali e disegno di campionamento dei Ghiacciai del Sorapiss. A sinistra è rappresentato il Ghiacciaio Occidentale, a destra quello Centrale. I puntini colorati sono posizionati in corrispondenza delle diverse unità ambientali individuate lungo le piane proglaciali. –– Morena anni '70-80; –– Morena anni '20; –– Morena PEG Tardiglaciale.

Fig. 3. Piana proglaciale del ghiacciaio Occidentale con, ben evidenti, i complessi apparati morenici che lo caratterizzano.

genee (Fig. 2) nelle quali sono stati fatti rilievi di vegetazione e artropodi. Dall'unità ambientale più recente (dove il ghiaccio è ancora presente) a quella liberata dal ghiaccio da maggior tempo si distinguono, quindi, per entrambi i ghiacciai: il detrito epiglaciale, la piana proglaciale recente corrispondente alla porzione di terreno compresa tra la fronte e l'avanzata glaciale degli anni '80, una morena messa in posto negli anni '80, una morena degli anni '20, una morena della Piccola Età Glaciale (PEG) e il substrato libero dal ghiaccio da più di 15.000 anni (Tardiglaciale).

Ad ognuna di queste unità ambientali è stata associata una comunità vegetale differente (Tognetti, 2019): il detrito deglacializzato dopo la PEG si presenta come detrito instabile vegetato in modo discontinuo e poco evidente da specie erbacee sporadiche; la morena della PEG è occupata da prateria a *Carex firma* (firmeto) discontinua nelle aree più stabili (Ghiacciaio Centrale) e da comunità a *Dryas octopetala* (driadeto) nelle aree più disturbate (Ghiacciaio Occidentale); la morena del Tardiglaciale mostra vegetazione di mugheta, in presenza di molta roccia affiorante, di lariceta, in presenza di suoli più profondi. Per il presente lavoro si farà riferimento a queste unità.

Materiali e metodi

Piano di campionamento e analisi dei dati

Vegetazione e artropodofauna sono state studiate durante il periodo giugno-settembre 2017 effettuando campionamenti su sei unità ambientali individuate per ogni ghiacciaio e corrispondenti a differenti età di deglaciazione (Fig. 4). All'interno di ogni unità ambientale (definite nel paragrafo precedente) sono stati individuati 2 plot, ad eccezione delle morene PEG del ghiacciaio Occidentale, dove sono stati stabiliti 3 plot. Ogni plot è stato a sua volta suddiviso in 3 punti di campionamento, dove sono stati effettuati il rilievo floristico e il campionamento dell'artropodofauna. Il totale complessivo dei punti di campionamento individuati sui due ghiacciai è di 75.

Il rilievo floristico è stato condotto in aree di 25 m^2 il più omogenee possibile sia per vegetazione che per substrato (Fig. 5). Per ogni punto di campionamento sono state rilevate coordinate (GD), altitudine (m s.l.m.), esposizione (°) e inclinazione (°); sono state inoltre segnate le coperture percentuali di ogni strato vegetale (arboreo, arbustivo, erbaceo e muscinale) e del detrito sciolto (pietrosità). È stato quindi redatto un elenco floristico in

Fig. 4. Punto di campionamento posizionato sul detrito epiglaciale del ghiacciaio Occidentale.

cui ad ogni specie è stato assegnato un valore di copertura approssimato al 5%; alle specie che coprivano tra l'1 e il 5% del rilievo è stato assegnato il valore +, mentre per quelle che coprivano meno dell'1% è stato usato il valore R.

Il rilievo dell'artropodofauna è stato realizzato mediante trappole a caduta, costituite da bicchieri in plastica (altezza 10 cm, diametro superiore 7 cm, diametro inferiore 4,5 cm) inseriti nel terreno fino all'orlo. Questi sono stati riempiti per 2/3 da una soluzione di acqua, aceto (dalla funzione attrattiva), sale a saturazione (con funzione anticongelante) e qualche goccia di detersivo (che riduce la tensione superficiale). Al fine di impedire la tracimazione del contenuto come conseguenza di eventuali giorni piovosi sono stati praticati due fori a circa 1 cm dal bordo superiore, mentre per impedire il danneggiamento delle trappole da parte della macrofauna, sono stati posizionati sopra alle trappole dei clasti di medie dimensioni, marcati con vernice spray per poterle facilmente individuare. La raccolta degli artropodi è stata effettuata ogni 20 giorni circa, ripristinando di volta in volta la trappola. È stato possibile ottenere un totale di 4 raccolte per il Ghiacciaio Occidentale e di 3 per quello Centrale.

Fig. 5. Punto di campionamento e rilievo di vegetazione sulle morene più antiche.

La fase di analisi dei dati vegetazionali ha visto in primo luogo l'inserimento delle specie riconosciute in una matrice specie-sito, in cui sono state riportate anche le informazioni stazionali. Questo ha permesso una prima analisi descrittiva che ha portato all'individuazione della ricchezza in specie di piante e artropodi (numero medio di specie per unità ambientale). Per la componente vegetale sono stati inoltre calcolati lo spettro biologico, usando le forme biologiche definite da Raunkiaer (1934), e lo spettro corologico, usando i corotipi di Pignatti (1982), raggruppati secondo lo schema presentato nell'Appendice 1.

Per l'artropodofauna è stata inoltre calcolata l'abbondanza di individui per ogni unità ambientale, utilizzando la Densità di Attività (D.A.): il rapporto tra il totale degli individui prelevati nel singolo punto di campionamento e il periodo di attività della trappola (numero raccolte *vs* intervallo).

La nomenclatura botanica segue quella di Bartolucci et al. (2018). Per la descrizione dei corotipi dell'artropodofauna è stato utilizzato il codice di nomenclatura proposto da Vigna Taglianti et al. (1999).

Risultati

Componente floristica

La *checklist* stilata include 122 specie (Appendice 2), rilevate in un intervallo di quota che va da un minimo di 1924 m s.l.m., nella mugheta e lariceta del Ghiacciaio Occidentale a un massimo di 2420 m s.l.m., a livello del detrito epiglaciale del Ghiacciaio Occidentale. Queste entità specifiche sono suddivise in 92 generi e appartengono a 40 famiglie (Appendice 3); quelle più rappresentate sono Asteraceae (15), Poaceae (10), Caryophyllaceae (9) Cyperaceae (9), Ericaceae (7) e Rosaceae (7).
Lo spettro biologico (Fig. 6) rivela una dominanza di emicriptofite (63%) di cui le specie scapose sono le più numerose, seguite dalle cespitose e da quelle a rosetta; le camefite e le geofite (rispettivamente il 18% e il 7% del totale) sono le altre forme biologiche più rappresentate. Il prospetto dettagliato delle forme biologiche è riportato in Tab. 1.
Dall'analisi corologica (Fig. 7) risulta che la parte più consistente della flora del Sorapiss appartiene alle orofite Europee (38%). Altre componenti importanti sono quella artico-alpina e quella boreale, che insieme contribuiscono con il 29% delle specie, legate ai climi freddi che caratterizzano i piani altitudinali in cui si sono effettuati i rilevamenti. Degne di nota sono le specie orientali, che costituiscono quasi 1/5 della flora e includono le endemiche Est-Alpiche e le orofite Sud-Est Europee.
Elementi alloctoni sono del tutto assenti, come del resto gli elementi steno-endemici.
Il numero medio di specie per rilievo è 9,2, ma va sottolineata una elevatissima variabilità tra rilievi, i quali possono ospitare un minimo di 0 specie -sul detrito epiglaciale del Ghiacciaio Centrale- e un massimo di 40 specie in un rilievo di mugheta sulla morena tardiglaciale del Ghiacciaio Occidentale. Questa grande variabilità è legata soprattutto al passaggio da comunità pioniere di recentissima formazione a morene deposte nel Tardiglaciale: tendenzialmente la ricchezza specifica aumenta allontanandosi dal ghiacciaio.

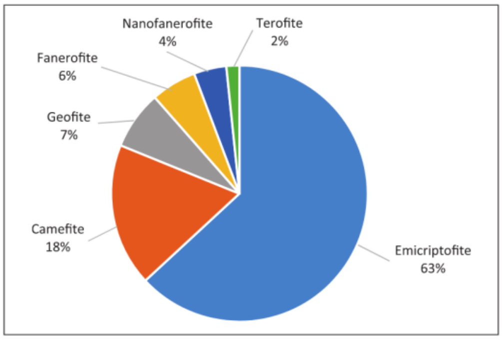

Fig. 6. Spettro biologico delle specie vegetali dei ghiacciai del Sorapiss.

Lungo la piana proglaciale e sul detrito epiglaciale del Ghiacciaio Occidentale del Sorapiss sono state campionate 94 specie vegetali, lungo quella del Ghiacciaio Centrale e sul rispettivo detrito epiglaciale 71. I risultati relativi alla distribuzione della ricchezza specifica e della copertura vegetale in corrispondenza delle diverse unità ambientali sono sintetizzati nei grafici (Fig. 8 e Fig. 9), unendo i valori relativi ai due ghiacciai.

Artropodofauna

L'identificazione dell'artropodofauna campionata ha permesso di ottenere una *checklist* comprensiva di 47 specie. Nello specifico sono state individuate 28 specie di Aracnidi appartenenti all'ordine degli Araneae (Appendice 4), incluse in 10 famiglie (Appendice 5), e 19 specie di Coleotteri Carabidi (Appendice 6). Questi *taxa* sono stati rilevati in un intervallo

Tab. 1. Tabella riportante il prospetto dettagliato delle forme biologiche rappresentate.

Emicriptofite H (%)		**Camefite Ch (%)**		**Nanerofite NP (%)**		**Geofite G (%)**		**Fanerofite P (%)**		**Terofite T (%)**	
H scap	32,17	Ch frut	6,09	G rhiz	6,09	NP	4,09	P caesp	2,61	T scap	1,64
H caesp	19,13	Ch sufr	4,35	G bulb	1,74			P scap	1,74		
H ros	12,17	Ch rept	4,35					P lian	0,87		
H bienn	1,74	Ch pulv	3,48					P rept	0,87		
H rept	1,74	Ch succ	0,87								

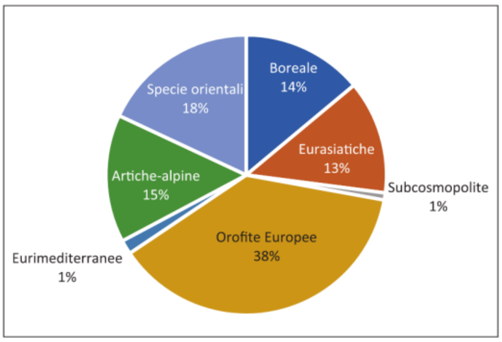

Fig. 7. Spettro corologico della flora proglaciale dei ghiacciai del Sorapiss, con ripartizione percentuale delle componenti.

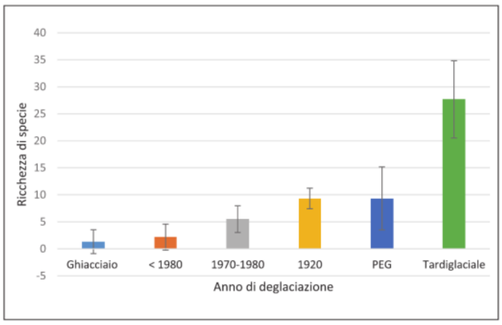

Fig. 8. Ricchezza di specie in funzione dell'anno di deglaciazione dei due ghiacciai del Sorapiss. La barra d'errore indica la deviazione standard.

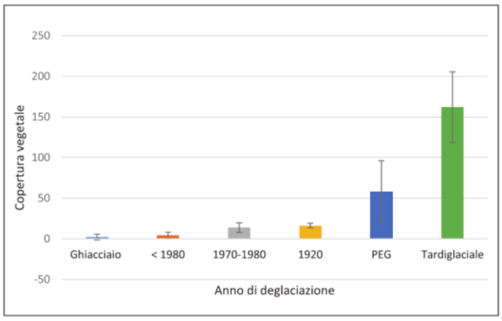

Fig. 9. Copertura vegetale in funzione dell'anno di deglaciazione dei due ghiacciai del Sorapiss. La barra d'errore indica la deviazione standard.

di quota che va da un minimo di 1924 m s.l.m, nella mugheta del Ghiacciaio Occidentale a un massimo di 2420 m s.l.m., a livello del detrito epiglaciale del Ghiacciaio Occidentale.

Il numero medio di specie di ragni per sito è 2,08, con minimi di 1 specie fino ad un massimo di 6, mentre i carabidi mostrano un maggior numero di specie per sito di campionamento, con un valore medio di 2,35 oscillando tra valori minimi di 0 e massimi di 7 specie (Fig. 10).

Discussione

Componente floristica

Sulla superficie glaciale è presente detrito con distribuzione e profondità variabile, poco coeso e instabile; le piante che lo popolano sviluppano apparati radicali superficiali che le rendono poco sensibili alle variazioni dello spessore del detrito. Il numero totale di specie osservate sul detrito epiglaciale è 8; le specie più frequenti sono *Hornungia alpina* e *Saxifraga sedoides* (Fig. 12), che è anche quella con valore di copertura più elevato, anche se molto ridotto (0,7%) a causa dell'instabilità marcata del substrato. In entrambi i ghiacciai, le specie di detrito epiglaciale non sono esclusive di questo ambiente, ma popolano anche le morene più recenti. Anche la porzione di piana proglaciale liberata dai ghiacciai dagli anni '80 è caratterizzata da detrito instabile, ma la ricchezza di specie e la loro copertura è maggiore (copertura media del 4,4%) rispetto a quella sul detrito glaciale. Si rilevano in totale 7 entità e le specie più tipiche di questi ambienti sono *Arabis alpina, Cerastium carinthiacum, Saxifraga sedoides*.

Sui substrati liberati dal ghiaccio nel 1970-1980 il numero totale di specie trovate è pari 15, la diversità floristica aumenta leggermente e alle specie precedenti si aggiungono, tra le altre, *Noccaea rotundifolia, Hornungia alpina, Sabulina austriaca, Poa minor e Papaver alpinum* subsp. *rhaeticum;* quest'ultima è la specie più abbondante.

Le piane proglaciali liberate dal ghiaccio da circa cento anni (età 1920) presentano dei substrati caratterizzati dalla componente detritica consolidata; questo permette la crescita di un numero di specie maggiore (ricchezza

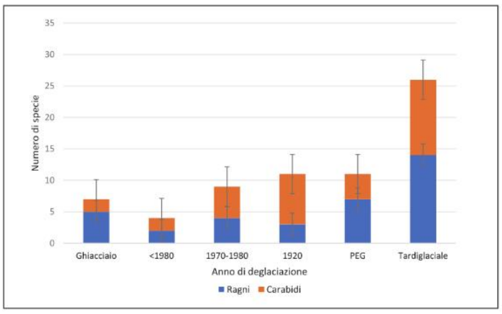

Fig. 10. Ricchezza di specie di carabidi e ragni in funzione dell'anno di deglaciazione.

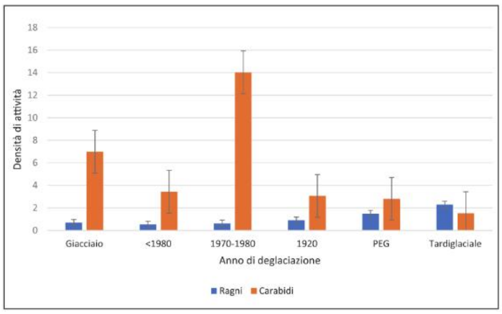

Fig. 11. Densità di attività totale di carabidi e ragni di entrambi i ghiacciai in funzione dell'anno di deglaciazione.

media di specie per rilievo è pari a 9,3) rispetto a quello dei substrati più giovani; lo stesso si osserva per la copertura vegetale (copertura media del 18%); Il numero di specie totale è 22 e *Papaver alpinum* subsp. *rhaeticum* è anche in questo ambiente una delle specie più abbondanti (Tab. 2), insieme a *Sabulina austriaca*.

Allontanandosi dalla fronte glaciale e raggiungendo i substrati liberati dal ghiacciaio verso la fine del 1800 si incontra una vegetazione di detrito più stabile e consolidato. Le specie trovate sono 42; la copertura vegetale di questi ambienti e la diversità floristica sono più alte rispetto a quelle rilevate sui substrati instabili, deglacializzati più di recente. Le specie più abbondanti sono *Dryas octopetala* e *Carex firma*, con una copertura media rispettivamente del 34% e del 22%.

La vegetazione dei substrati deglacializzati dopo il Tardoglaciale si distingue da quella degli altri substrati per una copertura del suolo molto maggiore (161,9%; questo valore è dovuto alla sovrapposizione di più livelli di copertura vegetale, erbaceo, arbustivo e arboreo) e da un elevato numero di specie per rilievo (33 specie). La struttura di queste vegetazioni è più complessa e compare una componente arbustiva e arborea caratterizzata da specie come *Pinus mugo* e *Larix decidua*. In totale sono state trovate 97 specie; la ricchezza floristica di questi ambienti è elevata e le specie erbacee più abbondanti sono *Sesleria caerulea*, *Carex firma*, tipiche di prateria, associate a specie come *Vaccinium myrtillus*, *Viola biflora*, *Rhododendron hirsutum*, *Geranium sylvaticum*, più tipiche degli arbusteti e dei boschi subalpini.

Per quanto riguarda la corologia, va segnalata l'assenza di elementi stenoendemici dolomitici d'alta quota. Questo è legato innanzitutto alla storia di questo massiccio, che durante le glaciazioni pleistoceniche era interamente coperto da calotte glaciali (Da Pozzo et al., 2016) e non poteva dunque fungere da rifugio; le specie presenti provengono quindi dalle aree limitrofe non glacializzate e non posso-

Fig. 12. *Saxifraga sedoides*, foto M. da Pozzo.

Unità ambientale	**Specie più frequenti**	**Specie con copertura maggiore**
Ghiacciaio	*Saxifraga sedoides, Hornungia alpina*	*Saxifraga sedoides*
Piana proglaciale (detrito instabile)	*Papaver alpinum subsp. rhaeticum*	*Papaver alpinum* subsp. *rhaeticum*
Piana proglaciale (detrito consolidato)	*Dryas octopetala*	*Dryas octopetala*
Prateria	*Anthyllis vulneraria, Saxifraga crustata, Carex firma, Bistorta vivipara e Dryas octopetala*	*Carex firma*
Lariceta	*Aposeris foetida, Carduus defloratus, Melica nutans, Prunella grandiflora, Trollius europaeus, Geranium sylvaticum, Lonicera caerulea, Juniperus communis, Vaccinium myrtillus, Viola biflora, Homogyne alpina*	*Larix decidua*
Mugheta	*Erica carnea, Juniperus communis, Salix waldsteniana, Pinus mugo, Thymus polytrichus, Vaccinium vitis-idaea, Vaccinium myrtillus, Galium anisophyllum, Rhododendron hirsutum, Trisetaria alpestris, Viola biflora, Parnassia palustris, Selaginella selaginoides, Campanula scheuchzeri, Sesleria caerulea, e Dryas octopetala*	*Pinus mugo*

Tab. 2. Specie più frequenti per unità ambientale.

no quindi essere steno-endemiche. Al termine dell'ultima glaciazione, la ricolonizzazione dei versanti del Sorapiss è avvenuta con un consistente intervento di elementi Est-Alpici e dei rilievi Sud-Est europei (Da Pozzo et al., 2016), la cui categoria corologica risulta quindi ben rappresentata nella flora analizzata.

L'assenza di specie stenoendemiche contribuisce a far sì che nell'elenco floristico stilato non risultino esserci specie soggette a particolari forme regionali di tutela.

Solo *Rhododendron hirsutum*, specie endemica di tutto l'arco alpino, figura nell'elenco delle specie protette dalla legge regionale n°53 del 15-11-1974. Tre sono le entità presenti inserite nella lista rossa italiana della IUCN: *Huperzia selago*, *Lycopodium annotinum* subsp. *annotinum* e *Selaginella selaginoides*. Sono tuttavia classificate come a minor rischio (*Least Concern* -LC) dalla suddetta lista.

Artropodofauna

In entrambi i gruppi tassonomici studiati, ragni e coleotteri carabidi, i valori massimi di ricchezza di specie si riscontrano nella lariceta e nella mugheta, dove oltre alle specie di ambiente più maturo, persistono anche le specie di ambienti pionieri (Tab. 3).

In generale, il detrito epiglaciale riesce a ospitare più specie di ragni e carabidi rispetto agli ambienti appena deglacializzati, antistanti la fronte (Fig. 10); con gli ambienti ancora più maturi si iniziano a registrare nuovamente ricchezze specifiche ben più elevate. La densità di attività dei ragni (Fig. 11) cresce progressivamente dal ghiacciaio agli ambienti più maturi del Tardiglaciale mentre quella dei carabidi registra un picco di massima sulle morene del 1970/80, seguito dal detrito epiglaciale, mentre negli altri ambienti si rilevano molti meno individui; questo non si osserva per le piante, che mostrano una ricchezza di specie e una copertura maggiore negli ambienti antistanti la piana rispetto al detrito glaciale.

Aracnidi Aranei

Le specie di ragni che caratterizzano i diversi ambienti mostrano un *turnover* ben definito in funzione dell'età di deglaciazione, con parziale coesistenza delle specie più abbondanti. Sulla superficie del ghiacciaio, per esempio, risulta come specie più frequente *Mughiphantes brunneri*, specie microterma appartenente alla famiglia dei Linyphiidae (come l'esemplare della Fig. 13).

Allontanandosi dal ghiacciaio si osserva un calo dell'abbondanza di *Mughiphantes brunneri* il quale inizialmente coesiste con *Acantholycosa pedestris*. A sua volta *Acantholycosa pedestris*, specie che predilige ambienti rocciosi e con abbondanza di detrito, risulta essere la specie più frequente nella piana proglacia-

Ambiente	Ragni più frequenti
Ghiacciaio	*Mughiphantes brunneri*
Piana proglaciale (detrito instabile)	*Acantholycosa pedestris, Mughiphantes brunneri*
Piana proglaciale (detrito consolidato)	*Acantholycosa pedestris, Xysticus alpinus*
Prateria	*Xysticus alpinus*
Lariceta	*Xysticus alpinus*
Mugheta	*Pardosa oreophila, Cybaeus tetricus, Alopecosa taeniata*

Ambiente	Carabidi più frequenti
Ghiacciaio	*Nebria germari*
Piana proglaciale (detrito instabile)	*Nebria germari*
Piana proglaciale (detrito consolidato)	*Nebria germari, Oreonebria diaphana*
Prateria	*Oreonebria diaphana*
Lariceta	*Carabus alpestris, Carabus creutzeri*
Mugheta	*Pterostichus jurinei, Carabus creutzeri*

Tab. 3. Specie di artropodi più frequenti per unità ambientale.

le, mentre in ambienti di prateria e lariceta la specie dominante per abbondanza diventa *Xysticus alpinus*.

Delle 28 specie individuate vanno evidenziate alcune di particolare rilevanza biogeografica: infatti 5 di queste sono endemiche alpine, ovvero *Acantholycosa pedestris, Drassodex heeri, Sittilong longipes, Troglohyphantes fagei e Xysticus alpinus,* quest'ultimo recentemente elevato a livello di specie (Ballarin et al., 2018). *Mughiphanthes brunneri*, già citato come specie più abbondante riscontrata nei campionamenti del detrito epiglaciale, risulta essere un endemismo italiano esclusivo delle Dolomiti venete e altoatesine.

Confrontando le specie di ragni censite nel Gruppo del Sorapiss con quelle presenti nel "Catalogo ragionato dei ragni del Veneto" (Ballarin et al., 2011) risultano come nuove segnalazioni per la fauna veneta tre specie: *Arctosa alpigena*, tipica di ambiente di brughiera, *Pardosa sordidata* di prateria alpina fino al limite degli alberi, e *Sittilong longipes*, specie strettamente di alta quota (oltre i 2000 metri).

Fig. 13. Esemplare di Linyphiidae sp. che si muove sul manto nevoso.

Coleotteri Carabidi

Le specie di Carabidi riscontrate con maggiore frequenza variano marcatamente con la distanza dal ghiacciaio. Sulla superficie del ghiacciaio infatti gli individui campionati appartengono interamente alla tribù dei Nebrini, della quale sono state identificate due specie: *Nebria germari* (Fig. 14) e *Oreonebria diaphana*. La prima rappresenta la quasi totalità degli individui campionati sulla superficie del ghiacciaio e nelle immediate vicinanze, mentre *Oreonebria diaphana* risulta essere più abbondante nelle raccolte effettuate in prossimità delle morene datate agli anni '80 e '20. Nei firmeti prevalgono invece specie appartenenti al genere *Carabus* (*C. creutzeri* e *C. alpestris*), mentre in ambienti di mugheta e lariceta si riscontrano con maggiore frequenza anche altre specie appartenenti al genere *Pterostichus*.

Delle 19 specie identificate nell'area di studio 10 risultano essere endemiche, di cui 8 considerate stenoendemiche delle Dolomiti orientali, ovvero: *Carabus alpestris*, *Carabus creutzeri*, *Laemostenus schreibersi*, *Nebria germari*, *Oreonebria diaphana*, *Pterostichus schaschli*, *Trechus dolomitanus* e *Trechus pallidulus*.

La comparazione delle specie censite in questo studio con quelle citate in Marcuzzi (1956) e quelle custodite nella Collezione Marcuzzi presso il Museo di Storia Naturale di Genova ha evidenziato, per la specie *Nebria germari*, un chiaro esempio di variazione temporale nel range di distribuzione altitudinale. Fino alla metà del secolo scorso veniva "*trovata sul Sorapiss a soli 1950 m*" (Marcuzzi, 1956). Gli esemplari di *N. germari* appartenenti alla Collezione Marcuzzi e raccolti nell'agosto del 1972 sono stati campionati a 2200 m s.l.m. I ritrovamenti di *N. germari* effettuati all'interno di questo studio sono avvenuti sempre a quote superiori i 2270 metri. Questo confronto evidenzia dunque una risalita altitudinale di *N. germari* di circa 300 metri nel corso degli ultimi 70 anni. Essendo una specie microterma sta migrando verso quote superiori dove può ritrovare temperature ottimali per la sua sopravvivenza (temperatura media annua = 0°C). Nel Gruppo del Sorapiss tali condizioni climatiche sono presenti unicamente in prossimità e sulla superficie dei ghiacciai del Sorapiss. Questo fenomeno di migrazione altitudinale di *N. germari* è confermato anche dalle osservazioni di Pizzolotto et al. (2014) in cui si dimostra l'estinzione di questa specie nei firmeti dolomitici delle Pale di San Martino posti a circa 2000 m s.l.m. dove, fino agli anni '80, era presente (Brandmayr & Zetto brandmayr, 1987).

Questo studio ha permesso di mettere in evidenza alcuni cambiamenti nelle biocenosi caratterizzanti gli ambienti di alta quota. Gli habitat studiati hanno dimostrato svolgere un ruolo importante per la sopravvivenza di specie microterme (qui particolarmente abbondanti o, addirittura, esclusive di questi ambienti, come nel caso del ragno *Mughiphanthes brunneri* e del carabide *Nebria germari*) e, quindi, vulnerabili a causa dei cambiamenti climatici.


Fig. 14. *Nebria germari* si sposta sulla copertura nevosa.

Ringraziamenti

Si ringrazia il Dott. Michele Da Pozzo (Parco Naturale delle Dolomiti d'Ampezzo) per aver supportato questo lavoro.

Si ringraziano inoltre il Dott. Davide Dalpiaz e il Dott. Fabio Pupin per aver fornito le fotografie degli artropodi.

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Appendice 1: classi corotipiche

Classi considerate nelle analisi	Corotipi compresi nelle classi
Boreali	- Circumboreali - Eurosiberiane - Orof. Circumbor. - Paleotemp.
Eurasiatiche	- Europ. - Centro-Europ. - Nord- e Centro-Europ. - Eurasiat. - Europeo-Caucas. - Eurasiat. Temp.
Subcosmopolite	- Subcosmopolite
Orofite europee	- Orof.S-Europ - Endem.-Alpica - Orof.S-Europ. (Alpico-Appenn.) - Orof. S- e Centro-Europ - Orof.Europ. - Orof.Eurasiat. - Orof.Centro-Europ. - Orof.SW-Europ. - Endem.S-Alpica - Orof.medioeurop. - Endem.
Eurimediterranee	- Euri-Mediterranee - NE-Medit.-Mont. - E-Stenomedit.
Artiche-alpine	- (Circum) Artico-Alp - Artico-Alp.-Euroamer. - Artico-Alp. - Artico-Alp. (Euro-Amer) - Artico-Alp. (Europ.)
Specie orientali	- E-Alpino-Dinarica - Orof.SE-Europ - Endem.E-Alpica - Orof. E-Alp.-Dinar - Subendem. - Alpino-illirica - Endem. SE-Alpico - Alpica (Sub-endem) - E-Alp.-Carpat. - Caucas. - Orof.- Alpico-Carpat. - E-Europ.

Appendice 2: elenco floristico

Nome specifico	Corotipo	Forma biologica
Huperzia selago (L.) Bernh. ex Schrank & Mart.	Subcosmop.	Ch rept
Lycopodium annotinum L.	Circumbor.	Ch rept
Selaginella selaginoides (L.) Schrank & Mart.	Circum-Artico-Alp.	Ch rept
Asplenium viride Huds.	Circumbor.	H ros
Larix decidua Mill.	Orof.Centro-Europ	P scap
Picea abies (L.) H. Karst.	Eurosib.	P scap
Pinus mugo Turra	Orof.-Eurasiat	P rept
Juniperus communis L.	Circumbor.	P caesp
Tofieldia calyculata (L.) Wahlenb.	Centro-Europ.	H scap
Veratrum album L.	Eurasiat. Temp	G rhiz
Lilium martagon L.	Eurasiat.	G bulb
Coeloglossum viride (L.) Hartm.	Circumbor.	G bulb
Epipactis atrorubens (Hoffm.) Besser.	Europeo-Caucas	G rhiz
Luzula sylvatica subsp. sieberi (Tausch) K. Richt.	Orof.S-Europ. (Alpico-Appenn.)	H caesp
Oreojuncus monanthos (Jacq.) Zav. Drabk. & Kirschner	Artico-Alp.-Euroamer.	G rhiz
Carex atrata L.	Artico-Alp. (Europ.)	H caesp
Carex austroalpina Bech.	Endem.	H caesp
Carex capillaris L.	Circum-Artico-Alp.	H caesp
Carex digitata L.	Eurasiat	H caesp
Carex ferruginea Scop.	Orof.S-Europ	G rhiz
Carex firma Host.	Orof.S-Europ	H caesp
Carex ornithopoda Willd.	Europeo-Caucas	H caesp
Carex parviflora Host	Orof.S-Europ	H caesp
Carex sempervirens Vill.	Orof.S-Europ	H caesp
Agrostis alpina Scop.	Orof.SW-Europ	H caesp
Calamagrostis varia (Schrad.) Host	Orof.Eurasiat	H caesp
Festuca pumila Chaix	Orof.S-Europ	H caesp
Koeleria pyramidata (Lam.) P. Beauv.	Nord- e Centro-Europ.	H caesp
Melica nutans L.	Europeo-Caucas	H caesp
Poa minor Gaudin	Orof.S-Europ	H caesp
Poa alpina L.	Circumbor.	H caesp
Sesleria coerulea (L.) Ard.	Orof.Medioeurop	H caesp
Sesleria sphaerocephala (Ard.) Deyl	Endem.SE-Alpica	H caesp
Trisetaria alpestris (Host) Baumg.	Orof.SE-Europ	H caesp
Aconitum lycoctonum L. emend. Koelle	Eurasiat.	H scap
Aconitum napellus L.	Europ.	G rhiz

Clematis alpina (L.) Mill.	(Circum) Artico-Alp	P lian
Thalictrum aquilegiifolium L. subsp. *aquilegiifolium*	Eurosib.	H scap
Trollius europaeus L.	Artico-Alp. (Euro-Amer)	H scap
Papaver alpinum L. subsp. *rhaeticum*	Orof.SW-Europ	H scap
Sedum alpestre Vill.	Orof.S-Europ	Ch succ
Saxifraga crustata (Ard.) Deyl	Endem. E-Alpino-Dinar.	Ch pulv
Saxifraga sedoides L.	Orof.SW-Europ	H scap
Saxifraga squarrosa Sieber	Subendem.	Ch pulv
Armeria alpina Willd.	Orof.S-Europ	H ros
Bistorta vivipara (L.) Delarbre	(Circum) Artico-Alp	G rhiz
Moehringia ciliata (Scop.) Dalla Torre	Alpino-illirica	H caesp
Moehringia muscosa L.	Orof. S- e Centro-Europ	H caesp
Sabulina austriaca (*Jacq.*) Rchb.	Endem. Alpico	Ch suffr
Sabulina verna (*L.*) Rchb. subsp. *verna*	Eurasiat.	Ch suffr
Atocion rupestre (L.) Oxelman	Artico-Alp. (Europ.)	H bienne
Cerastium carinthiacum Vest.	Orof.- Alpico-Carpat	Ch suffr
Heliosperma pusillum (Waldst. & Kit.) Rchb.	Orof.S-Europ	H caesp
Silene acaulis (L.) Jacq.	(Circum) Artico-Alp	Ch pulv
Silene vulgaris subsp. *glareosa* (Jord.) Marsden-Jones & Turrill	Orof.SE-Europ	H scap
Parnassia palustris L.	Eurosib.	H scap
Viola biflora L.	Circumbor.	H scap
Salix caprea L.	Euras.	P caesp
Salix glabra Scop.	Orof. E-Alp.-Dinar	NP
Salix reticulata L.	(Circum) Artico-Alp	Ch frut
Salix serpyllifolia Scop.	Orof.S-Europ	Ch frut
Salix waldsteiniana Willd.	E-Alp.-Carpat.	NP
Anthyllis vulneraria L.	Euri-Medit.	H scap
Lotus corniculatus subsp. *alpinus* (DC.) Rothm	Orof.S-Europ	H scap
Dryas octopetala L.	(Circum) Artico-Alp	Ch rept
Fragaria vesca L.	Eurosib.	H rept
Geum rivale L.	Circumbor.	H scap
Potentilla crantzii (Crantz) Beck ex Fritsch	(Circum) Artico-Alp	H scap
Potentilla erecta (L.) Raeusch.	Euras.	H scap
Sorbus chamaemespilus (L.) Crantz	Orof.S-Europ	NP
Geranium sylvaticum L.	Eurasiat	H scap
Arabis alpina L.	Circum.-Artico-Alp	H scap
Arabis caerulea All.	Endem.Alpica	H scap
Biscutella laevigata L.	Orof.S-Europ	H scap
Hornungia alpina (L.) O. Appel subsp. *alpina*	Orof. Centro e S-Europ	H ros

Noccaea rotundifolia (L.) Moench	Endem.Alpica	Ch pulv
Daphne striata Tratt.	Endem. Alpico	Ch suffr
Soldanella alpina L.	Orof.S-Europ.	H ros
Arctostaphylos alpinus (L.) Spreng.	Circum-Artico-Alp.	Ch frut
Erica carnea L.	Orof.S-Europ.	Ch frut
Rhododendron hirsutum L.	Endem. Alpico	NP
Rhodothamnus chamaecistus (L.) Rchb.	Endem. E-Alpico	Ch suffr
Vaccinium myrtillus L.	Circumbor.	Ch frut
Vaccinium uliginosum L	Circumbor.	Ch frut
Vaccinium vitis-idaea L.	Circumbor.	Ch frut
Galium anisophyllum Vill.	Orof. C. e S.Europ.	H scap
Gentiana bavarica L.	Endem.-Alpica	H ros
Gentiana clusii E. P. Perrier & Songeon	Orof.SE-Europ	H ros
Gentianella rhaetica (A.Kern. & Jos.Kern.) A. Love & D. Love	Centro-Europ.	H bienne
Betonica alopecuros L.	Orof.S-Europ.	H scap
Prunella grandiflora (L.) Scholler	Orof.S-Europ.	H scap
Thymus polytrichus Kerner	Orof. S.Europ.	Ch rept
Euphrasia salisburgensis Funck ex Hoppe	Orof. SE-Europ.	T scap
Bartsia alpina L.	Artico-Alp.	H scap
Linaria alpina (L.) Mill.	Orof.S-Europ	H scap
Pedicularis rostratocapitata Crantz	Orof.S-Europ.	H scap
Veronica serpyllifolia L.	Subcosmop.	H rept
Pinguicula alpina L.	Artico-Alp.	H ros
Imperatoria ostruthium L.	Orof.Europ.	H scap
Lonicera coerulea L.	(Circum) Artico-Alp.	P caesp
Valeriana montana L.	Orof.S-Europ.	H scap
Valeriana saxatilis L.	Alpica (Sub-endem)	H scap
Knautia longifolia (Waldst. & Kit.) W.D.J. Koch	Orof. SE-Europ.	H scap
Scabiosa lucida Vill. subsp. *lucida*	Orof.S-Europ.	T scap
Campanula scheuchzeri Vill.	Orof.S-Europ.	H scap
Phyteuma sieberi Spreng.	Endem. SE-Alpico	H scap
Achillea barrelieri (Ten.) Sch. Bip. subsp. *oxyloba* (DC.) F. Conti & Soldano	Endem.S-Alpica	H scap
Achillea clavennae L.	E-Alpino-Dinarica	H scap
Adenostyles alliariae (Gouan) A. Kern.	Orof.S-Europ.	H scap
Aposeris foetida (*L.*) Less.	Orof.SE-Europ.	H ros
Bellidiastrum michelii Cass.	Orof.SE-Europ.	H ros
Carduus defloratus L.	Endem. Alpico	H scap
Cirsium erisithales (Jacq.) Scop.	Orof.S-Europ.	H scap
Crepis jacquinii Tausch subsp. *kerneri* (Rech.f.) Merxm.	Orof.SE-Europ.	H ros

Doronicum austriacum Jacq.	Orof.S-Europ.	G rhiz
Hieracium alpinum L.	Circum-Artico-Alp.	H ros
Hieracium murorum L.	Euro-Sib.	H scap
Homogyne alpina (L.) Cass.	Orof.Centro-Europ.	H ros
Homogyne discolor (Jacq.) Cass.	Endem.E-Alpica	H ros
Leontodon hispidus L.	Europeo-Caucas.	H ros
Solidago virgaurea (L.) Arcang.	Circumbor.	H scap

Appendice 2. La nomenclatura delle specie elencate segue quella della *Checklist* aggiornata di Bartolucci et al. (2018). **Legenda: Forme biologiche:** Ch rept = Camefite reptanti, Ch succ = Camefite succulente, G bulb = Geofite bublose, G rhiz = Geofite rizomatose, H ros = Emicriptofite rosulate, H ros =Emicriptofite rosulate, H bienne = Emicriptofite bienni, H rept = Emicriptofite reptanti, P caesp = Fanerofite cespugliose, P lian = Fanerofite lianose, P rept = Fanerofite reptanti, P scap = Fanerofite arboree, T scap = Terofite scapose.

Appendice 3: Famiglie rappresentate

Famiglie	***Taxa***
Asteraceae	15
Poaceae	10
Caryophyllaceae	9
Cyperaceae	9
Ericaceae	7
Rosaceae	7
Brassicaceae	5
Salicaceae	5
Orobanchaceae	4
Ranunculaceae	4
Pinaceae	3
Caprifoliaceae	3
Gentianaceae	3
Lamiaceae	3
Saxifragaceae	3
Campanulaceae	2
Dipsacaceae	2
Fabaceae	2
Juncaceae	2
Lycopodiaceae	2
Orchidaceae	2
Apiaceae	1
Aspleniaceae	1
Celastraceae	1
Crassulaceae	1
Cupressaceae	1
Geraniaceae	1
Lentibulariaceae	1
Liliaceae	1
Melanthiaceae	1
Papaveraceae	1
Plantaginaceae	1
Plumbaginaceae	1
Primulaceae	1
Polygonaceae	1
Rubiaceae	1
Selaginellaceae	1
Thymelaeaceae	1
Tofieldiaceae	1
Violaceae	1

Appendice 4: Checklist Ragni Ghiacciai del Sorapiss

Nome specifico	**Corotipo**
Acantholycosa pedestris (Simon, 1876)	Endemico Alpino
Agroeca proxima (O. Pickard-Cambridge, 1871)	S Sibirico-Europeo
Agyneta rurestris (C. L. Koch, 1836)	Paleartico
Alopecosa taeniata (C. L. Koch, 1835)	Sibirico-Europeo
Arctosa alpigena (Doleschall, 1852)	Olartico
Centromerus pabulator (O. Pickard-Cambridge, 1875)	Sibirico-Europeo
Centromerus subalpinus (Lessert, 1907)	Sudeuropeo
Clubiona reclusa (O. Pickard-Cambridge, 1863)	Asiatico-Europeo
Cryphoeca sylvicola (C. L. Koch, 1834)	Paleartico
Cybaeus tetricus (C. L. Koch, 1839)	Centroeuropeo
Diplocephalus helleri (L. Koch, 1869)	Centroeuropeo
Drassodex heeri (Pavesi, 1873)	Endemico Alpino
Gnaphosa petrobia (L. Koch, 1872)	Sud-Europeo
Mughiphantes brunneri (Thaler, 1984)	Endemico Alpi orientali
Oedothorax apicatus (Blackwall, 1850)	Paleartico
Pardosa ferruginea (L. Koch, 1870)	Sibirico-Europeo
Pardosa oreophila (Simon, 1937)	Sud-Europeo
Pardosa sordidata (Thorell, 1875)	Europeo
Robertus arundineti (O. Pickard-Cambridge, 1871)	Paleartico
Robertus truncorum (L. Koch, 1872)	Centro-Europeo
Sittilong longipes (Canestrini, 1873)	Endemico Alpino
Tenuiphantes jacksonoides (van Helsdingen, 1977)	Sud-Europeo
Troglohyphantes fagei (Roewer, 1931)	Endemico Alpino
Walckenaeria capito (Westring, 1861)	Olartico
Walckenaria cfr obtusa (Blackwall, 1836)	Paleartico
Xysticus alpinus (Kulczyński, 1887)	Alpino
Xysticus desidiosus (Simon, 1875)	Sud-Europeo
Zora spinimana (Sundevall, 1833)	Paleartico

Appendice 5: Famiglie rappresentate

Famiglie	***Taxa***
Linyphiidae	10
Lycosidae	6
Cybaeidae	2
Gnaphosidae	2
Theridiidae	2
Thomisidae	2
Salticidae	1
Liocranidae	1
Clubionidae	1
Miturgidae	1

Appendice 6: Checklist Carabidi Ghiacciai del Sorapiss

Nome specifico	**Corotipo**
Abax parallelepipedus (Piller & Mitterpacher, 1783)	Europeo
Amara quenseli (Schönherr, 1806)	Olartico
Carabus alpestris Sturm, 1815	Centro-Europeo
Carabus creutzeri Fabricius, 1801	Centro-Europeo
Cychrus attenuatus (Fabricius, 1792)	Centro-Europeo
Cymindis vaporariorum (Linnaeus, 1758)	Sibirico-Europeo
Harpalus laevipes Zetterstedt, 1828	Sud-Europeo
Laemostenus schreibersi (Küster, 1846)	Sud-Europeo
Leistus nitidus (Duftschmid, 1812)	Centro-Europeo
Nebria germari Heer, 1837	Alpino-Orientale
Oreonebria diaphana (K. & J. Daniel, 1890)	Alpino-Orientale
Pterostichus burmeisteri Heer, 1837	Centro-Europeo
Pterostichus jurinei (Panzer, 1803)	Centro-Europeo
Pterostichus micropterus Péringuey, 1899	Olartico
Pterostichus schaschli (Marseul, 1880)	Alpino-Orientale
Pterostichus unctulatus (Duftschmid, 1812)	Centro-Europeo
Trechus dolomitanus Jeannel, 1931	Alpino-Orientale
Trechus pallidulus Ganglbauer, 1891	Alpino-Orientale
Trichotichnus laevicollis (Duftschmid, 1812)	Alpino

3.7 An empirical melt model of a small Alpine debris-covered glacier: the case study of the Amola Glacier (Italy)

PAPER IN SUBMISSION

Journal: Cold Regions Science and Technology

Title: An empirical melt model of a representative Alpine debris-covered glacier: the case study of the Amola Glacier (Italy)

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Abstract

Debris-covered glaciers are common in many regions of the world, and accurately modelling their melt is of increasing importance for water resources planning, and biological and ecological studies. In this study, we investigate meteorological and thermal conditions and estimate the melt of Amola Glacier (a small debris-covered glacier in the Adamello-Presanella Massif, Italian Alps) using an empirical approach, based on shortwave radiation, surface temperature, debris thickness and thermal resistance. Meteorological conditions are determined from a supraglacial automatic weather station, while the model is calibrated using i) field data acquired during the ablation season 2020, including a network of ablation stakes and thermistors, ii) modelled solar radiation and iii) thermal imagery from Landsat 8 OLI.

The analysis of glacier meteorological conditions shows a high prevalence of cloud-covered (50.60% of daytime observations) and humid conditions, with a high daily thermal range (22.24 °C). Analysis of thermistor data suggests that a linear thermal gradient of the debris layer can be assumed when the model is run at daily resolution. Modelled debris thickness, surface temperatures and melt capture patterns observed on the field, including the decrease in debris thickness and increasing melt with elevation and their variability across the glacier surface; the root mean square error between measured and observed melt is 0.16 m. Improvements to the model would require measuring all energy fluxes on the glacier from a weather station and investigating their spatial distribution on the glacier surface.

1. Introduction

During the current phase of global warming, alpine glaciers are exhibiting two major trends: a general retreat, due to cumulated negative mass balances (Roe et al., 2017; Marzeion et al., 2017) and an increase of debris cover on the ice surface due to an intensification of cryo- and thermo- clastism (Paul et al., 2007, Azzoni et al., 2018).

When this debris cover is consistent and mantles most of the ablation area, the glacier can be considered a debris-covered glacier (Benn and Evans, 2010). When a retreating glacier becomes a debris-covered glacier and the debris reaches a “critical thickness” (*sensu* Mattson et al., 1993), it slows its recession since the debris cover causes a logarithmic reduction of the ablation rate and, consequently, of the frontal variations (Nakawo & Rana, 1999, Belloni & Pelfini, 1995). This allows glaciers to reach lower elevation such as Miage and Belvedere Glaciers (Italian Alps) where the terminus is at an altitude lower than the treeline (Tampucci et al., 2016). However, local areas of high melt also develop at supraglacial ponds and exposed ice cliffs (Stefaniak et al., 2021). Debris-covered glaciers are becoming increasingly frequent in mountain environments of all middle and low latitudes (Benn et al., 2014; Mihalcea et al., 2008a, 2008b; Kirkbride 2010; Soncini et al., 2015; Bocchiola et al., 2018) and several studies analysed the relationship between debris thickness and ice melt rates (Han & alii, 2006; Nicholson & Benn, 2006; Brock & alii, 2010; Reid & Brock, 2010; Shukla & alii, 2010; Bocchiola & alii, 2010; 2015 Lejeune & alii, 2013).

The cryosphere is an important source of freshwater (Huss et al., 2017) that regulates the hydrological cycle of Alpine basins and influences the development of alpine ecosystems (Chesnokova et al. 2020, Huss et al. 2018, Barnett et al, 2005, Beniston et al. 2003). In some mountain ranges such as the Karakoram, large debris-covered glaciers are prevalent, and their meltwater is crucial for industrial and domestic use (Senese et al., 2018a). Moreover, the glacier surface represents a favourable habitat for a large number of species (e.g. from bacteria, Franzetti et al., 2017, to arthropods, Gobbi et al., 2011, Valle et al., 2022, and plants, Caccianiga et al., 2011), and there is evidence that over the past decades a number of threatened high altitude and cold-adapted species have taken refuge on debris-covered glaciers in response to climate change (Valle et al. 2021, Gobbi et al., 2017; Tampucci et al., 2017), highlighting the great ecological and biogeographic importance of this peculiar habitat for high altitude biodiversity. For these reasons, the study of debris-covered glaciers is becoming crucial in order to predict the evolution of the cryosphere and its consequences on the biosphere.

Unlike for debris-free glaciers, modelling melt of buried ice requires more information and assumptions since the presence of debris modulates the melting of the covered ice; while progress has been made towards more accurate models since the first studies of debris covered ice melt (Nakawo & Young, 1981, Nakawo & Rana, 1999), several sources of uncertainty still exist. In fact, accurate knowledge of the properties of the debris layer are necessary in order to better quantify the energy available for melt at the debris-ice interface, including the thickness of the layer, its thermal conductivity and the temperature of the debris at the surface (Gibson et al., 2018). As surface temperature is generally difficult to accurately obtain across spatial and temporal scales, in some studies it is derived numerically from the inversion of the energy balance equation. For example, Nicholson and Benn (2006) applied a modified surface energy balance model to calculate melt beneath a debris layer from daily mean meteorological data; such an approach was further refined by Reid and Brock (2010) and Rounce et al. (2015), among others. These methods require the deployment of an automatic weather station on the glacier surface carrying all the necessary instruments to derive the energy fluxes, which is not always practical or possible on a glacier. Besides, as thermal conductivity is also influenced by the debris porosity (depending on grain size distribution), lithology and humidity (Mattson et al. 1993), extensive field data are required to determine these variables.

Thus, in other studies a simplified approach was proposed based on the computation of the conductive heat flux through the debris layer (Han and others, 2006), where surface temperature is derived empirically. Distributing the debris thickness of the glacier is also complicated and most approaches estimate it through satellite thermal data (e.g. Zhang and others, 2011; Fujita and Sakai, 2014; Minora et al., 2015; Senese et al. 2018a).

In this study, we used the empirical approach (see also Mihalcea et al., 2008a,b; Minora et al., 2015) which requires knowledge of patterns of incoming shortwave radiation, debris thickness, and surface temperature and thermal resistance of the debris layer. Our aims are:

1) To define meteorological and thermal conditions on Amola glacier
2) To model the melt of the debris-covered portions of Amola glacier using an empirical model driven mainly by surface temperature and thermal resistance of the debris layer.
3) To use off-glacier Automatic Weather Stations (AWS) to model incoming shortwave radiation and observe its impact on modelling sub-debris ice melt.
4) To compare debris thickness maps obtained from different satellite images and observe their effect on modelling sub-debris ice melt

2. Study area

The study was performed on the Vedretta d’Amola glacier (Eastern Italian Alps: 46°13'10.1"N 10°41'08.7"E, Fig. 1), a debris-covered glacier (0.68 km^2, Paul et al., 2020) that is located in the Adamello-Presanella Massif within the protected area of the Adamello Natural Park (Baroni et al., 2004). The glacier covers the altitudinal range from approximately 2570 and 3150 m a.s.l. (Paul et al., 2020). Vedretta d’Amola has an Easterly aspect and is surrounded by the Presanella (3557 m a.s.l.) and other peaks constituted by tonalite, a rock of the diorite class characterised by lower thermal conductivity and higher reflectance than most of metamorphic and sedimentary rocks (Bocchiola et al., 2015). Tonalite rocks cover almost the entire glacier ablation area (debris cover: 60%; 2020 satellite data), with a coarse grain size that ranges from a few millimetres to about 1 metre (Gobbi et al., 2017). Average annual precipitation in the area of the Park is about 1000 mm (Bocchiola & Diolaiuti, 2010). Several glaciers are hosted within the Park area, including the widest glacier of Italy, Adamello glacier (Maragno et al., 2009). Previous studies on Amola glacier have focused on the colonisation of supraglacial debris and the glacier foreland by ground-beetles, spiders and springtails (Tenan et al., 2016; Gobbi et al., 2017; Hagvar et al., 2020), on plant-insect interactions on the glacier and along the chronosequence of glacier retreat (Losapio et al., 2015) and a relatively uninterrupted series of terminus variations exists (Gobbi et al., 2017); however, detailed studies on thickness patterns of supraglacial debris and their influence on meltwater production are lacking for this glacier.

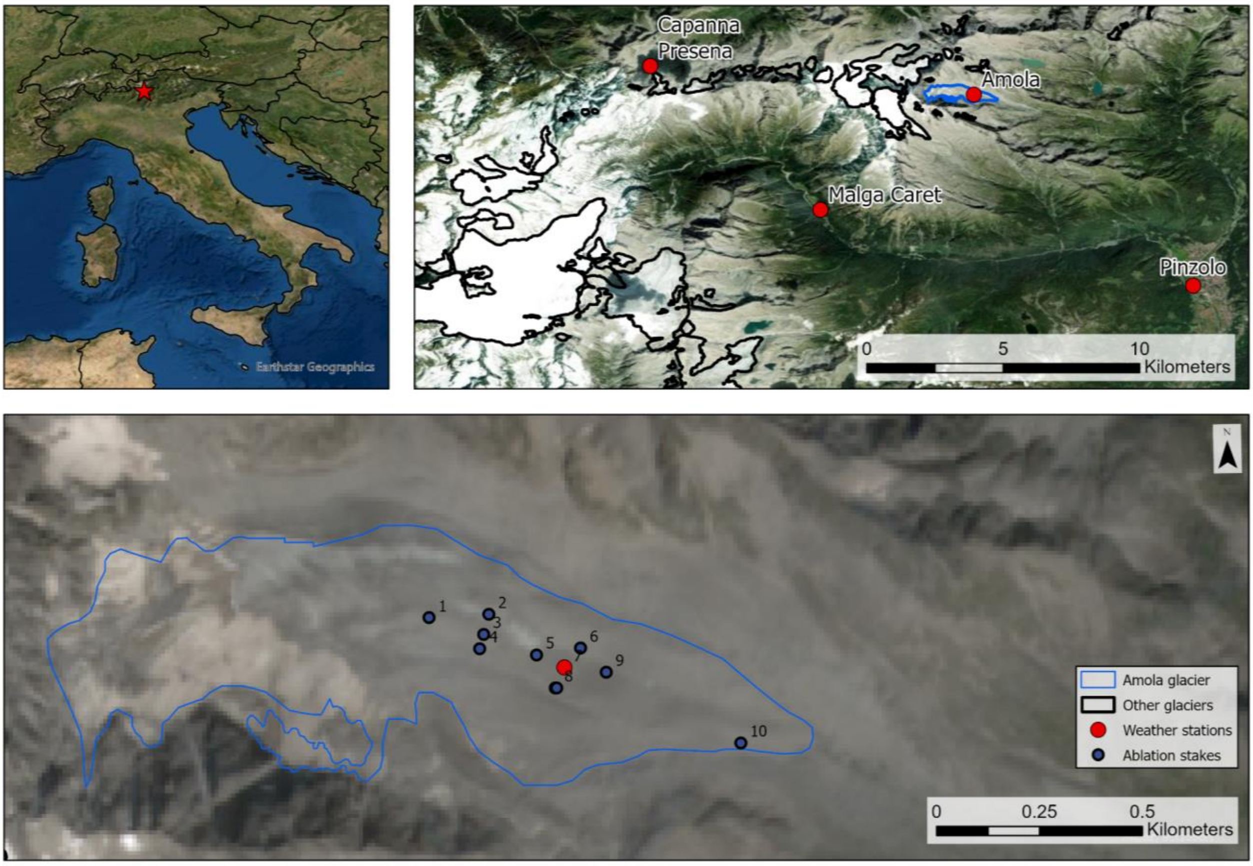

Figure 1*: Location of Amola glacier within Italy and Adamello Massif, with weather stations from MeteoTrentino (top). Zoom-in of Amola glacier with location of ablation stakes and thermistors and the automatic weather station (corresponding to number 7) (bottom).*

3. Data and methods

3.1. The automatic weather station AWS$_{\mathbf{amola}}$ and the observed meteorological data

An automatic weather station (AWS$_{\text{Amola}}$) was installed on 20 July 2020 on the debris-covered surface of the Amola Glacier (coordinates 46° 13’ 09.9’’ N and 10° 41’ 07.2’’ E, at 2689 m a.s.l., position number 7 in Fig. 1 and Fig. 2); it was then removed on 18th August 2020. The station was equipped with a four-component radiometer (CNR4, Kipp&Zonen, with an accuracy of ±5%), a naturally ventilated thermo-hygrometer (HygroVUE10, Campbell Scientific, with an accuracy of ±0.1°C for temperature measurements and ±2% for relative humidity), and a low power data logger (PCTDA041, MTX, with a 4 Gb SD card, 3.6V NiMH batteries and integrated 1 W solar panel); all instruments were mounted on a stainless steel tripod (AL300BA, MTX). Measurements of incoming and outgoing shortwave radiation (SWin and SWout), incoming and outgoing longwave radiation (LWin and LWout), air temperature (T) and relative humidity (RH) were sampled at 60-second intervals and minimum, mean and maximum values were recorded over a 30-minute time period. We used all meteorological data for assessing the micro-meteorological conditions of the glacier, while only SWin was used to quantify buried ice melt.

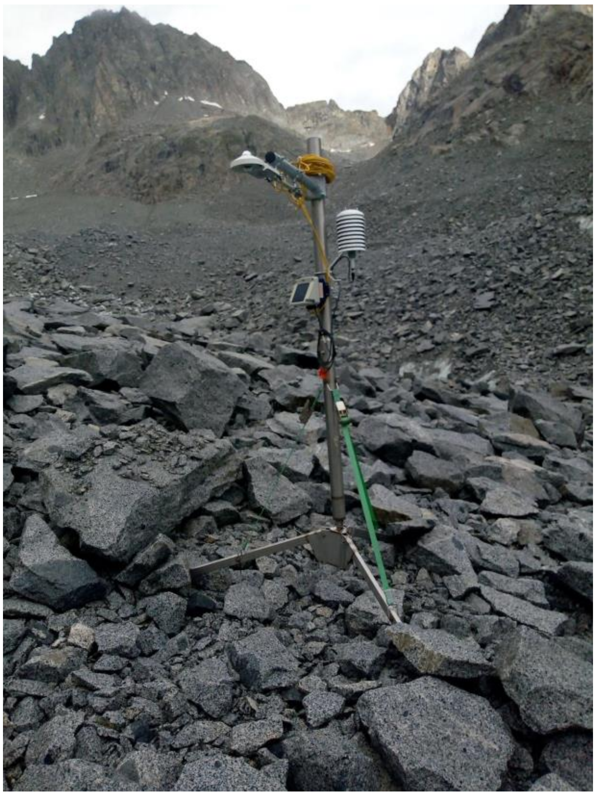

Figure 2: *The weather station on Amola glacier AWS*$_{Amola}$. *Typical clast size of supraglacial debris is also shown.*

The dataset was mostly uninterrupted, with gaps ranging from 27.6% to 31.5% of the total period depending on the parameter. Most of the gaps were due to a gradual night-time depletion of the batteries and therefore they occurred generally in the early hours of the day. During this period, SWin is null and therefore fortunately data gaps can be easily filled by setting SWin to 0 W m^{-2}. For the rest of the day (i.e. outside night-time), we derived missing values of SWin from clear-sky solar radiation (SWin$_{cs}$) and the atmospheric transmissivity depending on the cloud cover (τ) following Senese et al. (2016). Cloud transmissivity ranges between 0 and 1 and it is a factor that reduces the potential SWin of a quantity, which depends on the amount and type of clouds (Zhang et al., 1996). A value of $\tau = 1$ corresponds to a clear sky with no clouds (i.e. SWin = SWin$_{CS}$), whereas $\tau = 0$ means that no shortwave radiation reaches the surface at all. However, an overcast sky usually has $\tau > 0$ (i.e. SWin << SWin$_{CS}$), with different values for different cloud types. Firstly, we estimated SWin$_{cs}$ by means of an envelope of the SWin values measured by AWS$_{Amola}$ permitting to get an indication of the half-hourly maxima (clear sky radiation) corresponding to each half-hour of the day. While this clear-sky incoming solar radiation can in principle be overestimated owing to multiple reflections from snow-covered surrounding slopes, this does not affect our measurements, since we considered a snow-free period of the year (i.e. from 21 July to 18 August 2020).

Subsequently, we used SWin$_{cs}$ for calculating the half-hourly atmospheric transmissivity (Senese et al., 2020):

$$\tau = \frac{SWin_{Amola}}{SWin_{cs}} \tag{1}$$

where $SWin_{Amola}$ is the incoming solar radiation measured by the AWS_{Amola} in real atmospheric conditions. Compared to $SWin_{Amola}$, $SWin_{cs}$ does not take into account the reduction of solar radiation due to actual atmospheric conditions (e.g. clouds). We assumed that the conditions of the sky remain constant over short periods (a few hours). Thus, we calculated the missing SWin values by considering the τ value of the following or previous half-hour and inverting Equation 1. The reflected solar radiation data were filled considering an albedo of 0.18, which is the average of noon observations.

Regarding data gaps of the other meteorological parameters, we chose not to perform gap filling and to consider the actual measured value as these were not used in the ablation model but to define the micro-meteorological conditions.

By means of Stefan-Boltzmann law, we derived surface temperature (T_s) form the emitted longwave radiation (LWout):

$$T_S = \sqrt[4]{\frac{LWout}{\sigma}} \qquad (2)$$

where σ is the Stefan-Boltzmann constant equal to 5.67×10^{-8} W m^{-2} K^{-4}.

3.2. Measurements of ablation, supraglacial debris temperature and thickness

Nine 2 m long ablation stakes made out of bamboo were drilled into the ice with a manual auger to evaluate ice melt under different conditions of debris thickness (according to the method introduced by Kaser et al., 2003). The stakes were placed on a longitudinal transect along the glacier centerline with two transverse intersecting transects (see numbers from 1 to 6 and from 8 to 10 in Fig. 1) and ice melt from 20 July 2020 to 18 August 2020 was measured. Except for stake 9 which was drilled in bare ice, all stakes were installed over a debris-covered surface. Debris thickness (DT) was measured in correspondence of each ablation stake and at the AWS_{Amola} in July; the debris was manually excavated before inserting the stake and care was taken to maintain the same thickness and stratigraphy after drilling. DT was also measured in August, and for some stakes differences were found between July and August observations owing to the movement of the glacier; we therefore calculated the average of the two observations when this occurred.

Additionally, we measured debris surface temperature (T_s), which is a key element in calculating the energy available for melting of debris-covered ice, by means of Gemini Tinytag Plus thermistors (models TGP-4020, TGP-4500, TGP-4520 with a stated accuracy of 0.40°C, 0.50°C, 0.40°C at 20°C, respectively) at the location of the ablation stakes (except for stake 9 that was on bare ice). Each sensor probe was fixed with duct tape under a flat stone (2 cm thick) with a diameter of about 10 cm close to the stake in order to protect it from direct solar radiation, following Brock et al. (2010); the stone was then placed on the debris surface. The data recorded at this depth (2 cm) are normally considered indicative of point surface temperature, and used within several international protocols to study permafrost and frozen ground (see Osterkamp, 2003; Guglielmin, 2006; Guglielmin et al., 2008). Each data logger was programmed to record average measurements every 60 min. At stake 5 (see Fig. 1), the thermistor malfunctioned and it was therefore not possible to retrieve T_s; however, we placed an additional thermistor close to stake 8 (called T8+), and obtained a dataset of 9 T_s records.

3.3. Incoming solar radiation model

To distribute the incoming solar radiation (SWin) over the Amola Glacier surface, we applied the algorithms tested over another Italian glacier, Forni Glacier, by Senese et al. (2016). The CNR4 net radiometer installed at the AWS_{Amola} is of the same type as that running at the AWS of the Forni Glacier (Senese et al., 2018b), therefore providing homogeneity of the two datasets and then the applicability of the same model. For each grid cell we modelled SWin considering astronomical and geographical factors:

$$SW_{0-point} = I_0 \cdot E_0 \cdot k \cdot [(\sin\sin\delta \cdot \sin\sin\Phi \cdot \cos\cos S) \cdot (w_{ss} - w_{sr}) - (\sin\sin\delta \cdot \cos\cos\Phi \cdot \cos\cos S \cdot \cos\cos A) \cdot (w_{ss} - w_{sr}) + (\cos\cos\delta \cdot \cos\cos\Phi \cdot \cos\cos S) \cdot (\sin\sin w_{ss} - \sin\sin w_{sr}) + (\cos\cos\delta \cdot \sin\sin\Phi \cdot \sin\sin S \cdot \cos\cos A) \cdot (\sin\sin w_{ss} - \sin\sin w_{sr}) - (\cos\cos\delta \cdot \sin\sin A \cdot \sin\sin S) \cdot (\cos\cos w_{ss} - \cos\cos w_{sr})] \tag{3}$$

where I_0 is the average solar irradiance at the mean Earth-Sun distance (equal to 1367 W m^{-2}), E_0 is the eccentricity factor, k is a factor to express SWin in the correct measure unit, δ is the solar declination, Φ is the latitude, S is the slope, w_{sr} and w_{ss} are the sunrise and sunset hour angles, respectively, and A is the aspect. Moreover, we estimated shading due to surrounding orography and the atmospheric absorption taking into account actual meteorological conditions.

Senese et al. (2016) validated the approach by comparing the modelled SWin against the one measured at 18 sites along the glacier tongue, during summer 2011 and 2012. The modelled values agreed well with observations with a correlation coefficient of 0.97 and a root mean square error of 0.095 MJ m^{-2}.

For the last step regarding the atmospheric absorption, we tested the performance of the model comparing SWin values measured by AWS_{Amola} ($SWin_{Amola}$) with the ones obtained using data acquired by different automatic weather stations off-glacier from 21 July 2020 to 18 August 2020. Firstly, we used half-hourly data from the stations located at Malga Caret (Val Genova, 46.1814° N, 10.6348° E, 1418 m a.s.l., data from 06-10-2011, $SWin_{Caret}$), Pinzolo (46.1565° N, 10.7575° E, 760 m a.s.l., data from 01-01-1921, $SWin_{Pinzolo}$) and Cima Presena (46.2200° N, 10.5835° E, 3015 m a.s.l., data from 14-12-1994, $SWin_{Presena}$). These stations were chosen since they are the closest to the Amola Glacier at a distance of 5.9 km, 9 km and 8.3 km, respectively (Fig. 1). Data can be freely downloaded from the website of Meteotrentino (https://www.meteotrentino.it/#!/content?menuItemDesktop=111).

3.4. Debris thickness model

Previous studies have observed good correlations between temperature observed from satellites and thickness of supraglacial debris. Mihalcea et al. (2008a) used different linear relationships to estimate DT from satellite T_s by dividing the surface of Miage glacier (Italy) into elevation bands; conversely, on Baltoro glacier a single exponential relationship was found as the best fit by Mihalcea et al. (2008b) and by Minora et al. (2015). We calculated surface temperature using a Landsat 8 TIRS image from 28 July 2020; compared to previous sensors of the Landsat family and ASTER used in other studies

(Mihalcea et al., 2008a,b; Minora et al., 2015), the sensor has two thermal bands centred at 10.90 μm and 12 μm and therefore it is possible to derive T_s using a split-window approach (Rozenstein et al., 2014), which corrects for atmospheric absorption by water vapour by taking into account the different absorption features of the two thermal bands. We used SPT, a QGIS plugin, to perform the extraction. The relationship between Landsat derived T_s and DT was then estimated using all available DT observations at the ablation stake sites, except for DT observed at AWS_{Amola} which was used for validation. Given the small elevation range of Amola glacier, we preferred to use a single relationship and not divide the glacier into elevation bands. An exponential relationship was found as the best fit (equation 4), with an R^2 of 0.65:

$$DT = 0.221e^{0.297T_s} \tag{4}$$

3.5. Debris surface temperature model

As we could not estimate T_s from the inversion of the energy balance equation, we derived it by empirical correlation with SWin and DT. The relationship between these variables was demonstrated before on debris-covered areas (e.g. Mihalcea et al., 2008b): higher radiation fluxes and thicker debris lead to higher surface temperatures. First, we used T_s from thermistors, modelled SWin and DT measured at the 8 sites for the entire period of measurements (from 21 July 2020 to 18 August 2020) to establish a linear regression, with an R^2 of 0.47 (see eq. 5):

$$T_s = 0.079\, DT + 0.038\, SWin \tag{5}$$

This equation was then applied to estimate daily T_s across the glacier surface by using daily modelled SWin (see section 3.3) and DT (see section 3.4).

3.6. Debris-covered ice melt model

According to Minora et al. (2015), the amount of ice melt under a debris cover (M, m of surface lowering) depends on the energy available at the debris–ice interface that can be estimated assuming a linear temperature gradient from the top of the debris layer (T_S) to the ice surface (T_i) for mean daily conditions (e.g. Nakawo and Young, 1981):

$$M = \frac{(T_S - T_i)\cdot \Delta t}{DR \cdot \rho_i \cdot L_m} \tag{6}$$

where Δt is the time step, ρ_i is the ice density, DR is the effective thermal resistance of the debris layer (m^2 °C W^{-1}) and Lm is the latent heat of melting (3.34×10^5 J kg^{-1}). We set the ice surface temperature to the melting point, 0°C, neglecting refreezing phenomena, which generally do not occur during the main ablation season (Minora et al., 2015). An ice density of 917 kg m^{-3} was used (Senese et al., 2018b). The assumption of a linear temperature gradient along the debris cover is given by the fact that if the physical properties in the debris layer are constant with depth, the heat flux depends linearly on the surface temperature for steady-state conditions. The thermal resistance can be assumed constant over an ablation season as it mainly depends on debris thickness, which is generally considered stable over short periods (1–2 months; Fyffe et al., 2014). To derive DR for each grid cell, an empirical relationship was applied based on DT (Minora et al., 2015) measured at the ablation stakes, with a R^2 of 0.67:

$$DR = 0.0056\, DT + 0.0341 \tag{7}$$

To restrict the melt model to the debris covered portions, a normalised difference snow index (NDSI) mask was computed from Landsat 8 OLI bands, using a threshold of 0.3 to separate ice/snow from the debris covered parts (Gjermundsen et al., 2011).

4. Results

4.1. Meteorological conditions

The data collected by the $\text{AWS}_{\text{Amola}}$ are summarized in Figure 3. Half-hourly average values of air temperature and relative humidity, incoming and reflected solar radiation, clear-sky solar radiation, and incoming and outgoing infrared radiation are shown. The figure highlights the prevalence of data gaps during night-time as reported in section 3.1.

Air temperature ranges from +1.76°C (recorded on 4 August at 12 PM) to +16.92°C (recorded on 28 July at 1 PM) with a half-hourly mean value of +9.24°C. Generally, minima occur during nighttime or just before dawn. The minimum value recorded by the $\text{AWS}_{\text{Amola}}$ at 12 pm is due to very cold conditions that occurred during that day (Fig. 3a). The mean daily range is 5.66°C, ranging from 2.00°C (recorded on 16 August) to 10.39°C (recorded on 28 July). Therefore, the warmest conditions and the widest amplitude occurred on 28th July. Most of the time (77.60%), half-hourly mean temperatures between +6°C and +12°C prevail: 6-8°C for 23.13%, 8-10°C for 31.65% and 10-12°C for 22.82% of the considered period.

The half-hourly air relative humidity ranges between 99.5% (recorded on 27 July at 8 PM) and 29.32% (recorded on 28 July at 12:30 PMand 1 PM) with an average of 78.02% (Fig. 3b). Humid conditions prevail; in fact, there is only one half-hour with relative humidity lower than 40%. Moreover, 76.66% of time relative humidity is higher than 70% and 50.26% of time >80%.

As regards solar radiation (Fig. 3c), most of the considered period is found to be very cloudy since the clear sky index is lower than 0.40 for 50.60% of daytime observations (see Anslow et al., 2008). This high cloudiness can explain the data gaps, as the low wattage solar panel could not supply enough energy to the batteries during the day. Albedo is almost stable with a half-hourly mean value of 0.17. The maximum is equal to 0.30 even if only 6.65% of half-hourly values are higher than 0.25; these high values are due to the normal daily cycle of albedo and values at early morning or late afternoon are not completely representative of the actual surface conditions (Azzoni et al., 2016). Considering daily values, the albedo ranges from 0.12 to 0.21 with a mean value of 0.18. Lower albedo values can be probably caused by rainy conditions or meltwater rising to the surface by capillarity, since a wet surface reflects less than a dry one (Hartmann, 1994).

The outgoing longwave radiation (Fig. 3d) and debris surface temperature (calculated applying Eq. 2, Fig. 3e) follow the daily thermal cycle of the air: higher values during daytime (maximum of 436.78 W m^{-2} corresponding to +23.11°C recorded on 28 July at 1 PM) and lower ones during nighttime (minimum of 312.70 W m^{-2} corresponding to -0.64°C recorded on 6 August at 5:30 AM). Despite an always positive air temperature, the debris surface also reaches negative values even if this only occurs 1.05% of the time. The mean surface temperature is 8.73°C. On a daily scale, only 2 days (25 July and 6 August) are characterised by freeze-thaw conditions (i.e. min<0°C and max>0°C, Guglielmin et al., 2008). As regards thermal stress, the mean daily range is 13.42°C and the maximum is 22.24°C (on 28 July). These results suggest that supraglacial debris is more affected by thermoclastism and less by cryoclastism during the analysed period.

Moreover, from our findings, days with warmer air conditions occur with higher SWin fluxes (and higher τ) that heat the debris surface (i.e. higher T_s) which in turn emits more LWout that considerably affects air conditions with higher values of LWin.

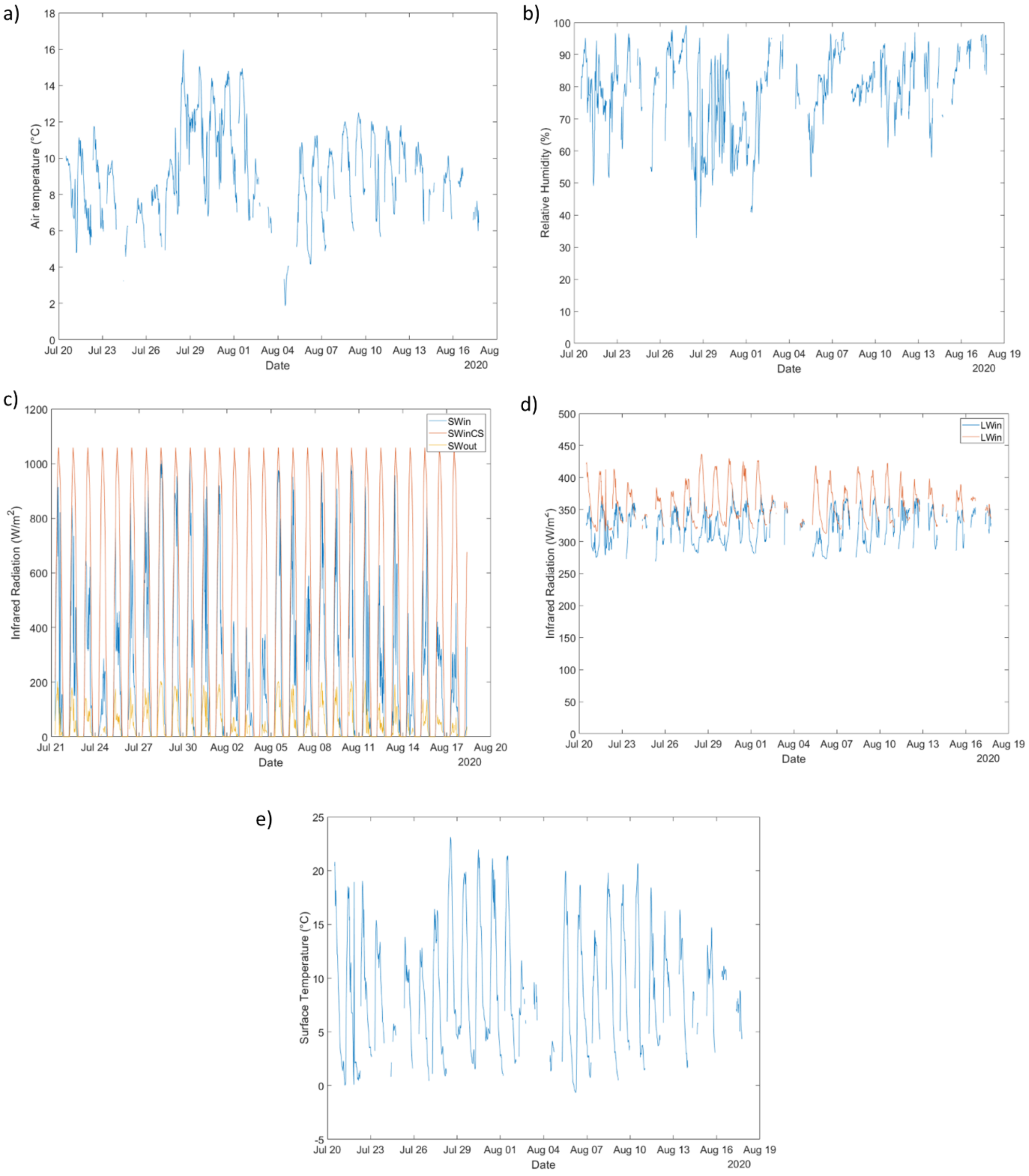

***Figure 3**. Half-hourly average values of air temperature (A), relative humidity (B), incoming and reflected solar radiation (C), clear-sky solar radiation (C), incoming and emitted infrared radiation (D), and surface temperature calculated from LWout (E) are shown.*

4.2 Observed debris thickness and surface/subsurface temperatures

Debris thickness measured on the field from the average of July and August observations ranged between 5 cm (at stake T3) and 32 cm (at T8+); at most (7) sites however the thickness of the debris layer was lower than 10 cm, and higher values were observed only at the terminus and other sites were local conditions favoured accumulation (e.g. at the base of lateral moraines).

Temperatures measured at the thermistor sites were rather homogeneous: for all thermistors except T8, the minimum temperature was recorded on the morning of 5 August, between 5 and 7 AM; the absolute minimum was -1.44 °C (T3, 5 AM on 5 August). Daily maxima were recorded on 28 July at 3 PM for T2, T4, T6, T8, T10 and T8+, and the absolute maximum was +42.06°C (T8+). Hourly Ts patterns are highly correlated, with R ranging between 0.77 (T3 and T10) and 0.99 (T2 and T6) (figure not shown). Averaging Ts from thermistors to daily means, the minimum Ts was recorded on 4 August and the maximum on 28 July. The correlation between the daily Ts from thermistors is even higher than for hourly values, ranging between 0.84 (T6 and T8) and 0.99 (T3 and T6), see Figure 4.

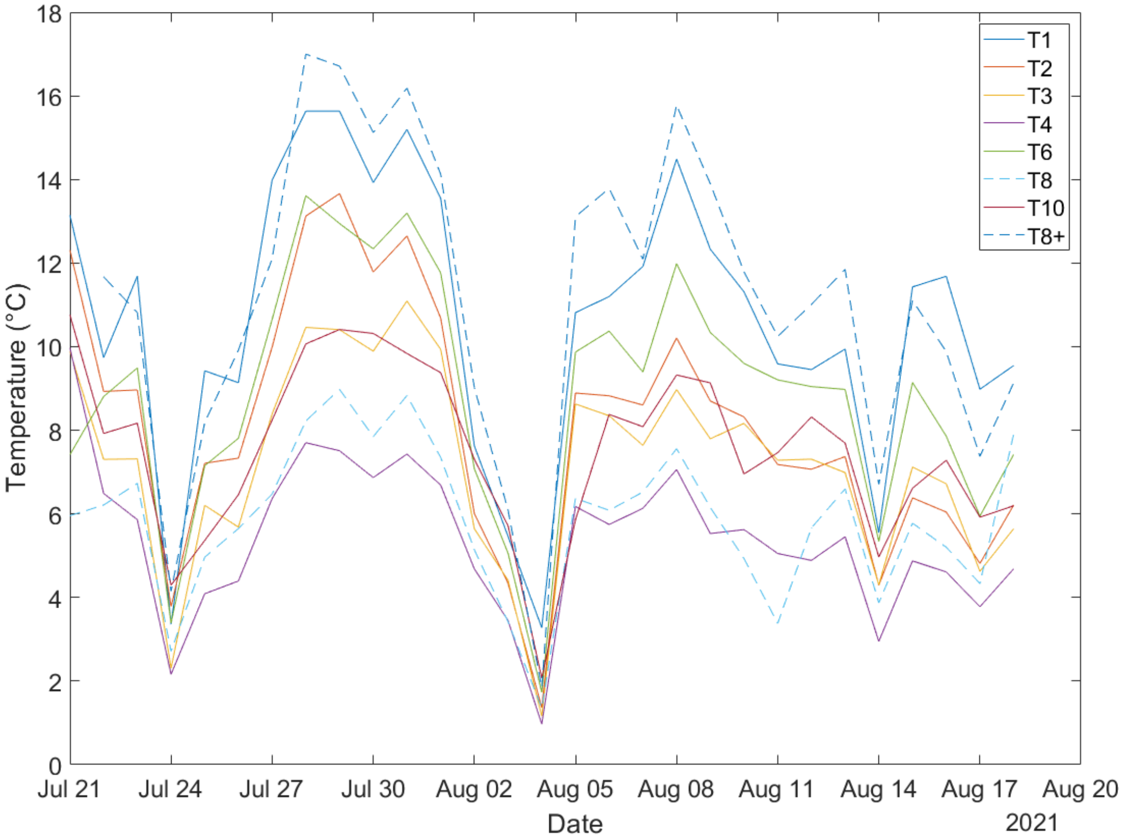

Figure 4: *Average daily debris surface temperature from thermistors located on Amola glacier.*

Considering debris T at different depths from thermistors T8+ and T10, hourly temperatures show the dampening of daily temperature cycles with increasing depth, as the amplitude of the daily temperature range is reduced. At thermistor T8+, the average daily range is 6.29°C at 1 cm thickness (close to the debris-ice interface) vs 24.81°C at 32 cm thickness, while at thermistor T10, it is 4.30°C at 10 cm thickness and 9.66°C at 30 cm thickness. A lag of 1-2 hours between T peaks and lows at different depths is also observed at both sites (see Figure 5). While the behaviour of hourly debris temperatures is non-linear, the opposite is true for daily temperatures, especially at thermistor T10 (see Figure 5). Considering a linear regression between temperature and depth, 15 out of 29 observations have a $R^2 > 0.85$ at T8+, while at T10 all observations have a $R^2 > 0.99$. This suggests that the assumption of a linear temperature gradient with debris depth when using a daily time step in computing sub-debris ice melt is reasonable.

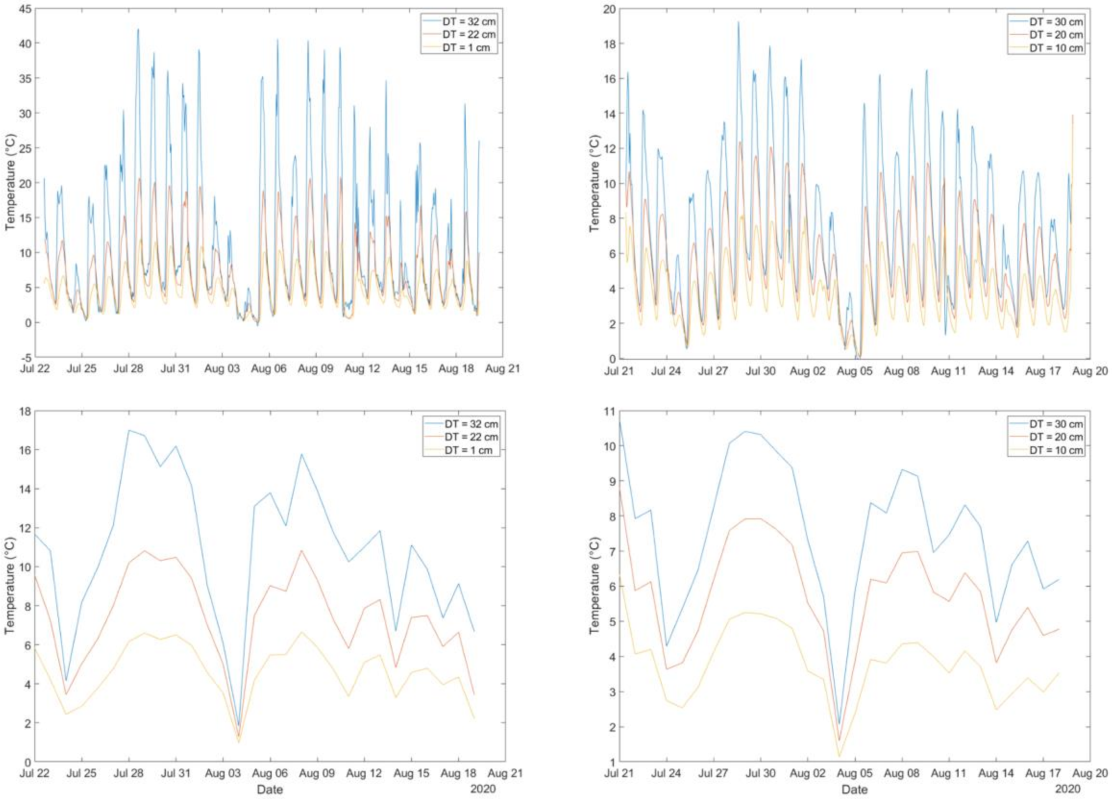

Figure 5: *Average hourly debris temperatures at different depths from thermistors T8+ and T10 (top left and right, respectively); daily debris temperature at different depths from T8 and T10+ (bottom left and right, respectively).*

4.3 Modelled debris thickness, surface temperature and buried ice melt

From the NDSI mask, we calculated a debris-covered area of 0.40 km^2, corresponding to 59% of the Amola glacier surface. Debris is found up to 2760 m a.s.l., except for isolated patches at higher elevations which might include dirty ice, with a temperature close to 0°C (see Figure 7a). The rest of the glacier surface is covered by snow at the time of satellite data acquisition (28 July 2020). The average debris thickness is 8.38 cm, with a maximum of 24.68 cm, which in general slightly underestimates ground observations. Higher DT is observed close to the terminus and the left flank of the glacier, and there is a general tendency towards decreasing DT with elevation (R^2 = 0.52). Two patches with lower DT are observed in the middle of the debris-covered part, likely because the lateral rock walls are the main source of debris. Ground observations confirm the presence of patchy debris cover in these areas. At the AWS_{Amola}, (number 7 in Fig. 1) a DT of 8.38 cm was calculated based on Landsat 8 TIRS, compared to an observed value of 5.5 cm.

Cumulated T_s follows the main pattern of debris cover, with a few differences (see Figure 7b): a longitudinal band of lower T_s along ice flow is observed at the terminus towards the hydrographic left part of the glacier, while on the hydrographic right flank higher T_s occurs. This might be caused by the influence of solar radiation, as in those areas the topographic characteristics (slope and aspect) cause a different radiative input. The correlation between daily modelled T_s and observed T_s at thermistor T7, by the AWS_{Amola}, is 0.80.

As regards glacier melt, the total cumulated amount is 295 m^3; the average total daily melt is 10.2 m^3 day^{-1} on the debris-covered part of the glacier or 3 cm day^{-1} for each glacier cell. The highest total melt of more than 1.5 m between 21 July and 18 August 2020 is observed at the upper reaches of debris cover (approximately 2760 m a.s.l.) while about 1 m is seen in the lower central portion of the tongue, owing to the combined effect of low DT and higher cumulated temperatures (see Fig. 7c). Comparing modelled melt with observed melt at the stakes between 21 July 2020 and 18 August 2020, the maximum difference is found for stake 1, where modelled melt is 0.36 m higher than measured melt, while the minimum difference is 0.01 m for stake 10 and stake 7, where AWS_{Amola} was located. Overall, the RMSE is 0.16 m, the bias is +0.03 m (modelled - measured) and the mean absolute error is 0.12 m, with a correlation coefficient of 0.50.

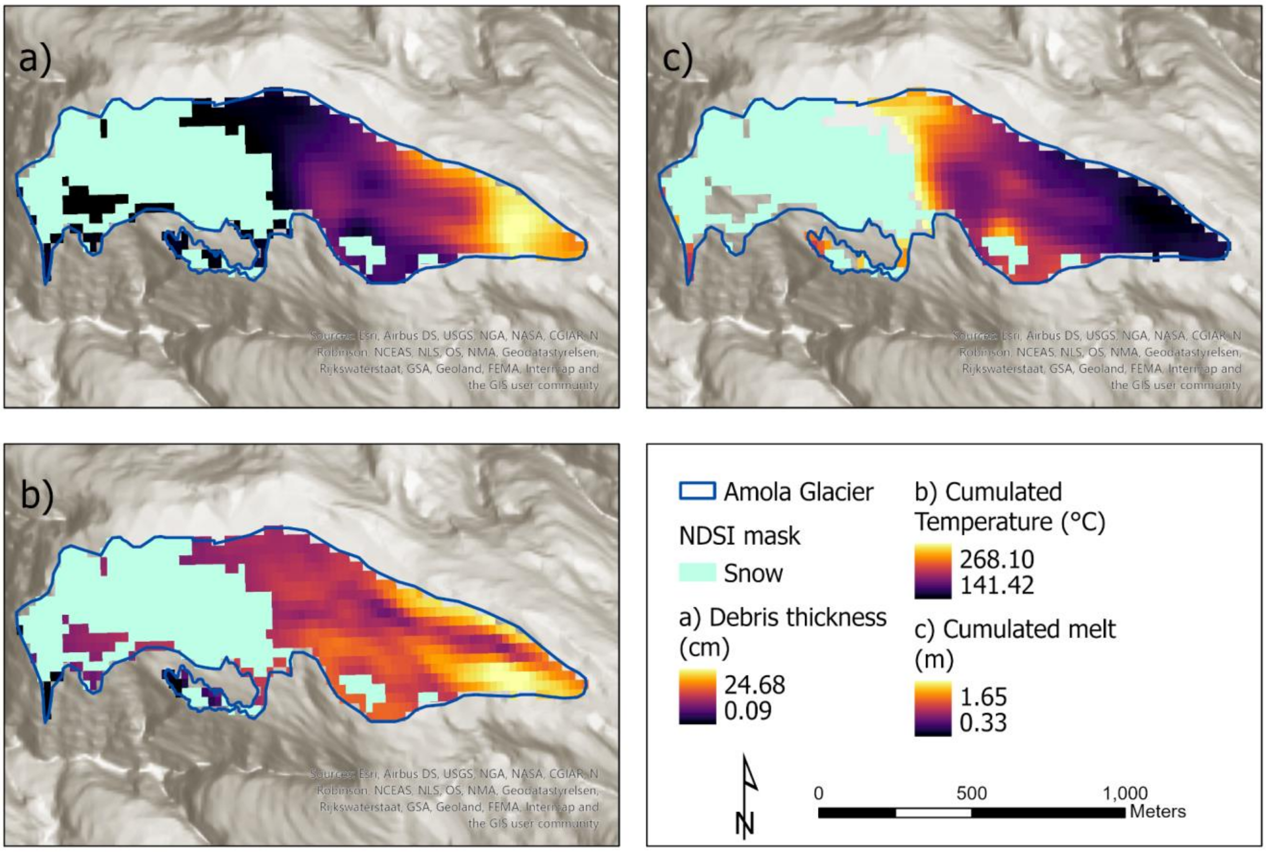

***Figure 6**: a) Debris thickness distribution obtained from Landsat 8 TIRS acquired on 28 July 2020; b) Cumulated temperature from 21 July to 18 August 2020 from equation 5; c) Cumulated melt between 21 July and 18 August 2020.*

5. Discussion

5.1 Using off- glacier weather stations to distribute incoming solar radiation

From the comparison between $SWin_{Amola}$ and the modelled values $SWin_{Caret}$, $SWin_{Pinzolo}$ and $SWin_{Presena}$ (Fig. 7), we found errors ranging from 153.46 W m^{-2} (84% of the half-hourly mean $SWin_{Amola}$) to 176.14 W m^{-2} (96% of the half-hourly mean $SWin_{Amola}$) (Tab. 1). The modelled values are generally underestimated if compared to the measured ones. This can be due to cloudy conditions prevailing at the three off-glacier AWSs, which reduce the radiative input. Moreover, the multireflection from the snow-covered surfaces surrounding the glacier could increase $SWin_{Amola}$ values. Another factor can be an incorrect shading estimation. In fact, in order to find the highest obstructing peak along the grid-point-to-the-Sun direction for each half-hour of the day, we set a grid step of 30 m. Probably choosing a lower grid step would produce a more reliable model.

Slightly better results were observed considering a daily time resolution: error from 30.92 W m^{-2} (17% of the daily mean $SWin_{Amola}$) to 68.13 W m^{-2} (38% of the daily mean $SWin_{Amola}$) (Tab. 1). These results suggest an extreme variability in hourly meteorological conditions among the sites and that no station is able to represent the same atmospheric absorption occurring over the Amola Glacier. Therefore, we decided to consider the SWin measured directly by the AWS_{Amola} in order to model the SWin distributed over the whole glacier surface. This assumption was applied by Senese et al. (2016) as well.

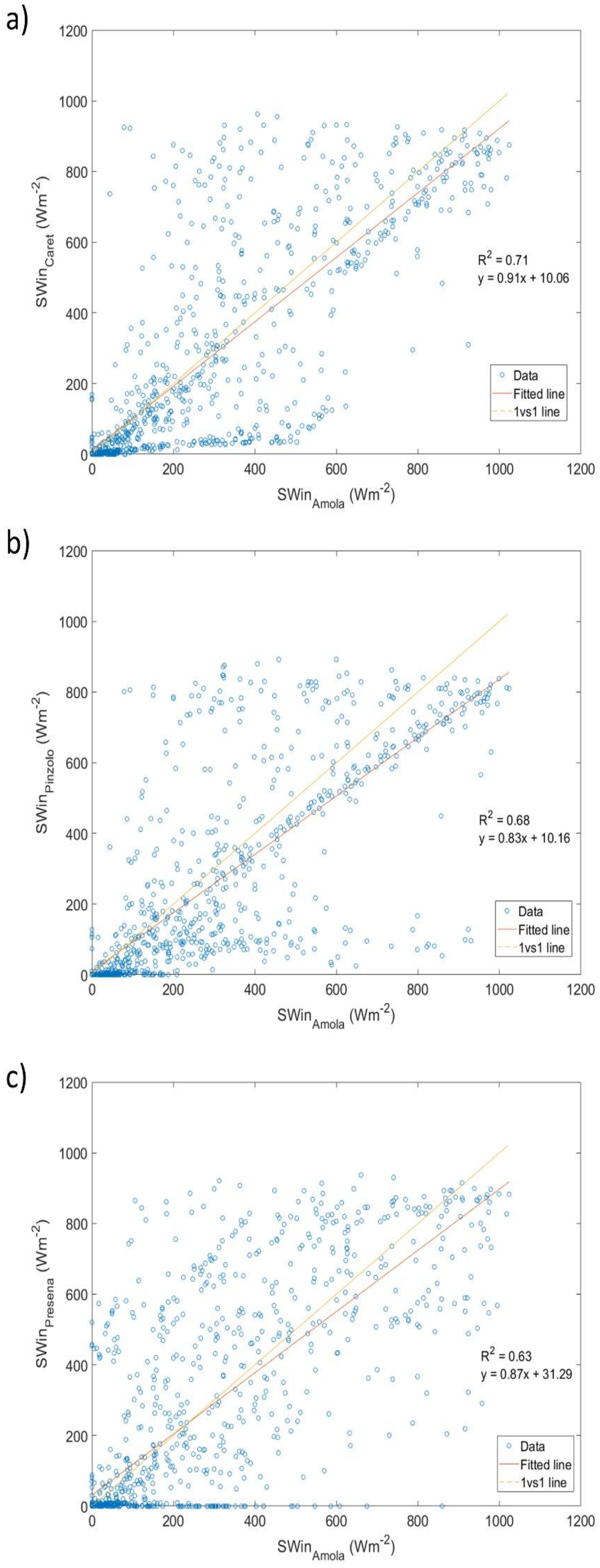

Figure 7*: Comparison between the incoming solar radiation measured by AWS$_{Amola}$ (SWin$_{Amola}$) and the modelled values using data acquired by the automatic weather stations at A) Malga Caret (SWin$_{Caret}$), B) Pinzolo (SWin$_{Pinzolo}$) and C) Cima Presena (SWin$_{Presena}$). Data are half-hourly averages from 21 July to 18 August 2020.*

	Half-hourly	Daily

	RMSE (W m^{-2})	%	r	Measured-Modelled >30 W m^{-2}	Measured-Modelled <-30 W m^{-2}	RMSE (W m^{-2})	%	r
SWin$_{\mathrm{Caret}}$	153.46	84%	0.84	27%	15%	30.92	17%	0.92
SWin$_{\mathrm{Pinzolo}}$	156.02	85%	0.83	34%	12%	43.29	24%	0.87
SWin$_{\mathrm{Presena}}$	176.14	96%	0.80	25%	20%	68.13	38%	0.77

***Table 1**: Comparison between the incoming solar radiation measured by AWS$_{amola}$ and the modelled values using data acquired by the automatic weather stations at Malga Caret (SWin$_{Caret}$), Pinzolo (SWin$_{Pinzolo}$) and Cima Presena (SWin$_{Presena}$).*

Although none of the three stations is able to accurately represent SWin$_{\mathrm{Amola}}$, it is still possible to estimate T_s using daily SWin from the off-glacier stations and the empirical formula in equation (5); we therefore calculated T_s and subsequently buried ice ablation from modelled daily SWin$_{\mathrm{Caret}}$, SWin$_{\mathrm{Pinzolo}}$ and SWin$_{\mathrm{Presena}}$**.** Similar melt amounts were found compared to SWin$_{\mathrm{Amola}}$; In fact, using SWin from AWS$_{\mathrm{Presena}}$ actually results in a slightly lower RMSE (0.15 m compared to 0.16 m for AWS$_{\mathrm{Amola}}$) if compared with observed melt at the stakes between 21 July and 18 August 2020, whereas a worse RMSE was found for the other stations, with the worst results for Caret (see Table 2). However, all off-glacier AWSs show a similar or worse MAE and a worse bias, with the worst result again obtained for Caret station (0.07 m).

Off-glacier AWS	**MAE (m)**	**MBE (m)**	**RMSE (m)**
Caret	0.12	0.07	0.18
Pinzolo	0.12	0.05	0.17
Cima Presena	0.14	-0.05	0.15

Table 2: Comparison between melt modelled using off-glacier SWin from three Automatic Weather Stations (AWS) and the observed melt at the stakes between 21 July and 18 August 2020. Statistics include the Mean Absolute Error (MAE), Mean Bias Error (MBE) and Root Mean Square Error (RMSE).

5.2 Modelling debris thickness from different satellite images

We checked the consistency of the DT - T_s relationship by using a Landsat 8 TIRS image outside of the observation period of AWS Amola. The image was acquired on 20 September 2020 and processed in the same way as the one from 28 July. The relationship between Landsat-derived T_s and DT was estimated with an exponential fit, with an R^2 of 0.63, slightly lower than using the image from 28 July (0.65). Landsat-derived T_s was generally lower on that day on the glacier at the time of image acquisition, with an average of 5.43°C compared to 7.27°C, compared to the image from 28 July. However, the relationship predicts larger DT, with a maximum of 70 cm and an average of 10.64 cm, compared to 24.68 cm and 8.38 cm, respectively. At $\text{AWS}_{\text{Amola}}$, the calculated DT in this case is 6.6 cm, compared to a measured value of 5.5 cm.

When using DT modelled from the Landsat 8 TIRS image acquired on 20 September, very small differences can be observed in modelled melt compared to the image from 28 July. All the statistics considered are the same, with a RMSE of 0.16, a MAE of 0.12 and bias of -0.03. This suggests that debris cover at the site is relatively stable and that using thermal images acquired up to one month outside of the field season does not produce further uncertainty when modelling sub-debris melt.

5.3 Model uncertainties and possible improvements

The comparison between the empirical melt model and measurements from ablation stakes highlighted some discrepancies between modelled and measured melt; several sources of uncertainty contribute to this result. Among them, the spatial scale has probably a large influence, owing to the small size of Amola glacier (0.68 km^2) and the spatial resolution of modelled incoming shortwave radiation (30 m) and thermal data (100 m from Landsat 8 OLI, interpolated to 30 m), which might not accurately represent local conditions. While modelling shortwave radiation at a higher spatial scale is complicated by the availability of high resolution digital elevation models and the high computing requirements necessary to calculate shading, higher resolution thermal data compared to Landsat 8 OLI might be acquired from UAVs, as done by Kraaijenbrink et al. (2017) or a thermal camera in a fixed position, as in the study of Tarca and Guglielmin (2022).

Beside modelled quantities, other sources of uncertainty are related to the measured data as well. Specifically, data gaps occurred in the meteorological record from $\text{AWS}_{\text{Amola}}$, and gap-filling of SWin was necessary to estimate daily T_s and melt. Measured ablation and debris thickness are also affected by uncertainties often difficult to quantify. In addition, they are point measurements and might not accurately estimate mass loss in an area of 30 m as used in the model, as differences of several tens of centimetres can easily develop during the ablation season between point measurements and nearby areas (Müller and Keeler, 1969). The same issue also affects temperature as measured from thermistor probes, which besides their inherent accuracy can undergo malfunctioning, as occurred in our case for the thermistor T5. To evaluate the potential of determining thermistor temperatures in case of malfunctioning, we compared T_s at the $\text{AWS}_{\text{Amola}}$ against temperatures derived from LWout and observed a high correlation coefficient (0.85). The relationship between the two variables is rather good for lower (< 10°C) and nighttime temperatures but the spread increases for higher ones, and temperature from LWout is overestimated compared to the one measured by the thermistor (see Figure 8), which was placed under a rock. A similar result was observed by Brock et al. (2010) for thermistors placed at 2-3 cm depth, and is probably related to the steep thermal gradients in the first few cm of debris (see also Figure 5). In addition, since the net radiometer is installed at a height of about 2 m, we can assume a contribution from the warm air layer between the surface and the sensor with a consequently overestimated measured LWout (Senese et al., 2012).

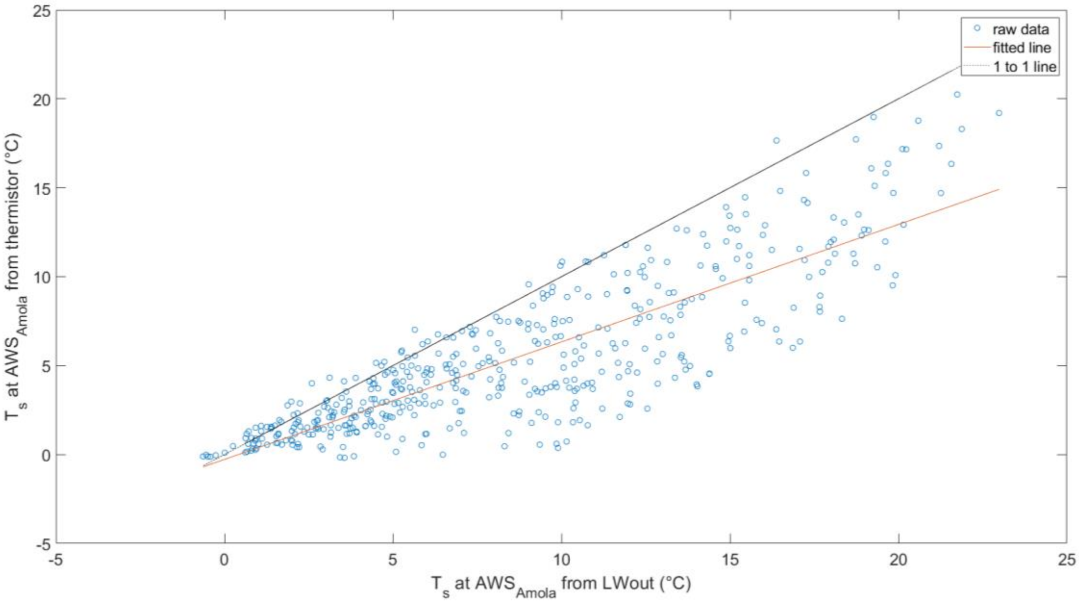

Figure 8: Comparison between T_s modelled from LWout and measured by the thermistor at AWS_{Amola} between 21 July 2020 and 18 August 2020.

In our model, we assumed a linear gradient of debris temperature with depth, and demonstrated that the assumption holds true for the daily scale (see Figure 5), but it is not verified for sub-daily time periods. This is in agreement with Nicholson and Benn (2006; 2013), who demonstrated this behaviour for debris of different lithology and grain size. To compute melt at an hourly scale, a different approach would therefore be needed. Most studies have done so by solving the energy balance at the debris surface using satellite surface temperature to derive DT, with meteorological data from an AWS as input (Foster et al., 2012; Rounce and McKinney, 2014). This approach however relies on the calculation of all energy fluxes at the surface and debris-ice interface including turbulent fluxes, which require a wind and pressure sensor not deployed on AWS_{Amola}, as well as the extrapolation of these fluxes from the AWS to the entire glacier surface, with uncertainties related to the distribution of air temperature as well as the estimation of surface roughness (Foster et al., 2012). However, the method might have the potential to be employed without field- and time-dependent calibration, used in the empirical approach, if meteorological parameters are acquired from reanalysis products (Schauwecker et al., 2015). Other approaches which are first calibrated using the glacier energy balance include a debris-enhanced T-Index model developed by Carenzo et al. (2016), which is based on the calculation of cumulated air temperature and shortwave radiation, and requires empirical coefficients for both as well as lag coefficients accounting for the delaying effect introduced by debris. Such a model might also be tested on AWS_{Amola}, although spatially distributing melt would also require the extrapolation of air temperature on the glacier surface.

Recent studies have adopted another methodology to derive debris thickness, by fitting the Østrem curve (relating debris thickness and melt) to sub-debris ice melt in energy balance simulations for varying debris thickness and then using it to estimate spatially distributed debris thickness from distributed melt. The latter is obtained from geodetic mass balance (Ragettli et al., 2015), potentially corrected for the ice flux divergence (Rounce et al., 2018). The advantage of this approach is that it does not require thermal data, which is limited by the coarse resolution of satellite sensors (100 m interpolated for Landsat 8/9 OLI and 90 m for ASTER TIRS) or the difficulties in undertaking and processing data from thermal surveys from UAVs or field-based cameras. Therefore, it has great potential to produce accurate estimates of debris thickness. Nevertheless, local calibration of the Østrem curve for the conditions at Amola glacier would be required, as well as a geodetic mass balance, ideally from high-resolution DEMs.

Finally, a global map of glacier debris thickness estimated using a sub-debris melt-inversion and temperature-inversion approach is available from Rounce et al. (2021); the maximum debris thickness modelled for Amola glacier is 16 cm, which clearly underestimates ground observations, and does not capture the patterns observed in Fig. 6 with our empirical approach; however, the approach uses calibration coefficients for the melt- and temperature-inversion from other nearby glaciers which might not be appropriate for Amola glacier.

6. Conclusions

In this study, we used an empirical model to estimate the melt of a small debris-covered glacier of the Italian Alps, Amola glacier, over the course of a month during the ablation season 2020. The model is based on incoming shortwave radiation, surface temperature, thickness and thermal resistance of the debris layer, assuming a linear temperature gradient within the debris mantle. Incoming shortwave radiation was obtained by estimating exoatmospheric radiation from a modelling approach and correcting it for local cloud conditions using observations from an automatic weather station; surface temperature was derived assuming a linear relationship with shortwave radiation and debris thickness; the latter was spatially extrapolated using satellite temperatures from Landsat 8 OLI while thermal resistance was calculated through a network of ablation stakes.

The model is able to capture debris thickness, surface temperature and melt patterns of Amola glacier, including the increase in debris thickness close to the terminus and the left flank of the glacier, with consequent lower melt, and the decreasing debris thickness with elevation, which leads to higher melt in the upper parts of the continuous debris mantle. Modelled melt ranges between approximately 30 cm and more than 1.50 m over approximately a month, with an RMSE of 0.16 m compared to ground observations from 9 ablation stakes.

We also tested varying inputs to the melt model, by using off-glacier weather stations to correct modelled exoatmospheric radiation and a thermal image acquired 1 month apart from field observations to model debris thickness. Observations from off-glacier automatic weather stations are unable to capture the local solar radiation receipts of Amola glacier, with an RMSE of 17-34% of daily incoming radiation. However, since the model empirically relates solar radiation to surface temperature in melt calculation, the stations can still be used for melt modelling without compromising the accuracy.

Similarly, using a thermal satellite image acquired 1 month apart does not result in a higher RMSE of modelled melt, which suggests a relative stability of the debris mantle during the ablation season.

Alternative approaches might be tested to improve the estimates of meltwater production of Amola glacier, based on solving the energy balance; as the approaches rely on a full set of meteorological parameters to be acquired, a comparison with off-glacier AWSs should also be performed to investigate whether the latter can be used to infer meteorological fluxes on the glacier surface.

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Chapter 4

Toward a synthesis of glacial ecology

4.1 Glacier fleas” (Hexapoda: Collembola) from supraglacial environment of European Alps: taxonomy, ecology and biogeography.

PAPER IN PREPARATION

Potential Journal: Proceeding of the Royal Society B

Title: "Glacier fleas" (Hexapoda: Collembola) from the supraglacial environment of European Alps: taxonomy, ecology and biogeography

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Keywords: biodiversity monitoring, climate change, glaciers, true ice-dwelling springtails, vanishing glaciers

INTRODUCTION

Alpine glaciers are currently threatened by climate change (Hock et al. 2019; Gobbi et al. 2021) that is leading them at least to the transformation into debris-covered glaciers (Azzoni et al., 2018; Kraaijenbrink et al., 2017; Tielidze et al., 2020) and ultimately to the total disappearance. Also permafrost and its more evident geomorphological manifestation, rock glaciers, are degrading under the effect of climate change as well, for instance through the thickening of the active layer and the reduction of ice extent (Biskaborn et al. 2019). Glacial and periglacial landforms are refugia for endemic and highly specialized high altitude organisms, which show physiological adaptation to live at low temperatures (e.g. Eisenbeis & Meyer 1999): if these landforms disappear, an important portion of biodiversity risk of disappearing with them (Cauvy-Fraunie & Dangles 2019; Gobbi et al. 2021; Brighenti et al. 2021; Valle et al. 2022). The urgency of studying glaciers and rock glaciers and their associated biodiversity for a future monitoring and for not losing this diversity is nowadays a conservation priority (Liu et al 2022; Gobbi et al. 2021).

Springtails are edaphic arthropods particularly linked to glacial habitat (Valle et al. 2021, 2022; Gobbi et al. 2021, Fjellberg 2010) and to cold biomes in general (Potapov et al. 2022), being also among the few terrestrial invertebrates able to colonize Antarctic continent (McGaughran et al. 2011). Among Alpine arthropods, only for springtails (Isotomidae family) is known the existence of cryophilic ice-dwelling species, i.e. adapted to survive only in direct contact to the glacial ice (Valle et al 2021, Buda et al. 2020, Fjellberg 2010). Eisenbeis & Meyer (1999) define these springtails "true ice-dwelling" cryophilic species. These species should be distinguished from "firn- and debris-dwelling" cryophilic ones, that occupy the habitat at the margin of the ice or on supraglacial debris (Eisenbeis & Meyer 1999). The main period of activity of ice-dwelling springtails occurs during winter months: during cold season the microhabitat they occupy is at the interface between ice and snow (Eisenbeis & Meyer 1999). Only when snow starts melting, they move up to the snow surface and, during summer, when snow is completely melted, they lay on the ice and into the ice interstice, down to a depth of about 30 cm (Eisenbeis & Meyer 1999). They are obligate ice-dweller, unable to survive elsewhere.

The peculiar physiological and ethological adaptation of springtails to survive under cold, and freezing conditions has been the object of many studies (e.g. Holmstrup 2018, Sinclair & Sjursen 2001, Eisenbeis & Meyer 1999, Sømme 1981). Steinböck (1939) demonstrated that glacial species (*Desoria saltans*) are capable of extreme adaptation to cold conditions, falling into chill coma at -16°C, whereas less adapted, not glacial species already become inactive at -6°C. Schaller and Zinkler (1963) found that *Desoria saltans* has comparatively high respiration rate close to 0°C, demonstrating high metabolism around the freezing point. At the same time, ice-dwelling springtails depend on a constant high humidity, differently from firn-dwelling species that during summer prefer snow-free zones with higher temperatures and drier air (Zopeszki, 1988; Eisenbeis & Meyer 1999).

By virtue of the very pioneer role of springtails in glacial ecosystems (Hågvar et al 2020) their importance is also ecological and is well summarized in the "springtail first principle" (Hågvar & Gobbi 2022): chlorophyll may be present in biofilm or tiny pioneer mosses, and pioneer springtails graze on these sources; the numerous predators that inhabit glacial habitat feed mainly on springtails community (Sint et al 2019; Valle et al 2020).

In high mountain areas, glaciers and rock glaciers probably act for ice-dwelling species like islands of ice in a matrix of rocky grounds, prairies, cliffs, woods and other ice-free landforms. In this situation, the patchily distributed ice-dwell springtail populations are good candidates for study the biogeography of Alpine high altitude environments, as suggested by Valle et al (2021) and as pointed out by the study of Fjellberg (2010) about the great diversity of cryophilic Isotomidae (both ice- and debris-dwellers) in southern Alaska and in the Canadian Rocky Mountains. Despite this, their diversity and distribution in the European Alps is still not well known and their diversity is probably undervalued (Valle et al. 2021, Eisenbeis & Meyer 1999).

The geologist Antonio Stoppani (1876) cited *Desoria saltans* in his essay "Il Bel Paese" for its showy, swarming and large assemblages on Alpine glaciers. For the following years this species was considered the only Alpine ice-dwelling springtail, the so called "glacier flea". In 1980 Haybach (1980) described a new species of ice-dwelling Isotomidae – *Vertagopus helveticus* (Haybach, 1980) – found on Morteratsch glacier (Bernina, Switzerland), under supraglacial stony debris. This species was taxonomically related to *Vertagopus alpinus* Haybach, 1972 discovered few years before for the snowy and high altitude habitats of Grossglockner, in particular close to Pasterze glacier (Austria). Only recently another ice-dwelling *Desoria* species was described from the last preserved glacier of Apennines (Abruzzo, Italy), *D. calderonis* Valle, 2021 (Valle et al., 2021) and *Vertagopus nunataki* Potapov & Kremenitsa, 2020 was described from the nival fauna of Caucasus (Lafooraki et al. 2020).

Another genus of specialized cryophilic Isotomidae was discovered in high altitudes of Pyrenées (Cassagnau 1957), *Gnathisotoma* Cassagnau, 1957, which was later then found also in Nord America (Fjellberg, 2010) and is considered a group evolved from *Desoria* and adapted to nival belt (Najt, 1981). *Gnathisotoma* has never been found on the Alps. Members of this genus from both Pyrenées and Alaska were found on the surface of water draining from the melting snow fields or on cold and wet mosses in the glacial streams (Fjellberg 2010; Cassagnau 1957), thus being “firn- or debris-dweller” cryophilic species (Eisenbeis & Meyer 1999).

Thus, as we currently know, in Europe, at least two genera of ice-dwelling Isotomidae seem to be related to the supraglacial habitat, *Desoria* Nicolet in Desor, 1841 and *Vertagopus* Bagnall, 1939; a third one, *Gnathisotoma,* is a debris-dwelling cryophilic springtail and, possibly, a key genus of glacier flea phylogenesis, still uncertain. The only morphological characteristic that separates *Vertagopus* from *Desoria* is the presence in *Vertagopus* of clavate tenent hairs; however, the shape of clavate hairs seems not a good phylogenetic trait, since this structure is strongly related to the environment (Christiansen 1961). Fjellberg (2010) highlighted how also the characteristics that define morphologically *Gnathisotoma* from *Desoria* – the reduced number of sensilla on the tergites, the modified maxilla and the absence of frontal setae on the ventral tube - are not unique to the genus and present a gradual difference between the two genera.

In this paper, we present the first comprehensive description of ice-dwelling springtails of European Alps through integrative taxonomy approach (Potapov et al. 2020), in order to investigate also their phylogeny and their potentiality as biogeographic indicators.

MATERIAL AND METHODS

Study area

The sampling was performed in the European Alps. (**Tab. 1; Fig. 1**). Sampling interested also a wide spectrum of geographic and climatic and substrate variability, in order to have sufficient data for biogeographic and ecological considerations. Nomenclature of Alpine sectors follows SOIUSA (Marazzi 2005)

Gnathisotoma specimens for phylogenetic analysis have been sampled on Pyrenées: *Gnathisotoma bicolor* in Troumouse (Gavarnie, 42°43'14.3"N, 0°07'32.8"E; 2500 m asl), *Gnathisotoma* sp.2 in Estarange (Aragnouet, 42°48'09.6"N, 0°08'10.0"E; 2490 m asl) (**Tab. 1**).

Figure 1*: Sites sampled during field work on European Alps. Red points = sites were specimens were found; orange points= sites were no specimens were found. Acronyms for sites are explained in Table 1.*

Sampling activity

The sampling activity was performed mainly during the summers 2020, 2021 and 2022. Sampling was performed on glaciers and rock glaciers from all areas of European Alps (**Tab. 1, Fig. 1**) Also snow patches in relict glacial site (i.e. glaciers where is not possible to find ice anymore, but there is still permanent or semi-permanent snow cover) have been checked. Specimens were searched on the supraglacial environments, in contact with the ice. Specifically, sampling consisted in hand-catching where springtails made consistent assemblages on snow or under the stones, and in floating method (Marshall et al. 1994, Valle et al. 2021) to collect the specimens occurring inside the supraglacial stony debris. For rock glacier it was not possible to reach the ice because of the deep debris layer and only surface interstitial habitat has been inspected.

Gnathisotoma species were sampled with floating method in the stony debris at the borders of snow-patches in relict glacial areas.

Table 1: *sampled sites, including those where no ice-dwelling springtails were found (grey) and those one where only few specimens have been found (blue). Legend: G= glacier, RG=rock glacier, N=snow-patch. FM=sampled with flotation method. "*" is associated to the dominant species of a glacier where also another species occurs: these glaciers are Morteratsch, Miage, Oberaar and Tour. Species name written in red are the three new species described hereafter. The last three populations are non-Alpine species used for phylogenetic analysis.*

glacier, rock glacier and snow-patches names	geographic area	land form	code	historical reports with reference	species name	country	sampling data	microhabitat	Latitude	Longitude	altitude (m asl)	Morphology	*cox1* (number of sequences)	*16S* (number of sequences)
Sforzellina	Ortles-Cevedale, Southern Rhaetian Alps, Eastern Alps	G	**SFO**		"species B"	Italy	05/08/2020	on supraglacial snow and in supraglacial debris (FM)	46°20'58.7"N	10°30'44.1"E	2859	Complete morphological description	10	8
Dosdè	Ortles-Cevedale, Southern Rhaetian Alps, Eastern Alps	G	**DOS**			Italy	05/08/2020	under stones on bare ice	46°23'34.8"N	10°12'58.9"E	2760		10	10
Agola	Brenta Dolomites, Southern Rhaetian Alps Eastern Alps	G	**AGO**			Italy	10/08/2020	on supraglacial snow and ice	46°08'57.9"N	10°51'27.0"E	2581		9	9
Predarossa	Valtellina, Southern Rhaetian Alps, Eastern Alps	G	**PRE**			Italy	Jul. 2021	under stones on bare ice	46°15'37.4"N	9°44'21.8"E	2850		9	6 (+4 to be sequenced)
Forni	Ortles-Cevedale, Rhaetian Alps, Eastern Alps	G	**GFO**	Isotomidae sp (Buda et al. 2020), "*Desoria glacialis*" (Stoppani, 1876)	"species A"	Italy	03/08/2020	under stones on bare ice	46°23'42.95"N	10°35'24.79"E	2630	Complete morphological description	10	7
Vedretta d'Amola	Adamello, Southern Rhaetian Alps, Eastern Alps	G	**AMO**			Italy	21/07/2020		46°13'8.95"N	10°41'12.25"E	2701		10	10
Giogo alto	Val Senales, Southern Rhaetian Alps, Eastern Alps	G	**GIO**			Italy	21/08/2020	under stones on bare ice	46°46'52.1"N	10°48'20.7"E	2843		13	9
Pers	Bernina, Wester Rhaetian Alps, Eastern Alps	G	**PER**			Switzerland	30/07/2o21	under stones on bare ice	46°24'25.9"N	9°57'32.4"E	2670-2700		10	8
Morteratsch*	Bernina, Western Eastern Alps	G	**MOR1**	*Vertagopus helveticus* (Haybach, 1980)		Switzerland	10/07/2021	under stones on bare ice	46°24'55.5"N	9°56'04.5"E	2200-2300		9	4
Mittelberg	Otztal Alps, Southern Rhaetian Alps, Eastern Alps	G	**MIT**	"cf *Desoria saltans*" (Kopeszki 1988)		Austria	20/08/2021	under stones on bare ice	46°55'09.5"N	10°53'43.7"E	2680-2700		6 (+3 to be sequenced)	6 (+4 to be sequenced)
Lang gletscher	Bernese Alps, Western Alps	G	**VAL**			Switzerland	10/08/2021	under stones on bare ice	46°27'28.3"N	7°55'55.8"E	2450-2550		6 (+ 3 to be sequenced)	6 (+ 2 to be sequenced)
Oberaar*	Bernese Alps, Western Alps	G	**OBE**	Isotoma 'sp. G' (Eisenbeis & Meyer 1999		Switzerland	14/08/2021	under stones on bare ice	46°32'08.6"N	8°13'12.4"E	2380-2440		6 (+4 to be sequenced)	6 (+4 to be sequenced)
de Moiry	Pennine Alps, Western Alps	G	**MOI**			Switzerland	11/08/2021	under stones on bare ice	46°05'15.5"N	7°35'25.3"E	2620-2660		10	10
Pièce	Pennine Alps, Western Alps	G	**PIE**			Switzerland	17/08/2021	under stones on bare ice	45°59'59.7"N	7°28'12.2"E	2750-2800		9	10
Pre de Bar	Mont Blanc, Graian Alps, Western Alps	G	**PDB**		***Desoria saltans* Nicolet, 1841**	Italy	25/07/2021	under stones on bare ice	45°54'08.9"N	7°03'04.2"E	2700	Morphological identification and notes	10	10
Glacier Blanc	Ecrins, Dauphiné Alps, Western Alps	G	**GLB**			France	08/08/2021	under stones on bare ice	44°56'46.6"N	6°23'48.8"E	2970		8	8
Scais	Orobian Alps, Eastern Alps	G	**SCA**			Italy	18/09/2020	in supraglacial debris (FM)	46°03'52.8"N	9°58'56.1"E	2815	-	5	-
Miage*	Mont Blanc, Graian Alps, Western Alps	G	**MIA1**		***Vertagopus alpinus* Haybach, 1972**	Italy	08/09/2020	in supraglacial debris (FM)	45°46'52.6"N	6°52'02.3"E	2075	Morphological identification and notes	14	12
Mer de Glace	Mont Blanc, Graian Alps, Western Alps	G	**MDG**			France	12/08/2021	in supraglacial debris (FM)	45°54'44.5"N	6°56'10.4"E	2040		10 to be sequenced	10
Pasterze	Grossglockner, Western Tauern Alps, Eastern Alps	G	**PAS**	*Vertagopus alpinus* Haybach, 1972		Austria	01/08/2021	in supraglacial debris (FM)	47°05'13.9"N	12°43'24.9"E	2340		10	6 (+4 to be sequenced)
Morteratsch	Bernina, Wester Rhaetian Alps, Eastern Alps	G	**MOR2**	*Vertagopus helveticus* (Haybach, 1980)		Switzerland	10/07/2021	under stones on bare ice	46°24'55.5"N	9°56'04.5"E	2200-2300		-	1
Orny	Mont Blanc, Graian Alps, Western Alps	G	**ORN**			Switzerland	17/08/2022	under stones on bare ice	45°59'59.8"N	7°04'03.7"E	2700		-	-
Pelerins	Mont Blanc, Graian Alps, Western Alps	G	**PEL**			France	23/08/2022	under stones on bare ice	45°53'43.9"N	6°53'04.9"E	2320		-	-
Tour*	Mont Blanc, Graian Alps, Western Alps	G	**TOU1**			France	24/08/2022	under stones on bare ice	45°59'44.8"N	6°59'07.4"E	2660		-	-
Tour	Mont Blanc, Graian Alps, Western Alps	G	**TOU2**		***Gnathisotoma* sp. 3** (few specimens)	France	24/08/2022	under stones on bare ice	45°59'44.8"N	6°59'07.4"E	2660	Morphological identification and notes	-	-
Glacier Noir	Ecrins, Dauphiné Alps, Western Alps	G	**GLN**		"species GLN"	France	09/08/2021	in supraglacial debris (FM)	44°55'11.3"N	6°23'37.8"E	2240	Complete morphological description	6	6

glacier, rock glacier and snow-patches names	**geographic area**	**land form**	**code**	**historical reports with reference**	**species name**	**country**	**sampling data**	**microhabitat**	**Latitude**	**Longitude**	**altitude (m asl)**	**Morphology**	***cox1* (number of sequences)**	***16S* (number of sequences)**
Peirabroc1	Maritime Alps, Western Alps	G	**PEI-a**		Unknown (few specimens)	Italy	14/09/2020	in supraglacial debris (FM)	44°07'18.7"N	7°24'51.1"E	2535	-	3	-
Peirabroc2	Maritime Alps, Western Alps	G	**PEI-b**		Unknown (few specimens)	Italy	14/09/2020	in supraglacial debris (FM)	44°07'18.7"N	7°24'51.1"E	2535	-	1	-
Clapier	Maritime Alps, Western Alps	G	**CLA**		Unknown (few specimens)	Italy	15/09/2020	in supraglacial debris (FM)	44°06'49.8"N	7°25'25.3"E	2730	-	3	-
Miage	Mont Blanc, Graian Alps, Western Alps	G	**MIA2**		Unknown (few specimens)	Italy	08/09/2020	in supraglacial debris (FM)	45°46'52.6"N	6°52'02.3"E	2075	-	2	2
Aletsch	Bernese Alps, Western Alps	G	-		-	Switzerland	01/08/2021	under stones on bare ice	46°26'36.2"N	8°04'41.5"E	2340	-	-	-
Diavolo in Tenda	Orobian Alps, Eastern Alps	N	-		-	Italy	19/09/2020	on snow and in the stony debris on the border of the snow (FM)	46°02'22.8"N	9°54'22.2"E	2390	-	-	-
Malgina	Orobian Alps, Eastern Alps	N	-		-	Italy	17/07/2020	on snow and in the stony debris on the border of the snow (FM)	46°04'49.5"N	10°03'01.8"E	2570	-	-	-
Secreti	Orobian Alps, Eastern Alps	N	-		-	Italy	18/09/2020	on snow and in the stony debris on the border of the snow (FM)	46°03'28.3"N	9°58'54.8"E	2700	-	-	-
Mandrone	Adamello, Southern Rhaetian Alps, Eastern Alps	G	-		-	Italy	25/08/2020	under stones on bare ice	46°11'5.80"N	10°33'34.67"E	2606	-	-	-
Marmolada	Marmolada Dolomites, Southern Rhaetian Alps, Eastern Alps	G	-		-	Italy	03/09/2020	under stones on bare ice	46°26'21.3"N	11°51'49.4"E	2900	-	-	-
Stelvio	Ortles-Cevedale, Southern Rhaetian Alps, Eastern Alps	G	-		-	Italy	19/08/2020	under stones on bare ice	46°30'29.6"N	10°28'06.7"E	3200	-	-	-
Ventina	Orobian Alps, Eastern Alps	G	-		-	Italy	05/09/2020	under stones on bare ice and in supraglacial debris (FM)	46°17'08.9"N	9°46'52.2"E	2100	-	-	-
Belvedere	Monte Rosa, Pennine Alps, Western Alps	G	-		-	Italy	10/08/2020	in supraglacial debris (FM)	45°57'33.5"N	7°54'47.0"E	2040	-	-	-
Cima uomo	Marmolada Dolomites, Southern Rhaetian Alps, Eastern Alps	G	-		-	Italy	25/08/2020	in supraglacial debris (FM)	46°24'33.5"N	11°48'21.1"E	2550	-	-	-
Lazaunkar	Val Senales, Southern Rhaetian Alps, Eastern Alps	RG	-		-	Italy	06/08/2020	ice not found, too deep	46°44'50.3"N	10°45'23.1"E	2540	-	-	-
Rock glacie Amola	Adamello, Southern Rhaetian Alps, Eastern Alps	RG	-		-	Italy	22/07/2020	ice not found, too deep	46°12'11.5"N	10°42'11.0"E	2460	-	-	-
Troumouse	Gavarnie, Pyrenées	N	**TGN**	*Gnathisotoma bicolor* (Cassagnau, 1957)	***Gnathisotoma bicolor* Cassagnau, 1957**	France	08/07/2021	stony debris at the border of a snowpatch, along the glacial stream (FM)	42°43'14.3"N	0°07'32.8"E	2500	Morphological identification and notes	9	10
Estarange	Aragnouet, Pyrenées	N	**ESTmg**	*Gnathisotoma bicolor* (Cassagnau, 1957)	***Gnathisotoma* sp.2**	France	07/07/2021	stony debris at the border of a snowpatch (FM)	42°48'09.6"N	0°08'10.0"E	2490	Morphological identification and notes	3	3
Calderone	Gran Sasso, Apennines	G	**CLA**	-	***Desoria calderonis* Valle, 2021**	Italy	08/07/2020	in supraglacial debris (FM)	42°28′16.2″ N	13°34′05.8″ E	2700	Complete morphological description in Valle et al. 2021	9 (from Valle et al. 2021)	9

Specimen conservation and preparation

Specimens are preserved in 96% ethanol at -20°C. For slide preparation they were passed in boiling alcohol for removing fats and cleared by a short immersion in 10% KOH solution. Then, they were passed in Chloralphenol aland finally mounted on slides using Swann medium as preservative solution (Rusek, 1975). Other specimens were initially cleared by a short immersion in 10% KOH solution and then mounted on depression slides using lactic acid or Marc André as a preservative solution for better preserve and observe the body shape. Morphological observations and pictures were made with a phase-contrast Leica DM2500 with phase and DIC contrasts and drawing arm, a Carl Zeiss Axiolab 5 with phase contrast light microscopes and a Quanta400 (FEI) scanning electron microscope..

DNA sequencing

Whole genomic DNA was extracted from ten specimens from each of the sampled population, using the Wizard®SV Genomic DNA Purification System (Promega, Madison, WI, USA). For each specimen we amplified and sequenced two markers. The mitochondrial marker analysed –cytochrome *c* oxidase subunit 1, 5P fragment (cox1) – was amplified by the primers GGTCAACAAATCATAAAGATATTGG (LCO, foreward) and AAACTTCAGGGTGACCAAAAAATCA (HCO, reverse) (Folmer et al. 1994). The ribosomial marker analyzed - *16S* ribosomal RNA (*16S*) – was amplified by the primers CCGGTCTGAACTCAAATCATGT (LR-J-12887M, foreward) and CGACTGTTTAACAAAAACAT (LR-N-13398M, reverse) (Simon et al. 1994, modified after Zhang et al. 2015).

For *Vertagopus sp n.* (GLN), *V. alpinus* (PAS, MIA, MDG) and *Gnathisotoma bicolor* (TGN) the primers aforementioned LCO-HCO (Folmer et al. 1994) did not amplify cox1; therefore, new primer HCO were designed for the same marker on the basis of a partial sequencing of the neighboring fragment COI. The amplification of COI fragment have been performed with COIa/f primers (Udayasuriyan et al. 2015). LCO has been corrected on the basis of the BOLD sequence of *Desoria tigrina* (OD987622.1 *Desoria tigrina*). Therefore, for *V. alpinus* (PAS, MIA, MDG) and *Vertagopus sp. n* (GLN) cox1 has been amplified with the primers TCAACAAACCACAAAGATATTGG ("LCO corrected for PAS, MIA, MDG", foreward) and TATACTTCAGGRTGGCCAAAAAATCA ("HCO corrected", reverse); for *Gnathisotoma bicolor* (TGN) cox1 has been amplified with the primers TCAACAAACCACAAAGATATTGG ("LCO corrected", foreward) and TAYACTTCTGGGTGCCCAAAAAATCA ("HCO corrected for TRO", reverse). PCRs were prepared with AmpliTaq Gold™ 360 Master Mix in a 10 μL reaction volume containing: 2 μL of whole genomic DNA, 0.5 μL of both forward and reverse primers (10 μM). Amplifications were run with the following conditions for each of the 35 cycles: a denaturation step at 95°C for 1 min, an annealing step at 50°C for 1 min and an elongation step at 72°C for 90 s. An additional initial denaturation step was set at 95°C for 5 min as well as a final extension step at 72°C for 7 min (5 min for COIa/COIf) (Valle et al 2021, Udayasuriyan et al. 2015). For TGN cox1 it has been necessary to run the amplifications for 40 cycles. For *Desoria calderonis* were sequenced from the 9 specimens of the original description (see Valle et al. 2021) also the *16S* marker. For ORN, TOU, PEL was performed only the morphological identification.

Phylogenetic analysis

Phylogenetic analysis was conducted on individuals coming from a total of 28 populations (26 for *cox1*, 23 for *16S*; population codes in **Tab.1**). Additional related sequences available from the literature were added as outgroups and/or to contextualize newly obtained sequences (7 for *cox1*, 2 for *16S*).

Phylogenetic analysis was conducted on the two markers separately. Sequences were imported in AliView (ver. 1.28; Larrson, 2014), aligned using the built in muscle function (ver: 3.8.425; Edgar, 2004), trimmed to an uniform length and collapsed to unique haplotypes using the DNAcollapser function through the FaBox webserver (https://birc.au.dk/~palle/php/fabox/). Final datasets included 218 sequences of 560 nucleotides for *cox1* and 188 sequences of 383 nucleotides for *16S* before collapsing and 121 and 45, respectively, after collapsing.

Differences among unique sequences were calculated as p-distances in Paup (ver. 4.0a168; Swofford, 2003). The best partitioning scheme and model of sequence evolution were identified in PartitionFinder 2 (Lanfear et al. 2012) sumbitting *cox1* sequences as three starting partitions (1st, 2nd and 3rd codon positions) and *16S* sequences as one starting partition. Phylogenetic analysis was conducted on each dataset using MrBayes (v. 3.2.7a; Ronquist et al. 2012) applying the best partitioning scheme and model, continuing the search for 50 million generations. After confirming convergence, the final tree was visualized in Figtree (v. 1.4.4; available at http://tree.bio.ed.ac.uk/software/figtree/).

After completing last *cox1* sequences (see **Tab. 1**), we will evaluate whether to analyse also a nuclear gene, 18S, and we will perform a phylogenetic analysis with the three genes combined.

PRELIMINARY RESULTS

Ice-dwelling springtails were found in 26 sites of European Alps (68% of the investigated sites), always on clean-ice glaciers and debris-covered glacier, never on snow patches and rock glaciers (**Tab. 1**). On three glaciers– Peirabroc and Clapier glaciers in Maritime Alps and Scais glacier in Orobian Alps – only very few specimens have been found. Thus, for these three sites only few sequences of *cox1* and no morphological notes have been provided, as a preliminary information.

From a morphological perspective, as a whole, five ice-dwelling species were found: *Desoria saltans, Vertagopus alpinus,* "Species A", "Species B" and "Species GLN". "Species B" occurs in the central area of Eastern Alps, others (*Vertagopus alpinus, Desoria saltans* and "Species A") occurred almost on the whole chain. "Species GLN" occurs only on Glacier Noir in Western Alps.

Usually only one species was found on each glacier, when the morphological approach was applied. However, on Oberaar (Bernese Alps) and Tour (Mont Blanc) two species have been found, one dominant and one rarer. On Oberaar, in addition to dominant "Species A", only few juvenile with strongly clavate tenent hairs have been found: this could suggest the co-presence of *Vertagopus alpinus*, but further sampling and studies on adult specimens are needed. On Tour glacier the dominant species is *Vertagopus alpinus*, very common on Mont Blanc, but few specimens (9) of *Gnathisotoma* sp. 3 have been found.

Phylogenetic results

The phylogenetic analysis has identified clusters with sequences very similar within the cluster, which, with few exceptions, corresponds uniquely to one or more groups of sampling sites. All clusters are well differentiated from each other. The average level of divergence within groups in the tree new described species is 1 % for *cox1* and 0.4% for *16S*, and between these three groups of 13% for *cox1* and 8% for *16S*. *16S* and *cox1* trees give concordant results on cluster identification. However, *cox1* highlights more intra-cluster variability than *16S*. In the absence of a specific species delimitation analysis, it is assumed that these groups observed in the phylogenetic trees are referable to good biological species, because of the sizeable gap observed between distances within a cluster and between clusters and the correspondence of some of these groups with already known species. These clusters well correspond to species identified morphologically.

Usually, also from molecular data only one species was found on each glacier; however, on Morteratsch (Bernina) and Miage (Mont Blanc) glaciers there are genetic evidences of the coexistence of two species, one dominant and one rarer, that was possible to identify for Morteratsch as “Species A” (dominant) and *Vertagopus alpinus* (**Tab. 1, Figg. 2,3**). On Miage glacier, two sequences of a different, separated species have been found (MIA2; **Figg. 2,3**). For Peirabroc and Clapier (Maritime Alps; PEI-a, PEI-b, CLA) and Scais (Orobian Alps; SCA) glaciers only few cox1 sequences are available and no morphological identification, since very few specimens have been found. Clapier hosts one species and Peirabroc hosts two different species that do not correspond to any other known sequences (**Fig. 3**). The five sequences of cox1 from Scais glacier indicates the presence of a *Desoria saltans* population in Orobian Alps (Southern Eastern Alps) (**Figg 3, 16**).

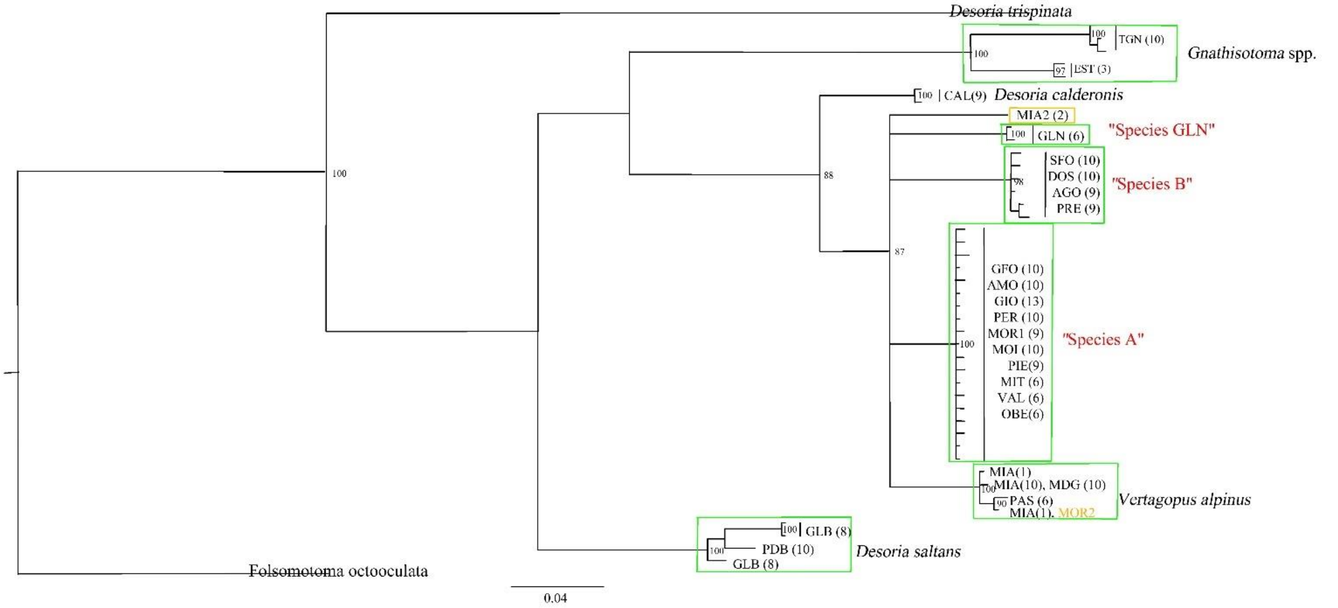

Figure 2 16S *phylogenetic tree. In green boxes, species sampled for this work for which we have morphological and genetic identification. In yellow boxes are highlighted species for which we have few sequences and no morphological identification. Species written in red are new species described for this work. In yellow are highlighted the second species of a population where another species is dominant. Bootstrap support is indicated if > 80*

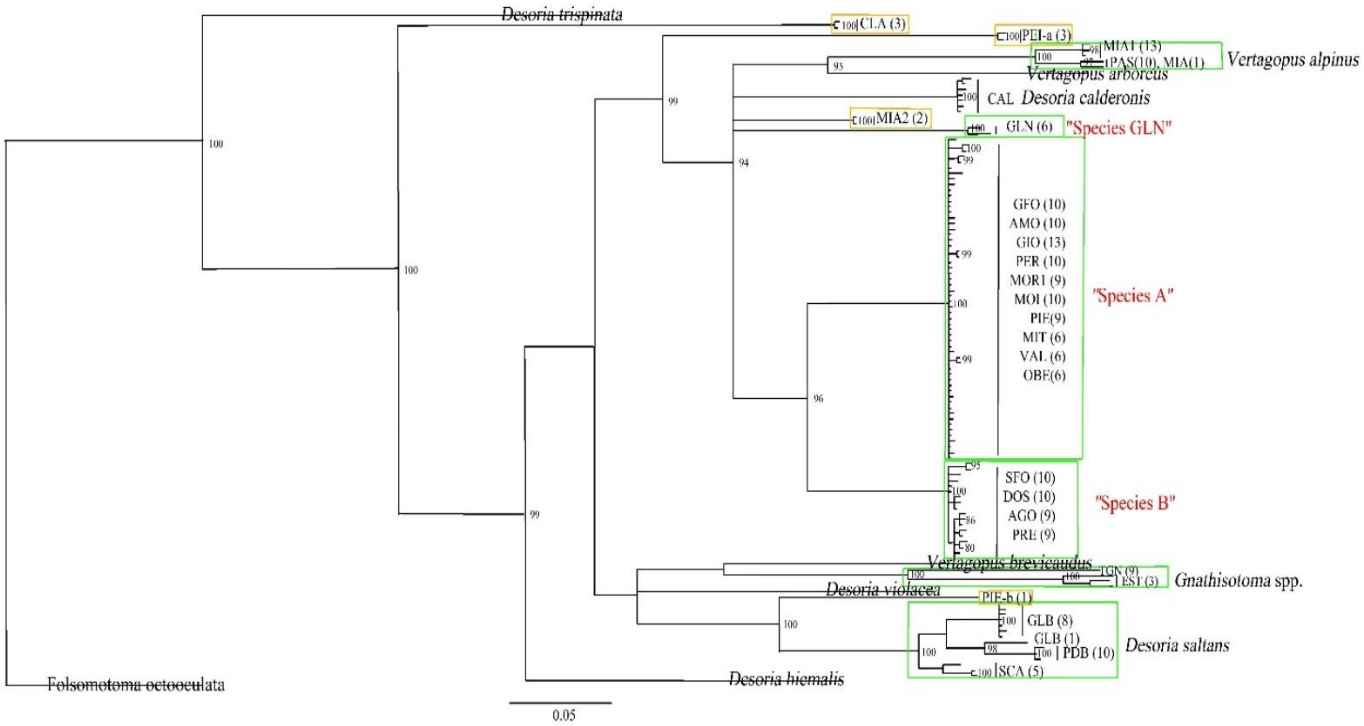

Figure 3 *cox1 preliminary phylogenetic tree. In green boxes, species sampled for this work for which we have morphological and genetic identification. In yellow boxes are highlighted species for which we have few sequences and no morphological identification. Species written in red are new species described for this work. Bootstrap support is indicated if > 80*

Species descriptions

From morphological and phylogenetic analyses it emerges that “Species A”, “Species B” and “Species GLN” are species new for sciences for which is necessary a morphological description belonging eather to *Vertagopus* or *Desoria* genus, see discussion below. For the already known *Desoria saltans, Vertagopus alpinus* and *V. helveticus* we present some morphological notes. From the two sequences found on Miage glacier that are not of *V. alpinus* (MIA2; Mont Blanc) and from Peirabroc and Clapier (PEI-a, PIE-b, CLA; Maritime Alps) *cox1* sequences there are evidences that they should be species new for science but there are too few specimens for describing them.

Abbreviations used in the text

Abd = abdominal segment; *accp*-setae = accessory p-row *s*-setae; *al*-setae = antero-lateral *s*-setae; Ant = antennal segment; AOIII = antennal organ III; *as*-setae = anterosubmedial *s*-setae; bl = basolateral field (mentum); bm = basomedian field (submentum); *ms*-setae = micro *s*-setae;
PAO = post antennal organ; Px = proximal field; Th = thoracic segment; Tita = tibiotarsus;
VT = ventral tube

Desoria/Vertagopus sp. n. “Species B” morphological description

Populations (SFO-DOS-AGO-PRE)

***Figure 4**: color pattern and general appearance of “species B”*

Body. Mean body length (without antennae) 1.49 (standard deviation: 0.29 mm on 11 specimens, see **Table 2**). Colour black, also juvenile (**Fig. 4**). Cuticle granulation fine and regularly distributed; all dorsal tergites clearly separated from each other (**Fig. 6A**). Abd. III and IV of approximately same width.

Chaetotaxy. Terga consisting of micro-, meso- and macrosetae, these latter well differentiated on last abdominal tergites (Abd. IV–VI, in median position), but not well distinguished from ordinary setae on other tergites (**Fig. 5G**). No setae in ventral side of Th. II-Th. III. All setae smooth. Macrosetae on Abd. V 0.6 times median length of tergite and 1.4 times as long as inner edge of Claw III (**Table 2**). Sensory chaetotaxy constituted by *ms*-setae, *accp*-, *al*- and *as*-setae. Only Th. II and Abd. III have *ms*-setae (formula 10/001). Dorsal *s*-setae constituted by single *al-s*eta on Th. II and Th. III, single *as*-seta on Abd. V and by *accp*-setae normally set within *p*-row (**Fig**. **5G**). The number of *accp*-setae can be expressed as (2)3, (2)3/(2)3, (2)3, 3, 4(5), 3(4).

Head. Antennae slightly longer than cephalic diagonal (D/A = 0.38, Antennae =0.43 mm). Ratio among Ant. I/Ant. II/Ant. III/Ant. IV is 1/1.5/1.4/2.7. There are often cases of asymmetry among *s*-setae between antennae of the same specimen. Ant. I has 12-23 *s*-setae in ventro-lateral position,(1)-2-(3) of them are shorter and in distal position; 2 microsetae in ventro-proximal position (**Fig**. **5B,5I**). Ant. II 4-6 *s*-setae in distal position. Ant. III has a sensory field that includes includes 2 inner *s*-setae of AO III, one lateral *ms*-seta and about 11-15 *s*-setae (**Figs 5C, 6D**). Ant. IV has one simple small subapical, peg-shaped organite and a bifurcate pin-like seta (**Fig. 5H**). Eye spots strongly dark pigmented with 8 + 8 ocelli (G and H smaller; **Figs 5A,6B**). PAO elongated about 2 times as long as diameter of nearest ocellus (**Fig. 5A**). Prelabral setae 4. Labral formula as 5,5 and 4 and 4 sharp papillae **(Fig. 5L).** Maxillary palp bifurcated and maxillary outer lobe with 4 sublobal hairs **(Fig. 6C).** Labial palp with 5 papillae and a total of 16 guard setae (Fjellberg 1999) distributed as: A_1, B_{1-4}, C_0, D_{1-4}, E_{1-7}. Hypostomal papilla with H shorter than h_1/h_2. Proximal (px), basomedian (bm) and basolateral (bl) fields of labium with 4, 4 and 5 setae, respectively and 4-8 postlabial setae. Mandible with well-developed molar plate . VT with 0+0 anterior, 4 + 4 latero-distal and (4)5-6 posterior setae with 2 in apical transverse row (**Fig. 5E**). Retinaculum with 4 teeth and 4-7 setae.

Furca. Furca almost as long as antenna (see **Table 2; Fig. 4)**; ratio of mucro/dens/manubrium = 1 / 25 / 16. Ventral setae on manubrium about 38-40 (in juvenile are less, and is possible to confuse them with specie A), including ventro-apical setae ((8)-10) that are usually larger than the others **(Fig. 5F)** with the exception of 1/2 + 1/2 shorter setae in apical-medial position; about 40 dorsal setae. Dens with dorsal crenulations, more than 90 ventral and 12-14 dorsal setae**.** Mucro quadridentate with apical tooth much smaller than subapical one (**Fig. 6E**).

Legs. 11 setae in the distal apical ring of Tita; 2-3-3 very weakly clavate tenent hairs (**Fig**. **5D**), shorter than inner edge of Cl. Claw of normal shape without lateral and inner teeth; empodium sometimes with a small inner tooth; pretarsus with a pair of setae **(Fig. 6F).**

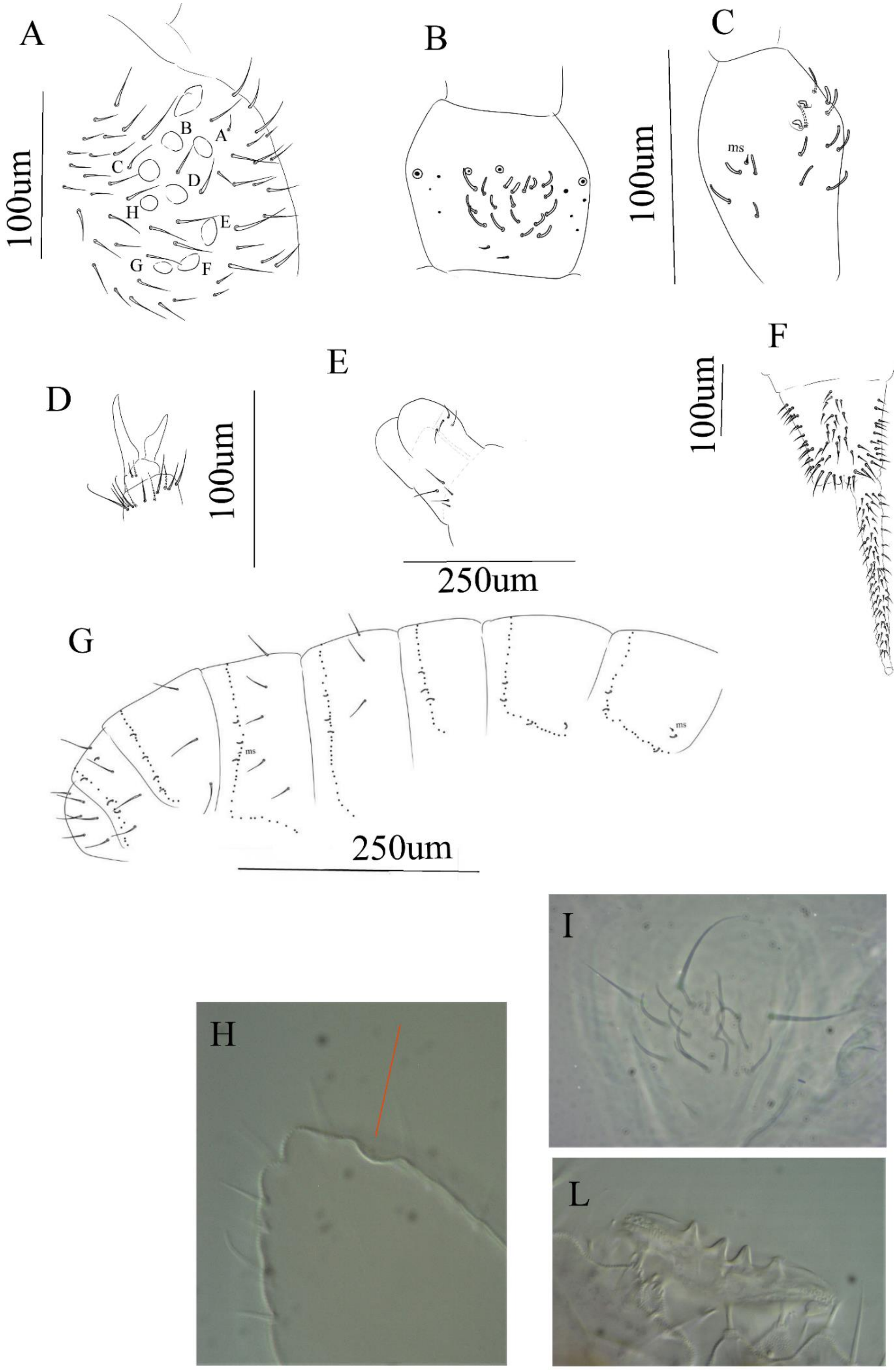

Figure 5 A-L: *drawing and pictures for "Species B" description. A: ocular plate (A-H: OMMA); B: Ant. I, ventral side; C: Ant. III; D: Claw III; E: latero-posterior side of VT; F: ventral side of furca; G: accp sens and macrosetae; H: Ant. IV organite and pin-like seta; I: ventral side of Ant. I; L: papillae labrum; I:*

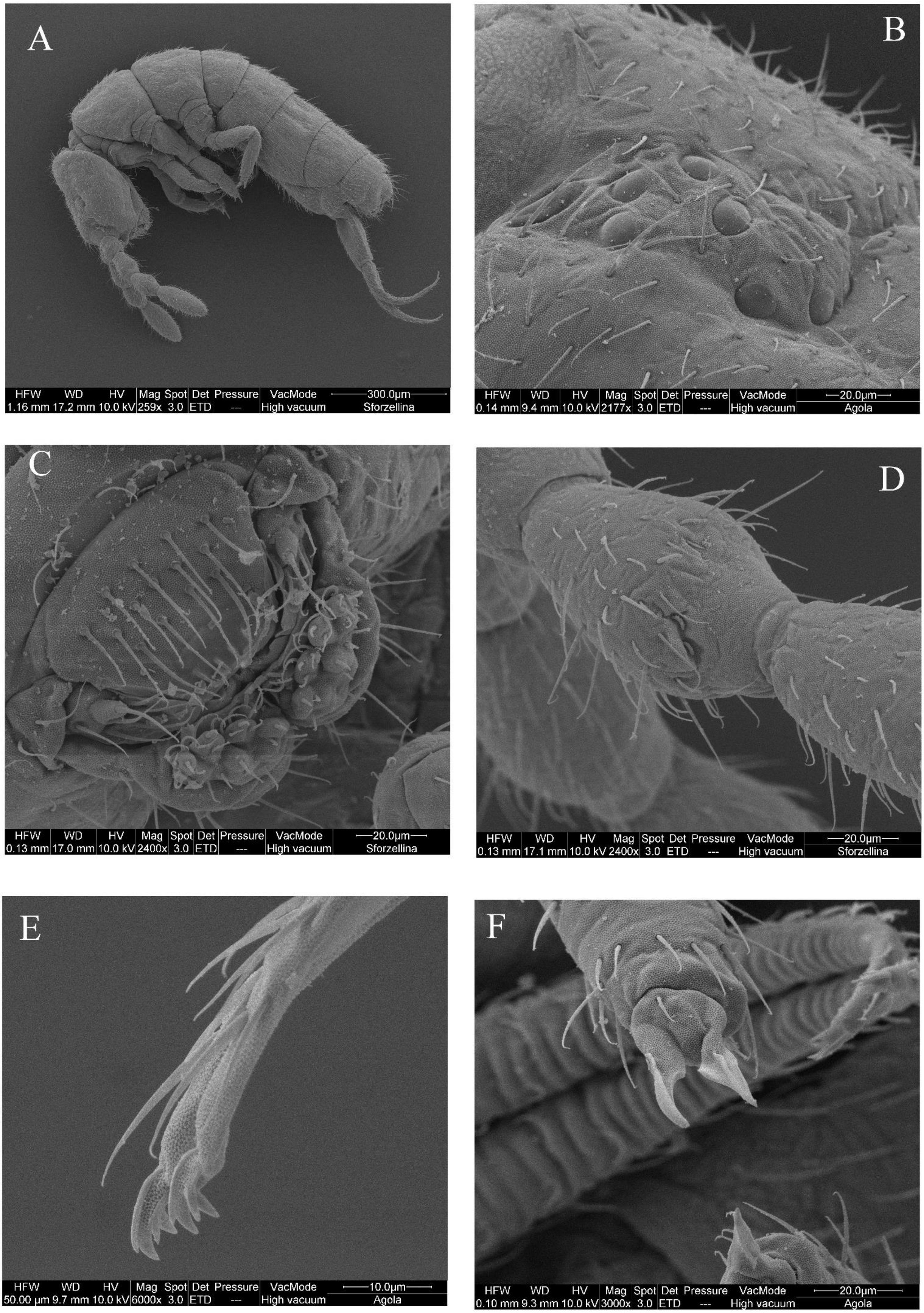

Figure 6 A-F: *drawing and pictures for "Species B" description. SEM pictures belong to SFO and AGO populations. Pictures at contrast microscopes are belong to DOS population*

Desoria/Vertagopus sp. n. "Species A" morphological description

Populations (GFO, AMO, GIO, MOR1, MOI, PIE, PER, MIT, VAL, OBE)

***Figure 7**: color pattern and general appearance of "species A"*

Body. Mean body length (without antennae) 1.73 mm (standard deviation: 0.34 mm on 29 specimens, **Table 2**). Colour black, also juvenile (**Fig. 7**). Cuticle granulation fine and regularly distributed; all dorsal tergites clearly separated from each other (**Fig. 9E**). Abd. III and IV of approximately same width.

Chaetotaxy. Terga, consisting of micro-, meso- and macrosetae, these latter well differentiated on last abdominal tergites (Abd. IV–VI, in median position), but not well distinguished from ordinary setae on other tergites (**Fig. 8D**). No setae in ventral side of Th. II-Th. III. All setae smooth. Macrosetae on Abd. V 0.5 times median length of tergite and 1.2 times as long as inner edge of Claw III (**Table 2**). Sensory chaetotaxy constituted by *ms*-setae, *accp*-, *al*- and *as*-setae. Only Th. II and Abd. III have *ms*-setae (formula 10/001). Dorsal *s*-setae constituted by single *al*-*s*eta on Th. II and Th. III, single *as*-seta on Abd. V and by *accp*-setae normally set within *p*-row (**Fig. 8D**). The number of *accp*-setae can be expressed as 2, 2/1(2), 1, 1-3, 2-3, 3(4).

Head. Antennae slightly longer than cephalic diagonal (D/A = 0.42, Antennae=0.45 mm). Ratio among Ant. I/Ant. II/Ant. III/Ant. IV is 1.0/1.6/1.5/3.0 (**Table 2)**. There are often cases of asymmetry among *s*-setae between antennae of the same specimen.-Ant. I has 8-24 *s*-setae in ventro-lateral position,1-(2) of them are shorter and in distal position; (1)-2-(3) microsetae in ventro-proximal position (**Fig**. **8B**). Ant. II 6 *s*-setae in distal position. Ant. III has a sensory field that includes 2 inner *s*-setae of AO III, one lateral *ms*-seta and about 10-13 *s*-setae (**Figs 8C**). Ant. IV with one simple small subapical, peg-shaped organite and a bifurcate pin-like seta (**Fig**. **8G**). Eye spots strongly dark pigmented with 8 + 8 ocelli (G and H smaller; **Figs 8A**). PAO elongated (sometimes is visible a weak median constriction) about 1.5 times as long as diameter of nearest ocellus (**Fig**. **9D**). Prelabral setae 4. Labral formula as 5,5 and 4 and 4 sharp papillae (**Fig**. **8H**). Maxillary palp bifurcated and maxillary outer lobe with 4 sublobal hairs (**Fig**. **9F**). Labial palp with 5 papillae and a total of 15-16 guard setae (Fjellberg 1999) distributed as: A_1, B_{1-4}, C_0, D_{1-4}, **$E_{1-6/7}$** (**Fig. 9D**). **Characteristic of this species is the variability in**

number of guard setae. Usually e7 is not present but it should be present and frequently the same individual has one labium with e7 and the other one without (see remarks below in “variability in labium setae”). Hypostomal papilla with H shorter than h_1/h_2. Proximal (px), basomedian (bm) and basolateral (bl) fields of labium with 4, 4 and 5 setae, respectively (**Fig**. X). 4-7 postlabial setae (**Fig**. **9F**). Mandible with well-developed molar plate. VT with 0+0 anterior, 4 + 4 latero-distal and (4)5-9 posterior setae with 2 in apical transverse row (**Fig**. **8F**). Retinaculum with 4 teeth and 5-7 setae.

Furca. Furca almost as long as antenna; ratio of mucro/dens/manubrium = 1 / 24 / 16 (**Fig. 8I**). Ventral setae on manubrium about 14-22, including ventro-apical setae (8) larger than the others (**Fig. 8I**) with the exception of 1(3) + 1(3) shorter setae in apical-medial position; about 50 dorsal setae on Man. Dens with dorsal crenulations, more than 60 ventral and 14-22 dorsal setae. Mucro quadridentate with apical tooth much smaller than subapical one (**Fig. 9C**).

Legs. 11 setae in the distal apical ring of Tita; 2-3-3 very weakly clavate tenent hair, shorter than inner edge of Cl (**Fig. 8E, 9A-B**). Claw of normal shape without lateral and inner teeth; empodium empodium sometimes with a small inner tooth (**Fig. 9A-B**); pretarsus with a pair of setae.

Variability in labium setae: checking 31 specimens (3-4 for every populations), 18 specimens have not e7, 7 specimens has e7 only on one side (usually on the right) and 6 have e7 on both sides. This characteristic is well distributed among populations.

Nota on Anterior setae of VT: in Dosdè (DOS) and de Moiry (MOI) glaciers in one specimens there are 1+1 anterior setae. It could be the link with *Vertagopus alpinus* (a pair of setae originally present and lost during evolution, expressed only for an error)

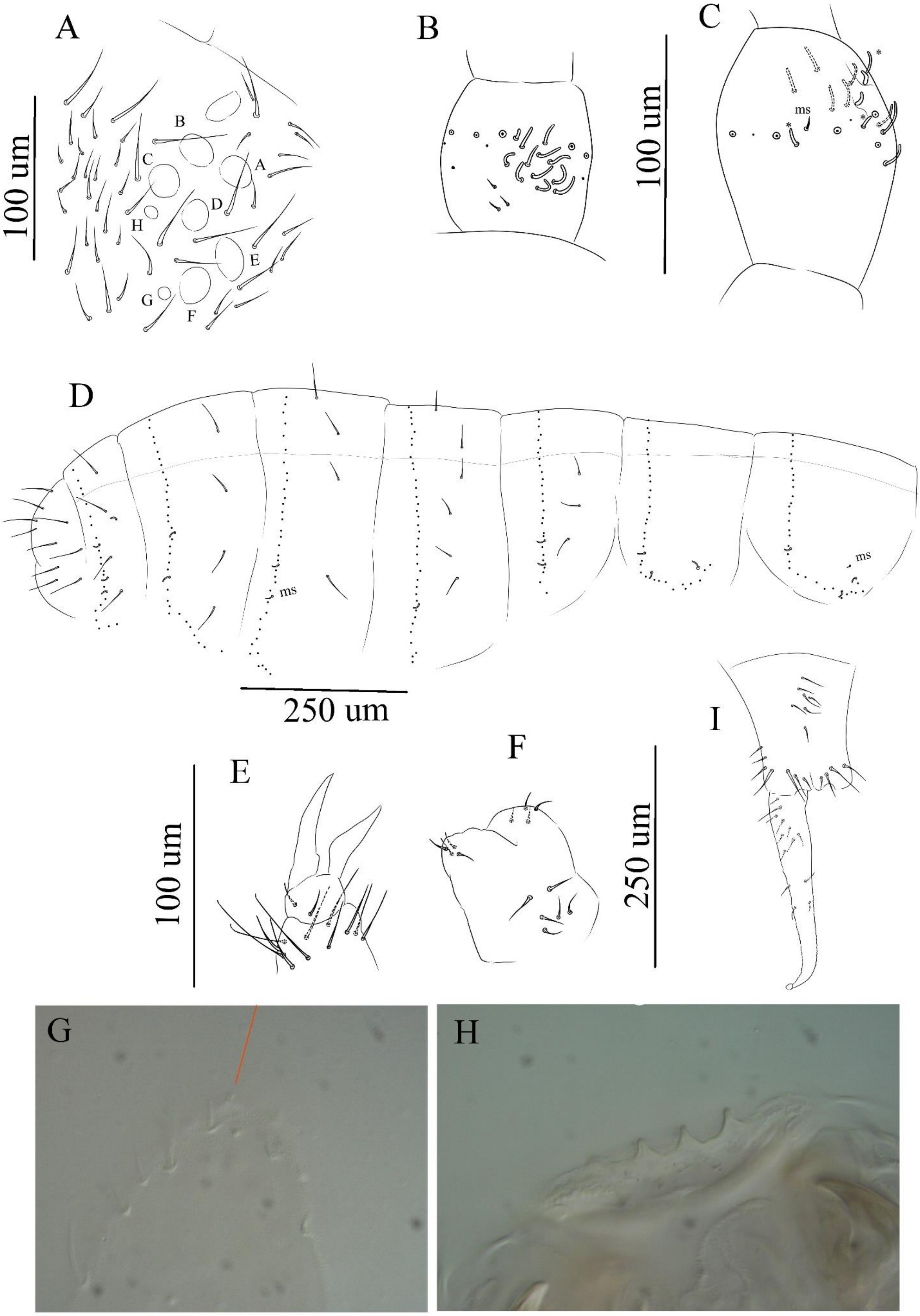

__Figure 8 A-I:__ drawing and pictures for "Species A" description. A: ocular plate (A-H: OMMA); B: Ant. I, ventral side; C: Ant. III; D: accp sens and macrosetae; E: Claw III; F: latero-posterior side of VT; G: Ant. IV organite and pin-like seta; H: papillae labrum; I: ventral side of furca.

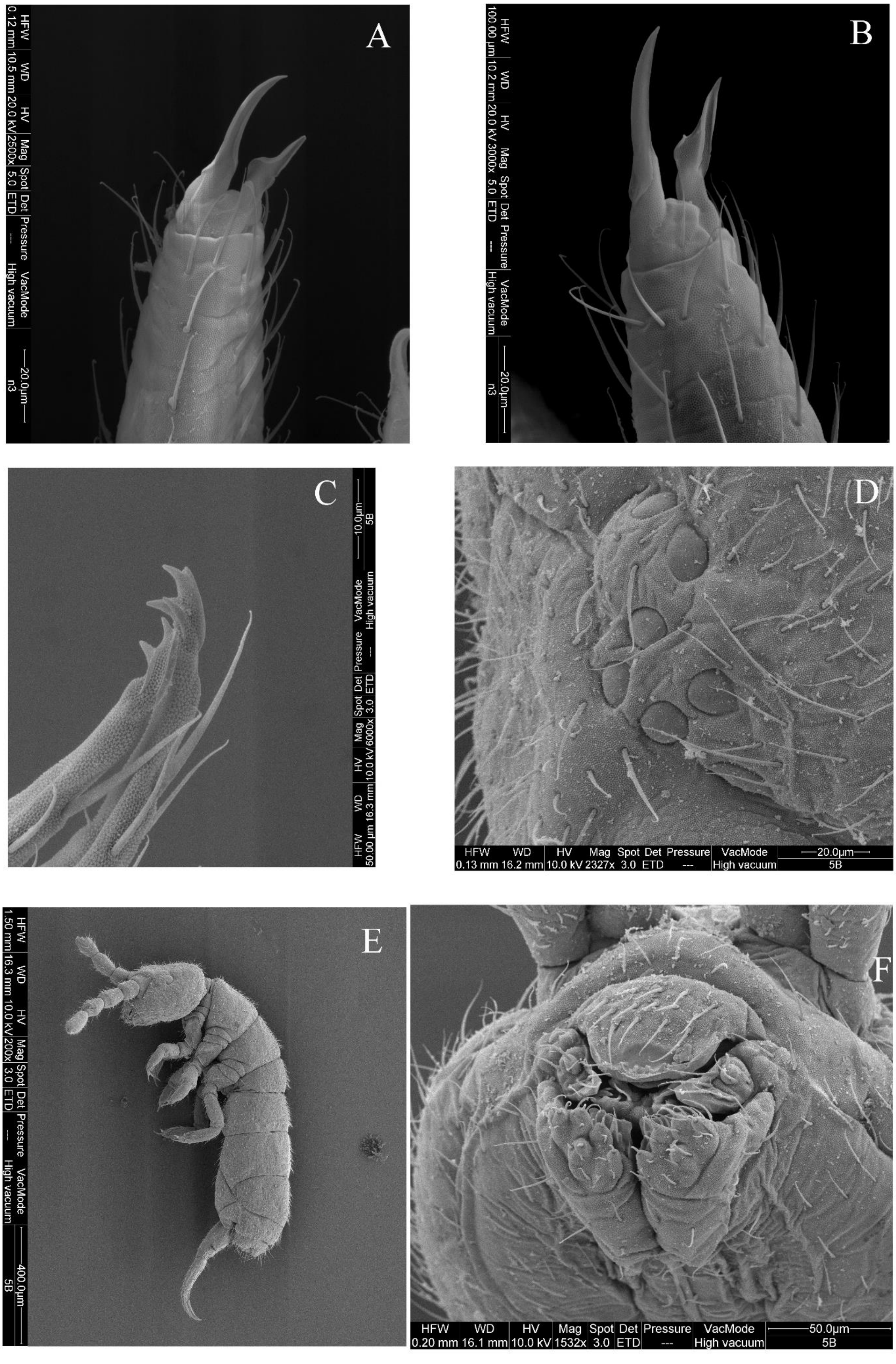

Figure 9 A-F: *SEM pictures of "species A". A-B: claws and empodium (emp in picture A without inner tooth, emp in picture B with inner tooth); C: mucro; D: Ocular plate; E: individual; F: mouth part*

Desoria/Vertagopus sp. n. “Species GLN” morphological description

Populations (GLN)

***Figure 10**: color pattern and general appearance of “species GLN”*

Body. Mean body length (without antennae) 1.3 mm (standard deviation: 0.1 mm on 10 specimens, **Table 2**). Colour black with appendages a little brownish, (**Fig. 10**); juveniles are brownish. Cuticle granulation fine and regularly distributed; all dorsal tergites separated from each other, **but Abd. V-VI are not clearly separated by a narrowing** (**Fig. 11G**). Abd. III and IV of approximately same width.

Chaetotaxy. Terga, consisting of micro-, meso- and macrosetae, these latter well differentiated on last abdominal tergites (Abd. IV–VI, in median position), but not well distinguished from ordinary setae on other tergites (**Fig. 11G**). No setae in ventral side of Th. II-Th. III. All setae smooth. Macrosetae on Abd. V 1 times median length of tergite and 2.2 times as long as inner edge of Claw III (**Table 2**). Sensory chaetotaxy constituted by *ms*-setae, *accp*-, *al*- and *as*-setae. Only Th. II and Abd. III have *ms*-setae (formula 10/001). Dorsal *s*-setae constituted by single *al-s*eta on Th. II and Th. III, two *as*-seta on Abd. V and by *accp*-setae normally set within *p*-row (**Fig. 11G**). The number of *accp*-setae can be expressed as 3, 3/ 3, 3, 3, 5, 3.

Head. Antennae longer than cephalic diagonal (D/A = 0.33, Antenna =0.38 mm). Ratio among Ant. I/Ant. II/Ant. III/Ant. IV is 1 / 1.7/ 1.6 / 2.9 (**Table 2**). There are often cases of asymmetry among *s*-setae between antennae of the same specimen. Ant. I has 8-13 *s*-setae in ventro-lateral position, 1-3 of them are shorter and in distal position; 2 microsetae in ventro-proximal position (**Fig**. **11B**). Ant. II has 6-11 *s*-setae in distal position. Ant. III has a sensory field that includes 2 inner *s*-setae of AO III, one lateral *ms*-seta and about 18 *s*-setae (**Figs 11C**). Ant. IV has one big subapical, spherical organite and a bifurcate pin-like seta (**Fig**. **11H**). Eye spots strongly dark pigmented with 8 + 8 ocelli subequal and very small (**Figs 11A**). PAO little elongated, about 3 times as long as diameter of nearest ocellus (**Fig. 11A**). Prelabral setae 4. Labral formula as 5-5-4 and 4 papillae **squared at the apex** (**Fig. 11I**). Maxillary palp bifurcated and maxillary outer lobe with 4 sublobal hairs. Labial palp with 5 papillae and a total of 16 guard setae (Fjellberg 1999) distributed as: A_1, B_{1-4}, C_0, D_{1-4}, E_{1-7}. Hypostomal papilla with H shorter than h_1/h_2. Proximal (px), basomedian (bm) and basolateral (bl) fields of labium with 4, 4 and 5 setae, respectively. 4-5 postlabial setae. Mandible with well-developed molar plate. VT with 0 + 0 anterior, 4 + 4 latero-distal and 4 posterior setae with 2 in apical transverse row (**Fig**. **11F).** Retinaculum with 4 teeth and 5-6 setae.

Furca. Furca longer than antenna; ratio of mucro/dens/manubrium = 1 / 25 / 13 (**Tab. 2**). Ventral setae on manubrium about 36, including ventro-apical setae (8) larger than the others with the exception of 1 + 1 short setae in apical-medial position; more than 40 dorsal setae on Man. Dens with dorsal crenulations, more than 60 ventral and 11-12 dorsal setae. Mucro quadridentate with apical tooth much smaller than subapical one (**Fig. 11D)**.

Legs. 11 setae in the distal apical ring of Tita; 2-3-3 very weakly clavate tenent hairs (**Fig**. **11E**), shorter than inner edge of Cl. Claw of normal shape without lateral and inner teeth; empodium without inner tooth; pretarsus with a pair of setae (**Fig**. **11E**).

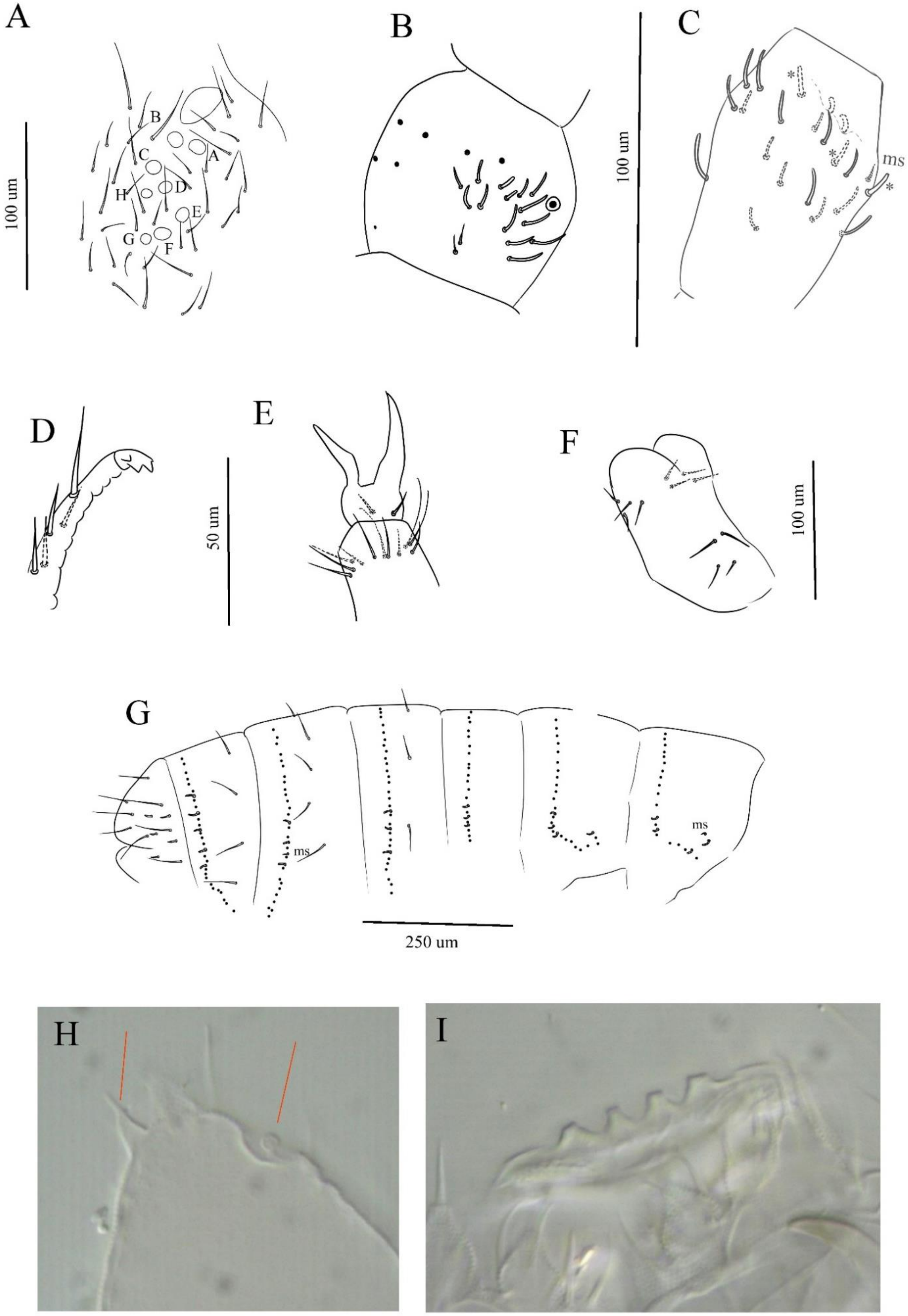

Figure 11 A-I: *drawing and pictures for Species GLN description. A: ocular plate (A-H: OMMA); B: Ant. I, ventral side; C: Ant. III; D: mucro; E: Claw III; F: latero-posterior side of VT; G: accp sens and macrosetae; H: Ant. IV organite and pin-like seta; I: papillae labrum*

Notes on *Vertagopus alpinus* Haybach, 1972 and *V. helveticus* Haybach, 1980

Populations (PAS, MDG, MIA*, MOR2*). **Figure 12**.

Figure 12: *general appearance of* Vertagopus alpinus *(PAS population).*

Taxonomic notes on *V. alpinus* have been made on the basis of Mer de Glace, Pasterze and Miage specimens:

<u>Antennae</u>: Ant I has 9-13 *s*-setae in ventro-lateral position, 1-2(3) of which are shorter in distal part; 2(3) microsetae in ventro-proximal position. Ant. II has about 5 *s*-setae in distal position. Ant. III has a sensory field that includes 2 inner *s*-setae of AO III, one lateral *ms*-seta and 8-10 *s*-setae. Ant. IV with one simple subapical, peg-shaped organite and a bifurcate pin-like seta.

<u>Sensory chaetotaxy:</u> Sensory chaetotaxy is very constant and is constituted by *ms*-setae, *accp*-, *al*- and *as*-setae. Only Th. II and Abd. III have *ms*-setae (formula 10/001). Dorsal *s*-setae constituted by single *al-s*eta on Th. II and Th. III, single *as*-seta on Abd. V and by *accp*-setae normally set within *p*-row. The number of *accp*-setae can be expressed as 3, 3/ 3, 3, 3, 3-4, 3.

The number of anterior setae on Man is very variable, from 20 to 32.
For body measurements see **Tab. 2**

Ecologic note: On Pasterze (Grossglockner), Mer de Glace and Miage (Mont Blanc) glaciers it has been only found inside supraglacial debris and not on bare ice. On Morteratsch (Bernina), Tour, Orny and Pèlerins (Mont Blanc) glaciers it has been sampled on bare ice, under stones.

Taxonomic notes: *V. helveticus* probably is not a valid species, as sampled population on Morteratsch (which should be *V. helveticus*) is genetically (but also morphologically) identical to *V. alpinus*. We don't have enough data to strongly support this finding, and further investigation is suggested.

Notes on two populations of *Desoria saltans* Nicolet, 1841

Populations (PDB, GLB). **Figure 13A-B.**

Figure 13 A-B: *A: general appearance of* Desoria saltans *(GLB population); B: bifurcated pin-like seta on Ant. IV (PDB population)*

Taxonomic notes on *D. saltans* have been made on the basis of Pre de Bar and Glacier Blanc specimens, since for Scais glacier only few specimens were available.

<u>Antennae</u> Ant. I has 2-5 *s*-setae in ventro-lateral position, and 5-7 shorter and thicker s-setae in distal part; 2/3 microsetae in ventro-proximal position. Ant. II has about 8-11 *s*-setae in distal position. Ant. III has a sensory field that includes 2 inner *s*-setae of AO III, one lateral *ms*-seta and 7-11 *s*-setae. Ant. IV with one simple subapical, **slightly bifurcated** rod-shaped organite and a bifurcate pin-like seta (basal process very small) (**Fig**. **13B**).

For body measurements see **Tab. 2**

Note on pigmentation: *Desoria saltans* is well distinguished from other ice-dwelling species by the very often visible purple reflections (**Fig. 13A**), especially in the juveniles.

Note on *Gnathisotoma* sp. 2

(population EST). **Figure 14A-B**.

Figure 14 A-B: *A: general appearance; B: mucro*

This *Gnathisotoma* species from Pyrenées has a maxilla with normal lamellae, not elongated as in *Gnathisotoma bicolor*. VT has no anterior setae, mucro has an apical dens slightly smaller than the subapical one (**Fig. 14B**). This species of *Gnathisotoma* does not correspond to any species described because of the shape of the maxilla, that is elongate in all known European species, and the pigmentation, and thus needs further investigations, since the low number of specimens collected does not allow to describe this species.

Note on *Gnathisotoma* sp. 3

(population TOU2)

Figure 15: *general appearance of* Gnathisotoma *sp. 3*

This species of *Gnathisotoma* from Mont Blanc is the first report of this genus for Alps. From preliminary morphological identification it shows a characteristic maxilla with all lamellae elongated and a mucro with an apical dens slightly smaller than the subapical one. The pigmentation is similar to that one of *Gnathisotoma bicolor* from Pyrenées (**Fig. 15**). Characteristic of *Gnathisotoma* sp.3 is the presence on ventral tube of 4+4 lateral, 3 posterior and 1+1 anterior setae.

		length (micrometers)																
		Head (dorsal)	head + body	AntI	AntII	AntIII	AntIV	**Antenna**	**Head + Body + Antenna**	Cephalic diagonal	Furca	man	dens	mucro	Mac (abdV)	AbdV	inner edge of Claw3	Mandible (from apex to molar plate, included)
species B	mean value	**314**	**1490**	**64**	**97**	**89**	**176**	**427**	**1922**	**381**	**447**	**168**	**267**	**11**	**53**	**92**	**39**	**85**
	standard deviation	46	291	7	9	9	16	36	308	20	30	19	30	1	5	12	2	8
	number of misuration	12	11	13	13	13	13	13	11	3	11	12	12	11	13	13	13	7
species A	mean value	**341**	**1729**	**64**	**102**	**94**	**190**	**451**	**2175**	**416**	**447**	**172**	**267**	**11**	**51**	**96**	**42**	**88**
	standard deviation	31	188	10	11	11	16	42	210	36	38	22	24	1	6	11	4	9
	number of misuration	29	29	33	33	33	33	33	29	5	29	31	29	31	30	28	29	14
specie GLN	mean value	**284**	**1296**	**53**	**90**	**85**	**153**	**380**	**1676**	**335**	**461**	**151**	**297**	**12**	**62**	**63**	**29**	**69**
	standard deviation	22	100	5	12	11	14	37	118	18	42	15	28	1	7	9	4	8
	number of misuration	10	10	10	10	10	10	10	10	3	10	10	10	10	9	9	8	7
Desoria saltans	mean value	**403**	**1864**	**68**	**119**	**109**	**233**	**529**	**2393**	**484**	**665**	**230**	**421**	**15**	**59**	**102**	**50**	**123**
	standard deviation	38	178	3	7	5	18	21	183	52	59	25	40	1	5	6	3	6
	number of misuration	10	10	10	10	10	10	10	10	4	10	10	10	10	10	10	10	6
Vertagopus alpinus	mean value	**288**	**1420**	**53**	**76**	**71**	**142**	**342**	**1757**	**330**	**473**	**154**	**304**	**11**	**36**	**73**	**33**	**77**
	standard deviation	24	157	5	3	3	12	17	173	17	62	28	37	1	5	14	5	9
	number of misuration	12	11	9	9	9	9	9	11	3	12	9	9	9	9	9	9	4

Table 2*: body measurements*

Distribution pattern of ice-dwelling species

Figure 16 reports the geographic distribution of the studied species. In the Northern part of Alps "species A" is the most frequent ice-dwelling springtail and shows a continue distribution from Pièce (Pennine Alps) to Mittelberg glacier (Oztal Alps); the Southernmost population of this species was found on the Amola glacier in Adamello massif (Rhaetian Alps, Italy), but most of the populations sampled are in Switzerland and Austria. "Species B" is the most common species in the Central-Southern Italian Alps, with a distribution almost limited to the Valtellina area (Rhaetian Alps, Italy). Both species are quite genetically homogeneous. *Vertagopus alpinus* and *Desoria saltans* have a more fragmented distribution: *D. saltans* have been found with two populations in Western Alps (Écrins and Mont Blanc) and a third population have been found on Scais glacier in Eastern Alps (Orobian Alps). *V. alpinus* spreads from Western Alps to the Nort-Eastern Alps, but it has been found only on three massifs, on Mont Blanc (Grain Alps, Western Alps) - where it is present on several glaciers – on Morteratsch glacier (Bernina massif, Rhaetian Alps; only few individuals) and on Pasterze glacier (Grossglockner, Western Tauern Alps). "Species GLN" have been found only on Glacier Noir (Écrins massif, France). Some important glacial areas host several species, in particular Mount Blanc, Ortles-Cevedale massif, Bernina massif and Écrins. *Gnathisotoma* sp. 3 has been found only with few individuals on Tour Glacier on Mont Blanc.

***Figure 16:** Distribution of ice-dwelling springtails. Orange= "species A"; green="species B"; red=* Vertagopus alpinus, *light-blue=* Desoria saltans*; violet="species GLN", yellow =* Gnathisotoma *sp.3, grey= unidentified species,*

PRELIMINARY DISCUSSION AND PERSPECTIVES

From these results we can, firstly, confirm the hypothesized existence of an unexplored biodiversity of ice-dwelling springtails on the European Alps: we added and described three new species to the two already known (*Desoria saltans* and *Vertagopus alpinus*). On the other hand, we suggest that *Vertagopus helveticus* probably is not a valid species, as an ice-dwelling springtails sampled on Morteratsch - the locus typicus of *V. helveticus* as described by Haybach, 1980 - is genetically identical to *V. alpinus* and the morphological traits of the two species are not clearly distinguishable. Comparing our findings with historical records, we could also hypothesize that the *Isotoma* 'sp. G' found by Eisenbeis and Meyer (1999) on Oberaar (Switzerland) and Rotmoos (Austria) glaciers and *Desoria saltans* found by Kopeszki (1988) on Mittelberg (Austria) were actually "species A". Kopeszki (1988), in fact, stated that the specimens he found did not fit with the descriptions of *D. saltans;* thus the next research step should be to check his original material for confirm this hypothesis.

Phylogenetic analysis is still ongoing thus it will be completed when all the genetic data will be available (*cox1* of some populations still lacks and also a nuclear gene will be sequenced, 18S), in order to have more robust results. However, we could already do some early considerations on the basis of morphological and genetic data available by now: the three new species we are going to describe belong to a phylogenetic group that includes *Vertagopus* and *Desoria.* There are evidences that both these genera need to be revised, especially *Desoria* that is clearly a paraphyletic genus, as observed in previous works (Stevens *et al.* 2006; Fjellberg 2007; Stevens & D'Haese 2017, Valle et a. 2021). Thanks to our data, it will be possible to compare all available sequences of *Desoria* and *Vertagopus* with our sequences and try to re-define these two genus and assign the new species to the proper one. Meanwhile we could hypothesize that *Desoria calderonis* (Valle et al. 2021) should be indeed *Vertagopus calderonis*. It is not clear what is the origin of *Gnathisotoma* genus, since its relations with respect to *Desoria* and *Vertagopus* branches changes considering *16S* or *cox1*.

An important morphological consideration on *Gnathisotoma* could be made on the populations of *Gnathisotoma* sp. 2 found on Pyrenées, with normal lamellae of maxilla, and *Gnathisotoma* sp. 3 found on Mont Blanc, with 2 anterior setae on VT. The genus was originally described by Cassagnau (1957) on the basis of *G. bicolor*, characterized by elongated lamellae of maxilla and the absence of anterior setae on VT. We confirm what hypothesised by Fjellberg (2010) regarding a wide spectrum of variability in *Gnathisotoma* and the evidence that none of the diagnostic characters are clearly inclusive of all species and unique to the genus. There is only a gradual difference between the *Gnathisotoma, Desoria* and *Vertagopus* species. Despite this, *Gnathisotoma* appear as a distinctly monophyletic group. We suggest as an important diagnostic constant feature for this genus the peculiar shape of the quadridentate mucro with an apical dens slightly smaller than the subapical one.

From the biogeographic point of view, we see a clear distribution pattern with the Northern part of Alps dominated by "species A", the Central-Southern part dominated by "species B"; both species are quite genetically homogeneous. *V. alpinus* and *D. saltans* have a more fragmented distribution; populations of *D. saltans* are genetically more differentiated. The low presence of *Desoria saltans* in our samplings is in contrast with many historical report for Switzerland and Austria: its presence in Eastern Alps is certain – since Lauteraar and Finsteraar in Switzerland (Bernese Alps) are the *locus typicus* (Nicolet, 1841; Handschin 1924) and we found also a population in Orobian Alps– but we suppose that many reports actually refer to other ice-dwelling species. Some example are Kopeszki's (1988) report (see above) or that one by Stoppani (1876), made without a morphological identification but only on the base of its ecology (in both cases, it was "species A").

Sites for which we have few genetic data that suggest the existence of several new species (PEI, CLA). These data suggest also that Maritime Alps, a peripheral mountain area already known as hotspots of biodiversity due to glaciation history (Medail & Quezel, 1999), could host isolated glacial species, well differentiated by the ones in Inner Alps. On the other hand, other important glacial areas host different species (Mount Blanc, Ortles-Cevedale massif, Bernina massif and Écrins), maybe indicating potential cold refugia during warm stages. From our data it emerges that a crucial area for "glacier flea" biogeography are the Western Alps and further investigations should consider to better detect this biodiversity. An important biogeographic datum regards the first record of *Gnathisotoma* for European Alps.

From the ecological point of view, ice-dwelling springtails seem a well defined cryophilic group of springtails, as suggested by Eisenbeis and Meyer (1999), and are differentiated by firn- and debris-dwelling cryophilic springtails like *Gnathisotoma.* In Alps, as in Pyrenées, this genus lives at the margin of the ice (in fact, we found only 9 specimens on a single Alpine glacier). Eisenbeis and Meyer (1999) affirmed that the intensive body pigmentation certainly functions as protection against the high radiation on the glacier surface: firn- and ground-dwelling cryophilic springtails are not so intensively pigmented, especially not on legs. From our data we could confirm this observation, being all supraglacial species completely dark, while only *Gnathisotoma* species show less pigmented appendages. Thus, also this evidence proves that *Gnathisotoma* sp. 3 from Mont Blanc – with yellow antennae - is a debris-dwelling cryophilic springtail. We could suggest this different pattern of pigmentation, from totally black to partially unpigmented on the appendages, as good indicators of the ecology of each species.

We did not find (or we found in very low number) springtails in some very polluted glaciers, like Stelvio and Giogo Alto glaciers, heavily impacted by skiing and plastic fragments. It should be interesting to deepen the sensitivity of these organisms to this type of pollutants and, possibly, also to that due to plastic tarpaulins used for reduce ice-melting.

Ice-dwelling springtails could not be found on rock glaciers: we suppose that it is due to the depth at which ice is located inside the stony debris. While we only sampled on the surface of the rock glacier. The potentiality of rock glaciers as habitat for these organisms is high, but we still have to overcome the difficulty in sampling at the deep interface rocks-ice.

As additional output of this paper, we will produce also an identification key for Alpine ice-dwelling springtails.

Preparation of an identification Key for Alpine ice-dwelling springtails:

Notes on differences among species:

- ***Desoria saltans*** is easy identifiable for the presence of anterior setae on VT (2-8), simple maxillary palp, few maxilla lamellae a little bit elongated, absence of clavate tenent hairs
- ***Vertagopus alpinus*** has short and clearly clavate tenent hairs (2-3-3) and about 28-32 anterior setae on Man
- In "**species GLN"** Abd. V-VI are not clearly separated by a narrowing.
- With only weakly clavate tenent hairs (2-3-3), there are "species A" and "species B": In "**specie B**" There is a cheta among OMMA A+B and C+D, differently from "**specie A**". In addition In "species B" there are only 14-22 anterior setae on Man, in specie A 38-40, while in GLN 36.
- ***Desoria calderonis*** has a very restricted distribution range (Calderone glacier, Gran Sasso)

Acknowledgments and fundings

BMR genomics (https://www.bmr-genomics.it/azienda/chi-siamo/).
This work was partially funded by the European Research Council under the European Community's Horizon 2020 Programme, Grant Agreement no. 772284 (IceCommunities) (G.F. Ficetola).

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4.2 Global scenario, local approach: challenges for alpine plants, insects and spiders in a warming world

PAPER IN PREPARATION

Potential Journal: Nature Climate Change

Title: Global scenario, local approach: challenges for alpine plants, insects and spiders in a warming world

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Plant and animal species are reacting to the ongoing climate change through a wide array of responses, depending on different time and spatial scales, including adaptation, speciation and extinction processes (Merila & Hendry, 2014; Schilthuizen et al., 2013; Bellard et al., 2014), migration along altitudinal or latitudinal gradients, local survival in refugia (Rull, 2009; Stewart et al. 2010, Lenoir et al., 2017, Gentili et al. 2020; Batori et al 2022) and consequent expansion, shrinking or displacement of their range distribution (Birks and Willis, 2008; Rull, 2009; Bellard et al., 2014). Individual species could show different responses in terms of direction, pace and intensity, potentially breaking up species assemblages and affecting their network of interaction (Brambilla and Gobbi, 2014).

Mountain areas of the world are hotspot of biodiversity, but increasing evidence indicates that species living at high altitudes are expected to be particularly threatened (Brambilla et al., 2016; Chamberlain et al, 2013; Viterbi et al., 2013, Monroy-Gamboa et al. 2021). However, plant and animal life in high-altitude ecosystems is affected by many ecological factors acting at different scale, from regional climate to local topographic, edaphic and microclimatic features (Hulsof & Spasojevic, 2020). The role of local ecological factors may overrule that of regional climate in terms of species survival in a given site (Corlett & Tomlisson,2020) and this, in turn, can make the difference for large-scale modelling of future species distribution. This is particularly true for a wide suite of living organisms with comparably small size and/or low mobility, that are particularly linked to the site-specific ecological profile. It is worth noticing that such organisms represent the vast majority, in terms of species and individual number, of the extant biodiversity, including microorganisms, algae, fungi vascular and non-vascular plants, mesofauna and arthropods (Gobbi et al. 2021). For this reason, a crucial and still underexplored challenge of modern ecology is that of including local ecological factors into regional-scale modelling of species responses to climate change, possibly taking into account different taxonomic groups at the same time.

Understanding the fate of high-altitude species in relation to the reduction of cold environments (e.g. cryosphere) and consequent mountain environment changes is among the most exciting challenges in mountain biodiversity conservation and global change biology. Despite this, two weaknesses are present in the scientific literature: 1) quantitative multi-taxa with detailed environmental data are available only at local scale, while an upscaling at regional level of such information is lacking.

Such task may be hindered by the need of field-based, homogeneous, detailed collection of biotic and abiotic data over a large area, coupled with the taxonomic knowledge of different organisms; however, such a “think globally, act locally” approach is needed to catch an elusive but fundamental component of organism responses to environmental change triggered by climate change; 2) few attention has been given to identifying climate refugia, at least in the near-term temporal scale. Such goal may be reached searching for ice-related landforms (i.e. rock glaciers, debris-covered glaciers; see Gobbi et al. 2021; Brighenti et al 2021) that, thanks to their insulating nature and thermal inertia are good candidates as warm-stage refugia for cold-adapted species. Demonstrating the role of these landforms in slowing down the extinction risk of some species during contemporary climate change could have great impact on environmental protection agencies deputies to develop active climate-adaptation strategies.

To evaluate the possible effect of high-altitude landform types and local topographic and ecological factors in regional-scale species responses to climate change, we planned a standardised sampling design aimed at recording data on vascular plants, ground beetles and spiders in high-altitude landforms of the Italian Alpine Arch. We obtained a dataset including presence and abundance data of 363 vascular plant, 52 ground beetle and 98 spider species in 463 sampling points (Figs. 1-2; Table 1); cutting species with less than 8 occurrences, we selected a database with 179 species of vascular plants, 23 of ground beetles and 25 of spiders. To the best of our knowledge it represents the most comprehensive dataset on high-altitude organisms simultaneously sampled on the European Alps. Sampling points were grouped in seven landform types representing the main high-altitude landform types, originated by gravitational, cryoclastic and/or ice-related processes, on the European Alps (Fig. 1). Species occurrence and abundance data were associated with five soil physical and chemical variables collected contextually on the field (see Tab. 1). These physical and chemical variables that could potentially contribute to the occurrence and abundance of the species we observed (Tab. 1).

Organisms with a potential negative fate (“losers”) are cold-adapted species that are linked to sites at high altitude but do not show the ability to live on ice-related landforms (Fig. 1). For this reason, they are not able to take advantage of the ecological heterogeneity at local scale to escape the progressive habitat loss due to the upshift of the altitudinal belts at regional scale (namely summit traps). Such species are mostly linked to high altitude grasslands and heathlands but also to rocky habitats, and include many plant and spider and some ground beetle species. Spiders seem to be particularly threatened by global warming because, respect to plants and ground beetles, they experience an overall higher percentage of losers. In addition, within this taxonomic group the percentage of losers in slightly higher respect to that of winners. The ability to colonize and survive on ice-related landforms may change significantly the fate of some cold-adapted species; in this case habitat loss may be locally dampened by the occurrence of landforms with a peculiar ecological profile behaving as refugia. The ultimate fate of these climate-change escaping species ultimately depends from that of the related landforms, whose thermal inertia may not last enough to assure their survival throughout a warm climatic cycle. However, the chance for a short-term, local survival could make the difference for the future scenarios of high altitude community composition.

Preliminary results and discussion

Spiders resulted the taxon with the higher percentage of species able of local and temporary survival on refugium areas (e.g. debris-covered glaciers, rock glaciers), followed by some plant species. A peculiar case is that of species that are able to take advantage of the primary succession triggered by glacial retreat. Such organisms, like some plant and ground beetle species, could experience a temporary advantage due to the increasing areas freed by vanishing glaciers thanks to their pioneer attitude. However, with succession proceeding, biotic interactions are ultimately supposed to cause the disappearance of specialized pioneers, and the biodiversity increase may represent a temporary phenomenon (Losapio et al. 2021).

We defined as “winners” all the species showing a preference for warmer sites within the range of our investigation sites (Fig. 1). Such species are generally negatively linked to altitude, have none or negative relationship with ice-related landforms, and are supposed to show a positive trend within the altitudinal limits of the investigated sites. We are aware of the fact that they may experience a negative trend at lower altitudes because of the increasing competition from incoming species presently occurring at even lower elevation. For this reason, the “winner” attribute may not represent the overall trend that a species is supposed to experience. Interestingly, both for plant and ground beetle species the percentage of winners is higher respect to the percentage of losers.

Species without a clear response pattern to environmental predictors are included into the “neutral” category (Fig. 1); some of them may show a significant positive ability to grow and reproduce on ice-related landform, with a probable increased survival possibility in these refuge areas. This is the case of several carabid and spider species, while plants show a lower percentage of neutral species.

Overall, ca. % (n=17) of the species are associated to ice-related landforms, 37% (n=7) of them experience a strong link/relationship with them.

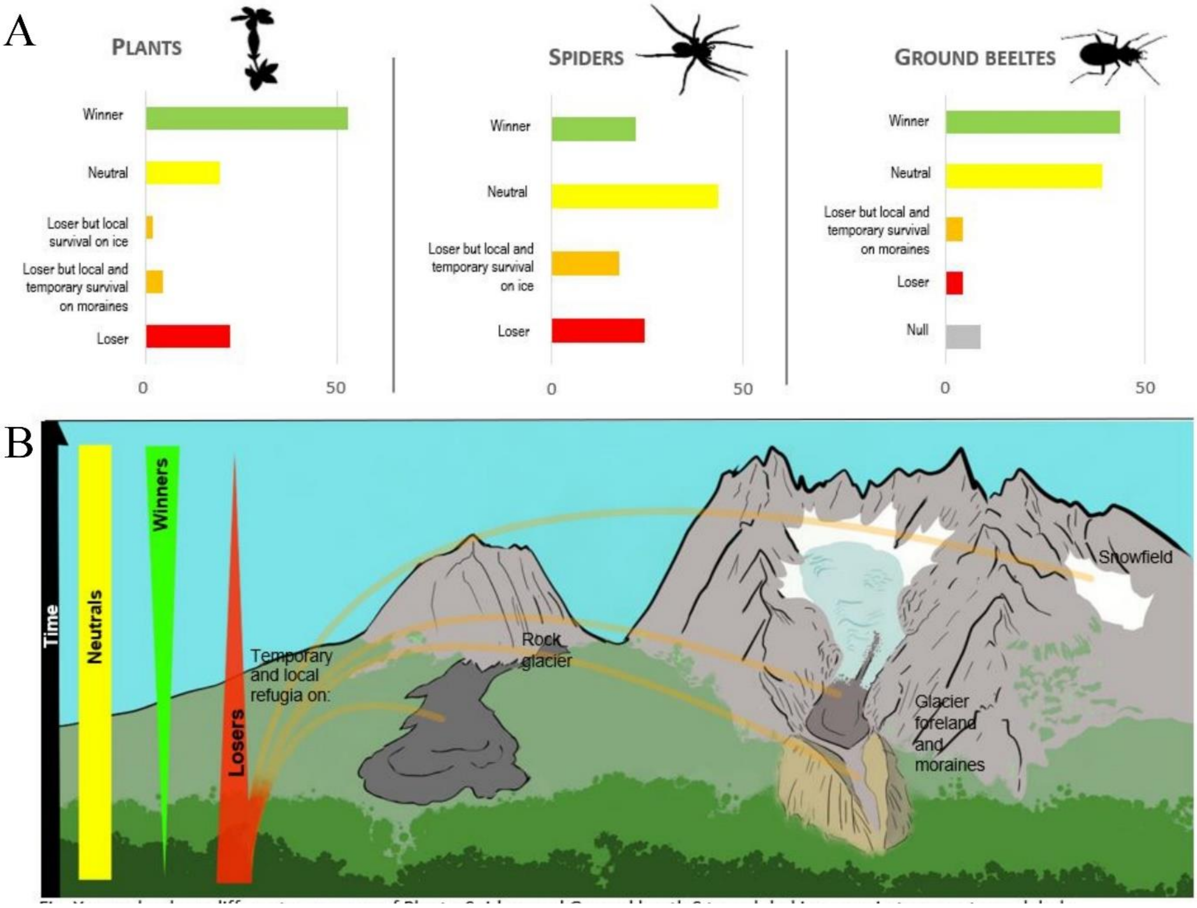

***Figure 1**: A: different responses of plants, spiders and ground beetles to a global increase in temperatures: B: general trends ad possible refugia for loser species (Illustration: B. Valle)*

These results highlight the importance of analytic works performed at local scale for finding general pattern of biodiversity trend: only a rich and detailed database is able to give reliable results and take into account local environmental conditions, whose role could be fundamental for present and future distribution pattern at regional scale. Thanks to these data we were able to predict which taxa will be among the most sensitive to climate change in glacial and periglacial habitats: conservation actions could necessary focus on these species. For some of these threatened species, usually cold-adapted and not competitive, we also predict potential local refugia on the basis of their preferences for ice-landform.

The analyses outlined different responses among the investigated taxa, particularly with regard to the capability of finding suitable refugia on ice-related landforms. This phenomenon could possibly affect the interaction networks within high altitude communities, with particular reference to food webs. Investigations on other key taxa are needed to shed light on this topic, taking into account primary consumers at the base of the food web such as springtails.

To positively assess the role of a specific landform as a refugium, an important point to be clarified is its survival under a prolonged unfavourable climatic period. Although the climatic inertia of rock glaciers and debris-covered glaciers has been already hypothesized, a long warm period could in any case lead to their disappearance, ultimately dooming to extinction their related ice-related biodiversity.

Methods

Study taxa

Vascular plants, ground beetles (Coleoptera: Carabidae) and ground-dwelling spiders (Arachnida Araneae) were selected as study models for the following reasons: i) they represent one of the best known component of high-altitude terrestrial communities from the taxonomical and ecological point of view (Hagvar et al 2020, Losapio et al 2021), ii) their sensitivity to environmental and climate changes is already acknowledged (Cauvy-Frauniè & Dangles 2019) iii) ground beetles and spiders are not directly trophically related to vascular plants because not phytophagous (Zou et al 2013), and iv) local-scale extinctions, altitudinal migration, or changes in population size, were already documented and forecasted (Losapio et al 2021; Pizzolotto et al 2014; Valle et al. 2020) (Fig. 2).

Investigated landform types

The most common high altitude landform types were investigated. Specifically, seven landform types were considered: stable slope (CS), active scree slope (SS), active rock glacier (RG), debris-covered glacier (DG), glacier foreland <100y (F1); glacier foreland >100y (F2), and snowfield (SF) (Fig. 2). A stable slope is characterised by i) terrain not directly affected by physical processes able to create disturbance, ii) vegetation at its last successional stage and ii) terrain ice-free since the Late Glacial (c. 10.000 y BP), thus not involved in Holocene glacial dynamics. An active scree slope is a slope mantled by a layer of relatively coarse, unconsolidated, rock debris, originated by gravitational processes which accumulate rock debris at the base of the cliff. An active rock glacier is a lobate or tongue-shaped landform consisting of coarse debris with interstitial ice or ice-core, characterized by creeping movement due to ice deformation; it is one of the most evident permafrost landforms. A debris-covered glacier (also known as black-glacier) is a glacial body where the largest part of the surface is covered by debris, which deeply influences glacier surface energy budget, ablation rates, long-term volume and surface variations. A glacier foreland is the area between the current leading edge of the glacier and the moraines of the latest Holocene maximum (about 200y ago in the European Alps). A snow field is a semipermanent accumulation of snow.

The investigated landform types were clustered in two groups on the base of the presence or absence of surface or interstitial ice: ice-related landforms (RG and DG) and landforms without ice (CS, SS, F1, F2 and SF).

Plants, ground beetles and spiders collection

Vegetation surveys were performed on 25 m2 surfaces at each sampling point: the cover of the whole plants and of every single species was estimated with a resolution of 5%. For species with a cover value lower than 5% was assigned a cover value of 3% or 1%, for rare and sporadic species, respectively

Ground beetles and spiders were sampled by pitfall trapping (see. Gobbi 2020). Specifically, a trap was placed in each sampling point and remained active during the snow free period (approximately early July - late September), being emptied and refilled approximately every 20 days. The sampled arthropods are stored in alcohol (ca. 70%) at MUSE-Science Museum of Trento collections.

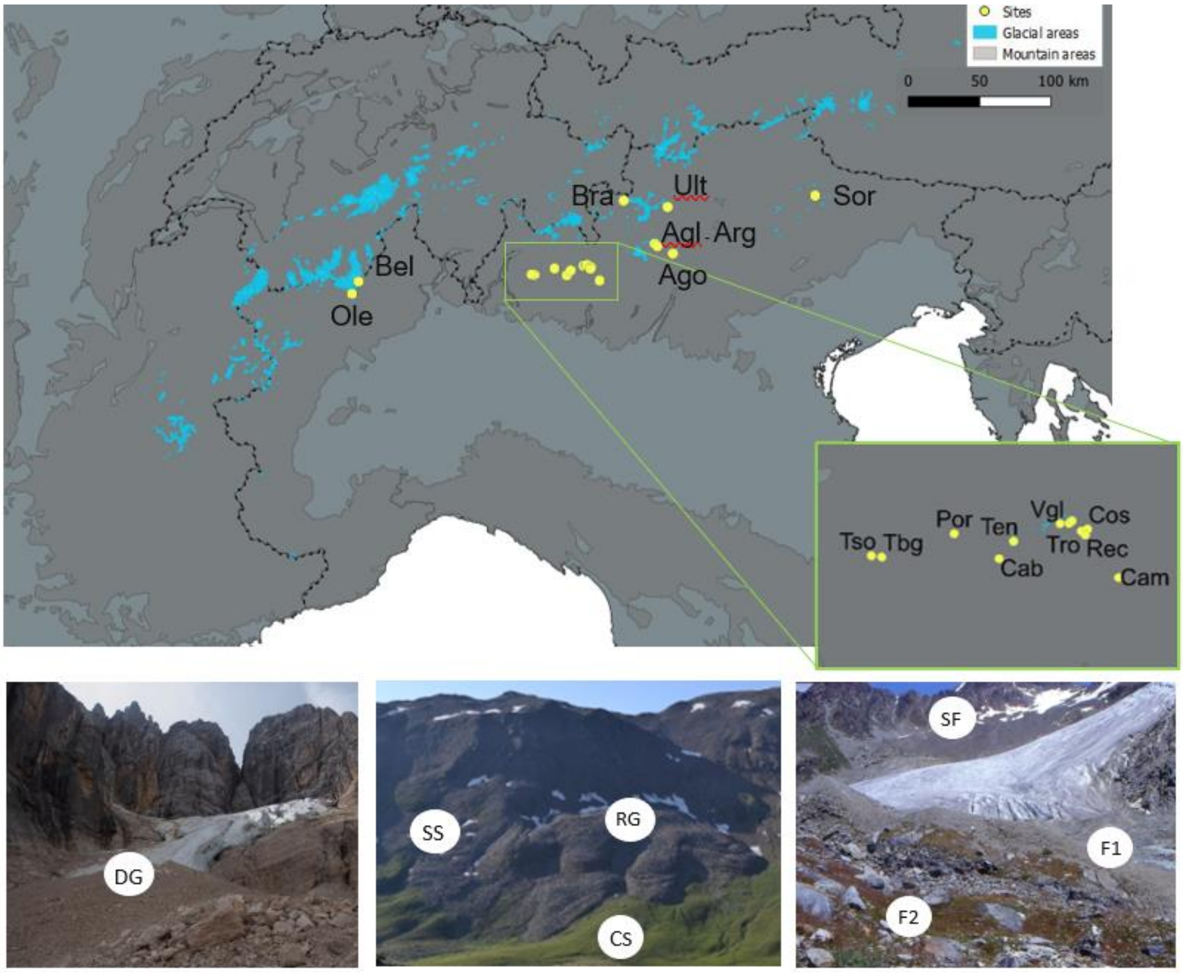

Figure 2: *sampling sites and landforms investigated. Legend landform: DG= Debris-covered glaciers; RG= Rock glaciers; SF=Snowfield; F1 and F2= glacier foreland successional stages (F1 < 100 years, F2>100 years); SS= scree slope; CS = Control slope. Legend site names: Ole= Col d'Olen, Agl=Val d'Amola (glacier), Arg= Val d'Amola (rock glacier); Tro = Trobio glacier; Vgl= Valmorta rock glacier; Tbg=Pizzo Tresignori (Bergamo province); Tso= Pizzo Tresignori (Sondrio province); Rec= Recastello; Por=Porcile Pass; Mal=Malgina; Cos=Costone mountain; Cab= Cabianca; Ten=Diavolo in Tenda peak; Cam= camino Peak; Sor= Sorapiss glaciers; Ago=Agola glacier. (Illustration: B. Valle)*

Environmental predictors

The following environmental predictors were considered: altitude (m asl) , solar radiation and soil variables (coarse debris fraction: sum of gravel and sand fractions expressed as percentage), soil pH ('pH') and organic matter content (expressed in g/kg). Specifically substrate samples were taken at the surface for physical and chemical analysis: at each sampling point a sample of ~2 kg was taken for particle size distribution analysis, and a sample of ~200 g was taken to measure soil pH (in 1:2.5 soil:water), and organic matter content (Walkley-Black method).

Statistical analyses

To explore the potential role of landform types, and especially with ice-related forms, we performed a three-step analysis. In step one, we evaluated what species display an occurrence pattern positively or negatively associated with landforms with ice (vs. landforms without ice), irrespectively of all other variables; species with a positive association with landforms with ice are those for which the former act, or could potentially act, as refugia. In step two, we assessed the effect of landforms with ice on species occurrence, considering also the effect of all other selected predictors and spatial autocorrelation; species positively associated at this step with landforms with ice are those that are actually exploiting the latter as refugia, benefiting from the presence of ice. In step three, considering only occurrence sites, we evaluated what environmental predictors affected local species abundance, considering the detailed effect of different types of landform (Tab. 1).

We standardized all continuous variables before running models, i.e. predictors were centered around their mean and scaled by standard deviation (Cade, 2015; Schielzeth, 2010). All variables were only weakly or moderately correlated (all $r < |0.4|$). To model the effect of the selected environmental variables on occurrence and abundance of our model species, we built generalized additive models (GAM), with binomial error distribution for presence/absence data and with Poisson distribution for abundance ones. To avoid too rare species (and sites with plenty of zeros), we restricted the analyses to those species occurring in at least 8 sampling points for presence/absence data, and in at least 30 sampling points for abundance data.

In step one, we only tested the potential effect of landforms with ice vs. landforms without. In steps two and three, we started by entering all the environmental variables in the GAM, and progressively simplified models, following a step-down procedure (Calvi et al., 2018; Zuur et al., 2009) (Zuur et al. 2009, Calvi et al. 2018), using p = 0.1 as threshold for variable removal (Brambilla et al., 2019). Continuous variables were tested as smooth terms; to control for spatial patterns in step two, a tensor term of longitude and latitude (full tensor product smooth; Wood, 2017) was entered in the model to correct for spatial autocorrelation patterns (often important for high-elevation species with low mobility; Gobbi and Brambilla, 2016) due to biogeographical, historical or local reasons. All analyses were performed in R (R Development Core Team, 2020), by means of the package 'mgcv' (Wood, 2019).

Then, on the basis of the models' outcomes, we assigned each target species to one of the categories summarized in Table 1, defined according to the response to the selected environmental predictors. This analysis being aimed at predicting high altitude species responses to climate change and so, to attitudinal shift of temperature and environments, the most important element in in order to predict these future scenario is the relation to altitude: in our categories, "Losers" and "Winners" are species with respectively a negative or positive significant response to altitude, "Neutrals" are species that do not show a response to this factor. Then, for Losers and Neutrals we considered species relation to other factors: species positively related to ice according to model 1 and 2 (and, secondarily, according to the model 3 and to abundance relation to landforms, DG, RG and SF) and species positively related to proglacial landforms (F1 and F2). These relations are particularly important for Losers, that can find on supraglacial/periglacial/proglacial landforms temporary refugium: these organisms are indicated with the category "Losers with local and temporary survival on ice and/or moraine"

Given that GAMs are highly suited to analyse spatially structured data, thanks to the flexibile spatial tensor, but is not possible to perform a full model validation of GAM models, to have more robust results other analyses (that can be fully validated) are currently in progress. Specifically, analyses using glmmTMB (with a spatial error) for presence/absence data, and GLS for abundance data, are presently ongoing.

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Table 1: *results of Gam models. Legend: p=plant; c=ground beetle; s=spider. Colours in "fate" column": red= loser; green=winner; yellow=neutral; orange = Loser but local survival on ice or moraines; grey=unpredictable.*

				LF_ICE		PA spatial tensor								LF_code abundance (no spatial tensor)												
ID	**name**		**FATE**	**coeff_LF_ICE**	sign_LF_ICE	NULL MODEL	**LF_ICE_presence/absence**	ELEVATION	SOLAR_AVG	SOIL_FINE	SOIL_REACTION	SOIL_ORGANIC_M	TE(X,Y)	NULL MODEL	CS	DG	F1	F2	RG	SF	SS	ELEVATION	SOLAR_AVG	SOIL_FINE	SOIL_REACTION	SOIL_ORGANIC_M
92	***Linaria.alpina***	p	🟥	0.21	0.5424			Ω+	+	-			+													
5	***Adenostyles.leucophylla***	p	🟥	-0.97	0.3603			Ω+	Ω				+													
12	***Androsace.alpina***	p	🟥	-0.74	0.1748			+			Ω+		+	x												
41	***Carex.rupestris***	p	🟥	-0.60	0.5766			Ω+				Ω														
44	***Cerastium.carinthiacum***	p	🟥	-0.36	0.6437		-	Ω+					+													
121	***Primula.glutinosa***	p	🟥	-15.26	0.9784			Ω+																		
134	***Salix.retusa***	p	🟥	-15.24	0.9848			Ω+					+													
140	***Saxifraga.caesia***	p	🟥	-1.00	0.1045			Ω+		?	+	Ω		x												
154	***Sibbaldia.procumbens***	p	🟥	-15.24	0.9848			+			-	Ω	+													

45	***Cerastium.cerastoides***	p	🟧	-15.24	0.9824		U+	Ω+				+								
31	***Campanula.carnica***	p	🟧	-15.26	0.9833		Ω+	+												
175	***Viola.comollia***	p	🟧	-0.36	0.6437		Ω+	+												
1	***Achillea.atrata***	p	🟧	-1.15	0.2708		Ω+		+			+								
119	***Primula.daonensis***	p	🟧	-15.25	0.9790		Ω+		Ω+		Ω-	+								
152	***Senecio.incanus***	p	🟧	0.27	0.5776		Ω+		Ω-	Ω-		+								
124	***Ranunculus.glacialis***	p	🟧	-1.26	**0.0390**		U+	?	Ω-	Ω		+	x							
173	***Veronica.aphylla***	p	🟧	-15.26	0.9833		Ω+			+	Ω-									
47	***Cerastium.uniflorum***	p	🟧	0.43	0.1814	-	+	-		Ω+		+	x							
103	***Oxyria.digyna***	p	🟧	-0.43	0.1785	-	Ω+	-	U-	Ω		+	x							
163	***Thlaspi.rotundifolium***	p	🟧	-1.02	**0.0219**	-	+	Ω-		Ω+	U-	+		+	+	-	+	-	+	
77	***Gnaphalium.supinum***	p	🟧	-1.82	**0.0132**	-	Ω+		Ω+	Ω-		+								+
132	***Salix.herbacea***	p	🟧	-2.72	**0.0075**	-	+		Ω+		Ω-	+	x							
172	***Veronica.alpina***	p	🟧	-0.99	**0.0115**	-	Ω+			?	Ω-	+			-	-	-	-	-	
176	***Hornungia.alpina***	p	🟧	-0.76	**0.0444**	-	+	Ω-		U+	U-									-
76	***Gnaphalium.hoppeanum***	p	🟧	-1.74	**0.0915**		Ω+	+		+		+								
112	***Poa.alpina***	p	🟨	-1.61	**0.0000**	-	Ω+	+	+	Ω+		+		-	-	+	-	-	-	+

75	***Geum.reptans***	p		-0.87	**0.0522**	-	Ω+	?		Ω	-	+				+	-	-	+		U+	
146	***Saxifraga.sedoides***	p		-1.13	**0.0352**	-				+		+			+	+				+	Ω-	
46	***Cerastium.pedunculatum***	p		1.16	**0.0020**		Ω		-	Ω		+			-	-			-	+	Ω	?
144	***Saxifraga.oppositifolia***	p		0.52	**0.0912**		Ω+			Ω+	-	+	x									
139	***Saxifraga.bryoides***	p		0.69	**0.0096**		Ω+	Ω-		Ω	U-	+	x									
86	***Juncus.trifidus***	p		-1.13	0.1296	-	Ω	Ω+	?		Ω	+										
33	***Campanula.scheuchzeri***	p		-1.60	**0.0084**		Ω	+	?	Ω-	+	+			-	+	-		-			
101	***Myosotis.alpestris***	p		-1.22	0.1009	-			U+	Ω	Ω-	+										
89	***Leontodon.helveticus***	p		-3.31	**0.0011**	-	?	Ω+	Ω+	Ω-	-	+			-	-	-	-	-			
52	***Cystopteris.fragilis***	p		-1.84	**0.0119**	-	?		U-			+			-	-	-	+	+			
64	***Festuca.halleri***	p		-0.23	0.6524	-				Ω-	-	+										
94	***Lotus.alpinus***	p		-1.58	0.1275	-	U			Ω-	-											
151	***Sempervivum.montanum***	p		-1.74	**0.0915**	-				Ω	Ω-	+										
16	***Arabis.alpina***	p		-0.41	0.2208	-		?	Ω-	+	U-	+				-	-	-	-			
137	***Saxifraga.aphylla***	p		-0.26	0.7385	-		Ω	-		-	+										
162	***Taraxacum.sp.***	p		-1.29	**0.0345**		Ω			+		+			-	+	-	+	-			
9	***Agrostis.stolonifera***	p		0.78	**0.0265**			-	U			+		+	+					Ω-	?	?

129	***Sagina.saginoides***	p		1.11	**0.0447**					Ω		+										
54	***Doronicum.clusii***	p		2.34	**0.0000**	+	Ω	U-		Ω-		+										
113	***Poa.laxa***	p		1.49	**0.0000**	+	Ω		-	Ω-	U+	+		+	+	+	+	+	+			
61	***Erigeron.uniflorus***	p		-0.09	0.8671	+	Ω		+	+	+	+										
95	***Luzula.alpino.pilosa***	p		-0.16	0.5570	+	Ω-	+		Ω-		+		+	+	+	+	-	+		Ω-	
21	***Artemisia.genipi***	p		-1.74	**0.0915**			+		Ω+		+										
32	***Campanula.cochleariifolia***	p		-1.71	**0.0201**		Ω	+				+	x									
19	***Arabis.pumila***	p		0.77	**0.0595**			-	?			+										
160	***Soldanella.alpina***	p		-2.01	**0.0502**				+	Ω	Ω	+										
36	***Carex.curvula***	p		-2.44	**0.0167**		?		Ω+	Ω-	Ω-	+									Ω-	
48	***Cirsium.spinosissimum***	p		-2.12	**0.0381**		Ω+	Ω+	-	Ω-	-											
109	***Phyteuma.hemisphaericum***	p		-2.55	**0.0124**		?	+	Ω	?						+	+		+			+
13	***Antennaria.carpatica***	p		-15.26	0.9833		Ω	+	+			+										
84	***Juncus.jacquinii***	p		-15.25	0.9858			+	Ω+													
34	***Cardamine.resedifolia***	p		-0.26	0.3623	-	Ω	+	-	Ω-		+		+	+	+	+	+	+			
114	***Poa.minor***	p		0.06	0.8693	-	U+	?			-	+		+	+	-	+		+	-	+	
79	***Helictotrichon.versicolor***	p		-15.27	0.9751		?	+	Ω		Ω-	+										

156	***Silene.quadridentata***	p		-15.25	0.9858		Ω	U+			-	+									
118	***Potentilla.nitida***	p		-15.24	0.9741		Ω	+	U+	U+											
98	***Minuartia.sedoides***	p		-15.26	0.9811			+		+	Ω-	+									
136	***Saxifraga.aizoides.***	p		-15.26	0.9833			+	Ω-	+	+	+									
53	***Daphne.striata***	p		-15.25	0.9858			+			Ω+										
51	***Cryptogramma.crispa***	p		-15.29	0.9726		Ω	-				+	x								
147	***Saxifraga.seguieri***	p		-15.25	0.9790			-	Ω-	Ω		+									
68	***Galium.anisophyllon***	p		-15.26	0.9760		Ω	+		-	-										
148	***Sedum.alpestre***	p		-0.53	0.1273	-	Ω+	U-	-	Ω-		+		+	+	+	+	+	?		?
20	***Armeria.alpina***	p		-15.24	0.9848				U+		Ω+	+									
85	***Juncus.monanthos***	p		-15.24	0.9848				+	Ω-	+										
168	***Vaccinium.myrtillus***	p		-15.27	0.9751				Ω	Ω-	+	+									
66	***Festuca.quadriflora***	p		-15.25	0.9737		Ω		+	Ω+	+	+									
72	***Gentiana.verna***	p		-0.81	0.2832		?		+	+	Ω										
78	***Helianthemum.alpestre***	p		-15.26	0.9811				Ω+	+	Ω+	+									
108	***Phyteuma.betonicifolium***	p		-15.25	0.9858				Ω+	Ω+		+									
115	***Polygonum.viviparum***	p		-16.29	0.9680		Ω-		+		Ω+	+			+			+	Ω +	U-	+

91	***Ligusticum.mutellina***	p		-15.46	0.9696	U-	Ω+	+	-		+			-	Ω +	-
15	***Anthyllis.vulneraria***	p		-15.27	0.9751			U+	Ω	Ω						
69	***Galium.pumilum***	p		-15.24	0.9848			U+			+					
123	***Ranunculus.alpestris***	p		-1.58	0.1275			U+	Ω		+					
23	***Aster.bellidiastrum***	p		-15.28	0.9729			+	Ω+	Ω						
37	***Carex.ferruginea***	p		-15.25	0.9840			Ω+	Ω+		+					
40	***Carex.parviflora***	p		-15.25	0.9840			+	Ω+		+					
142	***Saxifraga.exarata***	p		0.21	0.6582	Ω+		-			+					
42	***Carex.sempervirens***	p		-15.60	0.9694	Ω		+	Ω	Ω	+	-	-	-		Ω-
70	***Gentiana.bavarica***	p		-1.39	0.1827	?	Ω	+		U-	+					
49	***Corydalis.lutea***	p		-15.24	0.9796		Ω+	U-	-							
50	***Crepis.kerneri***	p		-15.25	0.9817	Ω		-	Ω+	+	+					
104	***Pedicularis.kerneri***	p		-15.27	0.9755				Ω	Ω-	+					
93	***Loiseleuria.procumbens***	p		-15.23	0.9770	Ω		Ω		-						
135	***Salix.cfr.breviserrata***	p		-15.25	0.9817					-	+					
145	***Saxifraga.paniculata***	p		-0.93	0.2171	Ω		-	Ω+	-	+					
63	***Euphrasia.salisburgensis***	p		-15.25	0.9817					Ω+						

150	***Selaginella.selaginoides***	p		-15.27	0.9755				?		+	+						
111	***Pinus.mugo***	p		-0.86	0.4189						+	+						
18	***Arabis.caerulea***	p		-0.11	0.7543					Ω+			x					
10	***Alchemilla.vulgaris***	p		-15.25	0.9840					Ω-		+						
106	***Petrocallis.pyrenaica***	p		-15.25	0.9858					+								
59	***Dryopteris.villarii***	p		-15.25	0.9817							+						
90	***Leucanthemopsis.alpina***	p		-0.13	0.6699		Ω-		Ω	Ω-								Ω +
102	***Nardus.stricta***	p		-15.25	0.9840			Ω		-		+						
125	***Ranunculus.montanus***	p		-15.25	0.9858					Ω-								
169	***Valeriana.saxatilis***	p		-15.23	0.9802					Ω+	Ω							
11	***Alnus.viridis***	p		-15.26	0.9833			?										
58	***Dryopteris.dilatata***	p		-15.24	0.9824				Ω	-								
74	***Geum.montanum***	p		-15.23	0.9802			?	Ω			+						
120	***Primula.glaucescens***	p		-15.25	0.9840				?									
157	***Silene.rupestris***	p		1.02	**0.0168**	-					U	+						
164	***Thymus.sp.***	p		-15.24	0.9848		Ω	U				+						
130	***Salix.appendiculata***	p		1.16	**0.0020**		Ω+			+		+		-	-			
6	***Agrostis.alpina***	p		-15.49	0.9696				+	Ω-	Ω+	+				+	+	

27	***Bartsia.alpina***	p	🟨	-15.57	0.9694	Ω		Ω+	Ω	+			-	+					
7	***Agrostis.rupestris***	p	🟨	-0.12	0.6709	?	Ω+	Ω+	Ω-	-	+	-	-	+	-	-	-	U	+
8	***Agrostis.schraderiana***	p	🟩	-15.26	0.9733	?	+		-		+								
17	***Arabis.bellidifolia***	p	🟩	-15.26	0.9733		Ω+				+								
35	***Carduus.carlinaefolius***	p	🟩	-15.25	0.9840		Ω+				+								
55	***Doronicum.grandiflorum***	p	🟩	-15.65	0.9693	Ω	+				+			+		+	+		+
60	***Epilobium.fleischeri***	p	🟩	-15.24	0.9848		+				+								
2	***Achillea.clavenae***	p	🟩	-15.27	0.9751	Ω-			Ω+		+								
3	***Achillea.moschata***	p	🟩	-15.25	0.9840	Ω-			Ω+		+								
29	***Botrychium.lunaria***	p	🟩	-15.26	0.9811	Ω-			+		+								
30	***Calamagrostis.villosa***	p	🟩	-15.24	0.9848	-			U-		+								
39	***Carex.ornithopoda***	p	🟩	-15.27	0.9779	-					+								
65	***Festuca.nigrescens***	p	🟩	-15.23	0.9802	Ω-	Ω		U		+								
73	***Geranium.sylvaticum***	p	🟩	-15.25	0.9858	-			-		+								
99	***Minuartia.verna***	p	🟩	-15.46	0.9696	Ω		Ω			+							-	
105	***Pedicularis.rostrato.capitata***	p	🟩	-15.24	0.9848	-				Ω	+								
110	***Pinguicula.alpina***	p	🟩	-15.26	0.9811	-			Ω		+								

126	***Rhododendron.ferrugineum***	p		-1.89	**0.0097**	-	-		Ω	Ω-		+	-	-		+	-	U-		
127	***Rhododendron.hirsutum***	p		-15.26	0.9784		Ω-					+								
179	***Salix_serpyllifolia***	p		-1.21	**0.0116**		Ω-					+		-	+	+	+	Ω-	U	
	Saxifraga.crustata	p		-15.24	0.9824		Ω-			Ω+										
143	***Saxifraga.hostii***	p		-15.24	0.9848		-			Ω+	Ω	+								
149	***Sedum.atratum***	p		-15.23	0.9770		Ω-			+		+								
171	***Veratrum.lobelianum***	p		-15.25	0.9858		Ω-													
170	***Valeriana.supina***	p		-15.24	0.9848		U-		Ω	Ω+		+								
80	***Hieracium.bifidum***	p		-15.25	0.9817		-			+		+								
71	***Gentiana.purpurea***	p		-15.23	0.9802		Ω-	U-		-										
83	***Huperzia.selago***	p		-15.26	0.9733		Ω-		Ω+	Ω-	Ω									
81	***Hieracium.glanduliferum***	p		-15.27	0.9779		Ω-		Ω+			+								
117	***Potentilla.crantzii***	p		-15.24	0.9848		-		+			+								
153	***Sesleria.sphaerocephala***	p		-15.27	0.9713		-		U+	Ω		+						U-		Ω-
38	***Carex.firma***	p		-15.69	0.9692		Ω-		+		Ω	+		-	-		-		U-	
56	***Draba.aizoides***	p		-15.23	0.9802		Ω-		+			+								
166	***Trifolium.pratense***	p		-15.24	0.9848		-		Ω-	Ω		+								

97	***Minuartia.austriaca***	p	🟩	-15.25	0.9737		Ω-		-			+											
22	***Asplenium.viride***	p	🟩	-15.35	0.9703		Ω-					+		+	+		+	+	U-	Ω-			Ω-
26	***Avenella.flexuosa***	p	🟩	-15.26	0.9811		-				Ω-												
165	***Trifolium.pallescens***	p	🟩	-15.24	0.9796		-		Ω		-	+											
43	***Cerastium.arvense***	p	🟩	-15.26	0.9833		-		Ω-	Ω-	-												
25	***Athyrium.distentifolium***	p	🟩	-15.26	0.9811		-				Ω+	+											
122	***Primula.latifolia***	p	🟩	-15.26	0.9784		-				Ω+	+											
57	***Dryas.octopetala***	p	🟩	-15.78	0.9690		Ω-				+	+								-			
133	***Salix.reticulata***	p	🟩	-15.25	0.9817		-		Ω+	+	+	+											
174	***Viola.biflora***	p	🟩	-15.23	0.9802		-			Ω-	+	+											
178	***Sesleria.caerulea***	p	🟩	-15.49	0.9696		Ω-	U-				+											+
28	***Biscutella.laevigata***	p	🟩	-15.24	0.9796		Ω-	+			Ω	+											
88	***Larix.decidua***	p	🟩	-0.67	0.1739	-	-	+		+		+	-	-	-				U-				
107	***Peucedanum.ostruthium***	p	🟩	-15.25	0.9790		Ω-	+		-													
138	***Saxifraga.aspera***	p	🟩	-0.60	0.5766		Ω-	+				+											
87	***Juniperus.nana***	p	🟩	-15.24	0.9796		Ω-	Ω+	Ω+	-	Ω+	+											
167	***Vaccinium.gaultherioides***	p	🟩	-15.49	0.9696		Ω-	+	Ω+	Ω-	Ω-								-				

116	***Potentilla.aurea***	p		-15.28	0.9729		Ω-	+			Ω-	+										
161	***Solidago.virgaurea***	p		-15.26	0.9733		Ω-	+			+	+										
24	***Astrantia.minor***	p		-15.26	0.9760		Ω-	Ω+			Ω+	+										
158	***Silene.vulgaris***	p		-15.23	0.9770		Ω-	U+		U+	Ω+	+										
4	***Achillea.oxyloba***	p		-15.24	0.9824		Ω-	Ω-				+										
62	***Euphrasia.minima***	p		-1.09	**0.0246**	-	?	+				+	x									
155	***Silene.acaulis***	p		-2.17	**0.0000**	-	?		+	Ω		+		-	-	+	-	-	-		-	-
96	***Luzula.lutea***	p		-0.16	0.7812	-	Ω-				U	+										
128	***Rumex.scutatus***	p		0.44	0.3442	-	-			Ω+	-	+										
100	***Moehringia.ciliata***	p		-0.80	0.1961	-	-	U-		+		+										
159	***Soldanella.alpicola***	p		-1.49	**0.0438**	-	-	Ω	Ω		Ω-	+					-		-			
14	***Anthoxanthum.alpinum***	p		-2.57	**0.0115**	-	Ω-	Ω				+										Ω+
82	***Homogyne.alpina***	p		-3.33	**0.0010**	-	Ω-	-	+	Ω-	Ω+	+				-	-	-	-		Ω-	
177	***Papaver_raethicum***	p		-1.48	**0.0020**	-	?		-	+	-	+				-	-	-	-	Ω-		
67	***Festuca.varia***	p		-2.32	**0.0229**	-	-	+				+		-	-				-			
131	***Salix.helvetica***	p		-0.27	0.6806	-	Ω-	Ω+	+	-	-	+										
200	***Abax.arerae***	c		-15.25	0.9790		-	Ω+				+										

201	***Amara.alpestris***	C	🟩	-15.26	0.9784			-	+	Ω-	-		+					
202	***Amara.erratica***	C	🟨	-0.74	0.4899						Ω-		+					
203	***Amara.quenseli***	C	🟨	-0.86	0.4189								+					
204	***Carabus.adamellicola***	C	🟧	-15.36	0.9701			Ω+					+		+			
205	***Carabus.alpestris***	C	🟩	-15.29	0.9726			Ω-					+					
206	***Carabus.castanopterus***	C	🟩	-2.16	**0.0349**			-					+	X				
207	***Carabus.concolor***	C	🟨	-15.25	0.9765				?	?	?		+					
208	***Carabus.creutzeri***	C	🟩	-15.31	0.9708			Ω-		+			+		+	+		-
209	***Carabus.depressus***	C	🟩	-15.25	0.9765			-			Ω-	Ω-	+					
210	***Carabus.sylvestris***	C	🟨	-15.25	0.9858					Ω		Ω	+					
211	***Cymindis.vaporariorum***	C	🟩	-1.24	0.2365			-					+					
212	***Leistus.nitidus***	C	🟩	-15.24	0.9824			-	-		-	+						
213	***Nebria.germari***	C	🟧	1.16	**0.0001**			Ω		?	-	-	+				-	
214	***Oreonebria.castanea***	C	🟧	0.35	0.2568			?	-	Ω-			+			+		
215	***Oreonebria.diaphana***	C	🟧	0.18	0.6411		-	Ω+	-	Ω			+	X				
??	***Oreonebria.lombarda***	C	🟨			X												
216	***Oreonebria.soror.soror***	C	🟧	0.989	**0.0671**		-		-		?	U	+					
??	***Oreonebria.soror.tresignore***	C	🟨			X												
217	***Platynus.teriolensis***	C	🟩	-15.242	0.9796			-	+	Ω	-		+					
218	***Pterostichus.cribratus***	C	🟨	-15.255	0.9833				Ω			+	+					
219	***Pterostichus.lombardus***	C	🟨	-0.456	0.4727								+					

220	***Pterostichus.multipunctatus***	C	🟩	-1.763	**0.0163**			Ω-		Ω	-	Ω	+	X									
221	***Acantholycosa.pedestris***	S	🟥	-0.963	**0.0739**	-		Ω+	+			-	+		-	-	-						
222	***Anguliphantes.monticola***	S	🟧	0.693	0.1774			+		U-			+										
223	***Centromerus.pabulator***	S	🟩	-15.255	0.9833			-			-		+										
224	***Coelotes.pickardi.pastor***	S	🟨	-15.233	0.9802				?	Ω			+										
225	***Coelotes.pickardi.tirolensis***	S	🟥	-0.124	0.7085			Ω+				+	+						+		-	Ω +	
226	***Coelotes.rudolfi***	S	🟩	-15.243	0.9848			-					+										
227	***Diplocephalus.helleri***	S	🟩	-1.221	0.1009		-				+	-	+										
228	***Drassodex.heeri***	S	🟥	-0.872	0.2478			Ω+															
229	***Entelecara.media***	S	🟥	-0.965	0.3603			Ω+	Ω-				+										
230	***Gnaphosa.petrobia***	S	🟥	-15.242	0.9824			Ω	+		+	+	+										
231	***Meioneta.rurestris***	S	🟧	2.678	**0.0010**					Ω+			+										
232	***Mughiphantes.brunneri***	S	🟧	2.252	**0.0000**		+						+										
233	***Mughiphantes.handschini***	S	🟩	-1.131	0.1296		-		-				+										
234	***Mughiphantes.variabilis***	S	🟧	1.053	**0.0780**			+					+										
235	***Oedothorax.agrestis***	S	🟨	4.231	**0.0000**			-	Ω+	-													
236	***Pardosa.blanda***	S	🟨	-15.255	0.9833			Ω	?			-	+										
237	***Pardosa.nigra***	S	🟧	1.356	**0.0000**		+			+	Ω		+					+		+			+
238	***Pardosa.oreophila***	S	⬜	-15.242	0.9796						-	+	+										
239	***Pardosa.saturatior***	S	🟧	3.177	**0.0000**		+		Ω+														
240	***Robertus.truncorum***	S	🟩	-0.681	0.3713			-				Ω	+										

241	***Sitticus.longipes***	S	🟨	0.56	0.2324				+		+	
242	***Tenuiphantes.jacksoni***	S	🟨	-15.249	0.9840		Ω	Ω			+	
243	***Walckenaeria.capito***	S	🟨	-15.249	0.9840						+	
244	***Xysticus.desidiosus***	S	🟩	-15.256	0.9811	Ω-	?	-	+		+	
245	***Xysticus.alpinus***	S	🟧	-1.152	**0.0169**	+				Ω+	+	X

4.3 Ecosystem Birth Near Melting Glaciers: A Review on the Pioneer Role of Ground Dwelling Arthropods

insects

MDPI

Review

Ecosystem Birth near Melting Glaciers: A Review on the Pioneer Role of Ground-Dwelling Arthropods

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Received: 15 August 2020; Accepted: 16 September 2020; Published: 19 September 2020

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Simple Summary: Due to climate change, glaciers are retreating. On newly deglaciated ground, ecosystems gradually evolve through the process of primary succession. This gives scientists a unique opportunity to study how a new ecosystem is born. During the first few years, before plants establish, the barren ground of sand, silt, and stones close to the ice edge is conquered by a rich variety of insects, spiders, and other small animals. Many of these are predators and their prey are either transported by air or produced in situ. The real pioneers are, however, wingless springtails that graze on biofilm containing algae or cyanobacteria. Studies of two pioneer food webs showed differences in structure and function. In the one case, beetles, spiders, and harvestmen exhibit preferences for locally produced springtails, while predators in the other example relied mainly upon midges hatching from young ponds. Pioneer communities contain a mixture of generalists and specialists. Species composition vary under different climatic and geographical conditions, depending on the available candidate species in the surrounding areas. This study illustrates flexibility in the early phase of primary succession. Certain cold loving beetles, spiders, and springtails may become extinct if glaciers disappear completely.

Abstract: As glaciers retreat, their forelands represent "natural laboratories" for the study of primary succession. This review describes how certain arthropods conquer pristine ground and develop food webs before the establishment of vascular plants. Based on soil samples, pitfall traps, fallout and sticky traps, gut content studies, and some unpublished data, we compare early arthropod succession on glacial forelands of northern Europe (Iceland, Norway including Svalbard, and Sweden) and of the Alps (Austria, Italy). While macroarthropod predators like ground beetles (Coleoptera: Carabidae), harvestmen (Arachnida: Opiliones), and spiders (Arachnida: Araneae) have usually been considered as pioneers, assumed to feed on airborne prey, this review explains a different pattern. Here, we highlight that springtails (Collembola), probably feeding on biofilm made up of algae or cyanobacteria, are super-pioneers, even at high altitudes and under arctic conditions. We also point out that macroarthropod predators can use locally available prey, such as springtails or non-biting midges (Diptera: Chironomidae). Pioneer arthropod communities vary under different biogeographical and climatic conditions. Two pioneer food webs, from northern Europe and the Alps, respectively, differed in structure and function. However, certain genera and orders were common to both. Generalists and specialists live together in a pioneer community. Cold-adapted specialists are threatened by glacier melting.

Keywords: arthropods; Collembola; food web; foreland; glacier; pioneers; succession

1. The Questions

Due to climate change, glaciers are retreating [1–3]. The freshly deglaciated areas left behind after glacier retreat represent unique "ecological laboratories" that can be used to study primary succession (Figures 1 and 2). We observe how pioneer species arrive, how communities establish and how food webs develop. While the establishment and succession of plants has been well studied in glacial forelands [4–10], the colonization of animals has been investigated less. Here, we summarize and discuss recent European studies (Figure 3) on the role of arthropods during early succession. The number of years since deglaciation varies between studies but is always less than 50 and several studies focus on the very first few years. Figure 1 illustrates a large retreat during one summer [11]. These small animals reveal a great ability to conquer virgin ground and in certain ways challenge our ecological thinking.

Figure 1. Rapid glacier retreat: In 2010, the Hardangerjøkulen glacier in Southern Norway receded 34 m, corresponding to the area behind the person. From [11]. Photo: Daniel Flø.

We discuss how the demands of various pioneer species can be fulfilled within the harsh and unstable environmental conditions on newly deglaciated ground. How do local conditions in habitat structure, shelter, climate, and food availability influence colonization? We describe how species must pass through certain "ecological filters" to become pioneers and ask whether they are specialists or generalists. Furthermore, why are the taxonomic structures of pioneer arthropods communities within a restricted geographical area rather predictable? We also discuss why certain early species are gradually pushed-out of the community, challenging the principle of persistence after colonization [12].

Figure 2. A well-studied site in Ötztal, Austria: The Rotmoos foreland. Past positions of the glacier front are shown. Photo: Rüdiger Kaufmann.

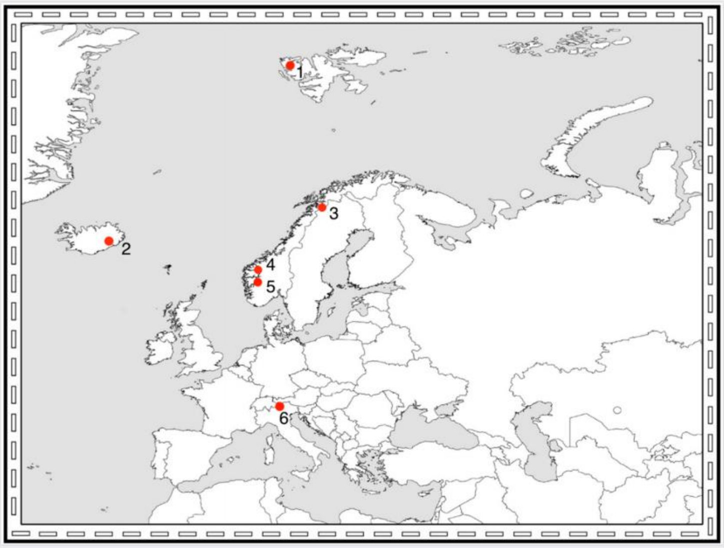


Figure 3. European glacial areas mentioned in this review. 1: Midtre Lovén-bre, Svalbard. 2: Vatnajökull, Iceland. 3: Ålmajallojekna glacier, Sweden. 4: Jostedalen and Jotunheimen, Norway. 5: Hardangerjøkulen, Norway. 6: Closely situated glaciers in the Alps (Italy and Austria).

A much-debated topic during the last two decades is the "predator first paradox": How is it possible for predators to establish almost immediately, before the presence of vascular plants and herbivores? It has been hypothesized that early predators like carabid beetles and spiders feed on airborne prey, and organic material blown in from the surrounding area supports scavenging detritivores like Collembola [13]. Here we present observations that shed new light on the "predator first paradox".

From community structure we go to discuss function. What do we know about early food webs? We compare two well-described pioneer food webs based on gut content studies—one from northern Europe (Norway) and one from the Alps (Austria). Both studies claimed to have "solved" the predator first paradox by documenting local production of prey, although different types of prey.

At the end, we will try to answer two main questions about early succession:

A. How "flexible" are arthropod communities in the early phase of primary succession?
B. Do pioneer arthropod communities under different conditions still have certain basic traits in common?

2. Conquering Newly Deglaciated Ground: A Passage through Ecological Filters

Early work introduced eight categories of colonizers, each characterized by their preference for food or substrate [14]. Here we present the colonization process of pioneer species in a slightly different light, considering a wider range of factors. Each pioneer species has to overcome certain obstacles, or "ecological filters", before it is able to establish its presence. Firstly, it must travel, which demands a sufficient dispersal ability. Secondly, it must find an acceptable habitat with tolerable climate and shelter to avoid hostile conditions. Thirdly, it must be able to find food and finally, a true pioneer species must also be able to reproduce. We now explore these filters further.

2.1. Ability to Disperse

Existing literature contains several observations on fallout of winged insects on glaciers and snowfields [13]. In alpine snow fields and glaciers of southern Norway and the Alps, as well as on Icelandic nunataks, even typical lowland-insects have frequently been recorded, lifted upwards by warm air currents (Hågvar, Kaufmann, and Gobbi, pers. obs.) [15–18].

The isolation of nunataks makes them especially interesting in studying the dispersal of non-winged arthropods. In Iceland, the microarthropod fauna of isolated nunataks was compared with that of non-isolated deglaciated areas [19]. They found that isolation of a few kilometers did not significantly affect the colonization of Collembola and oribatid mites, and it was assumed that these tiny animals were transported by wind.

We know therefore that dispersal occurs, but it is often difficult to quantify this. Evidence from Austrian fallout traps in Rotmoos valley produced Collembola catches and plant material; however, a reliable quantification was not possible [18]. In Norway, 30 fallout traps (diam. 6.5 cm) were operated during a four-week period on a five year old moraine [20]; 108 microarthropods: 26 Acari and 82 Collembola were caught. The total fallout in this period was calculated to 1080 microarthropods per m^2. Other arthropods in the traps included Diptera, especially chironomid midges, but also some wingless aphids. Interestingly, plant organic material in fallout traps included fragments and diaspores of mosses, often in considerable quantities, and of which several fragments had the potential to start new colonies.

Sticky traps in the same site showed that both arthropods and mosses were transported close to the ground, below about 40 cm height [20]. On a glacier foreland on Svalbard, nearly all flying insects which colonized pioneer ground were trapped below 25 cm height [21]. It was explained by a favorable microclimate with little wind near the ground, and that the "aerial transport" in this case was mainly due to active flight. On Iceland, sticky traps placed at 30 cm height on a medial moraine (debris cover that stretches from nunatak down-glacier to lowland) collected many Diptera compared to traps placed on white ice, indicating that active flight occurs over ice-free ground [16]. Active flight of winged insects on glacier forelands clearly occurs mainly near the ground but it is easy to imagine that episodic storms may carry both winged and wingless organisms high up and long distances.

Linyphiidae spiders are known to be efficient aerial dispersers, having the ability of long distance "aerial ballooning", hanging on silk threads. This has been well demonstrated in glacial forelands in Svalbard [13,21,22].

Certain Collembola are probably able to keep pace with the receding glacier front by jumping and walking. In Norway, the cold-adapted Collembola *Agrenia bidenticulata* was observed to make jumps on the surface of cold water, and after a glacier retreat of 30 m one year it was actively present 4 m from the ice edge [20]. On partly vegetated ground of 34–38 years age, pitfall catches revealed that Collembola were not confined to vegetated plots but showed a high surface activity on bare ground [23]. This is also true on young sites of Italian glacier forelands, even if the bare ground is coarse, highly irradiated and percolating and the dispersion seems not to be easy [10,24]. High surface activity of Collembola on newly deglaciated ground was likewise documented in Austria [25]. Furthermore, on Icelandic nunataks, pitfall catches documented that Collembola were active on bare ground, even on land younger than 10 years old [19].

The large and fast-moving harvestman *Mitopus morio* can easily trace the receding glacier on foot [26]. This may be true for all mobile macroarthropod colonizers. However, recently emerged Icelandic nunataks seem to be too isolated by snow and ice to be reached by *M. morio* [15].

2.2. Ability to Find Acceptable Habitat Qualities

In order to survive, arrivals must be able to avoid or overcome extreme microclimates including temperature and moisture extremes. Arrivals may also face surface flooding by meltwater, or unconsolidated soils and soil movement. Finding shelter to avoid these extremes, including use of sub-surface habitats between stones and gravel, will be important. An inability to avoid extremes, will mean non-survival. Bare rock surfaces are unfavorable. However, rock crevasses may be safe sites for colonization of arthropods.

Figure 4 visualizes high spatial heterogeneity on an eight-year-old moraine at Hardangerjøkulen glacier in Norway that creates a variety of microenvironments and habitats [27]. The morphologically varied terrain contained various surface structures, from fine-grained silt, sand, and gravel to larger stones and boulders, sometimes in a complex matrix. Fast-moving predators, like ground beetles and spiders hunt on such surfaces. Young ponds (some less than one m^2 in size) contained sediments rich in larvae of Chironomidae and Tipulidae. In the porous limestone bedrock areas of the Alps, the silt and clay proportions of pioneer ground are usually scarce compared to gravel and sand. In front of the Trobio glacier, soils younger than 30 years contained about 3% of silt and clay [10]. Ponds are less frequent because of the well-drained soil, however Chironomidae are able to colonize glacial streams and supraglacial lakes [28]. Vertical labyrinths created between stones and gravel and below surface stones, may offer shelter during day for nocturnal carabids and habitats for their larvae [29]. In Rotmoos valley, Austria, carabid larvae have been caught in specially designed traps, positioned at 0.5 m depth below the surface (Kaufmann, unpublished).

Microclimate and structural diversity are two closely connected parameters. For example, during sunny days, open ground, including stones, can be considerably heated due to the lack of shadow-producing vegetation. Heat can be slowly released afterwards, improving hunting conditions for predators and even some nocturnal species. Shallow ponds may also be considerably heated by sun. On windy days, stones create shelters, both horizontally and vertically. Figure 5 illustrates how wind-dispersed diaspores of pioneer mosses can aggregate and thrive alongside a large stone [30]. The effect of local microclimate for early succession has been well documented in the Austrian Rotmoos foreland [9,31]. Even small temperature changes by climate warming may profoundly speed up the initial colonization [32].

Figure 4. This picture from the foreland of Hardangerjøkulen glacier in southern Norway illustrates that pioneer ground may contain a variety of habitats. From [27].

Figure 5. Windblown moss fragments have aggregated along a stone and established a pioneer community before higher plants arrive. From [30].

On the barren moraine surfaces the situation is extreme, and in Rotmoos, daily amplitudes from −10 to + 60 °C locally have been measured in June. This heat stress, occurring together with desiccation pressure, requires good strategies for the colonizers to avoid the extremes, and to optimize their foraging. Winter under the snow cover is favorable, not only for the microbiota but also for certain carabids that are active beneath snow. Snow-free periods with the ground freezing at −30 °C will kill carabid larvae, consequently low adult numbers are present the next summer. Once a plant cover has developed, the situation becomes much less extreme.

Response to local environmental conditions can be demonstrated on the small scale in pitfall grids. In Rotmoos valley, the occurrence patterns of various carabid species remained stable over years. A non-continuous occurrence of *Nebria jockischii* illustrates the point: local conditions are decisive, not only site age (Figure 6, unpublished).

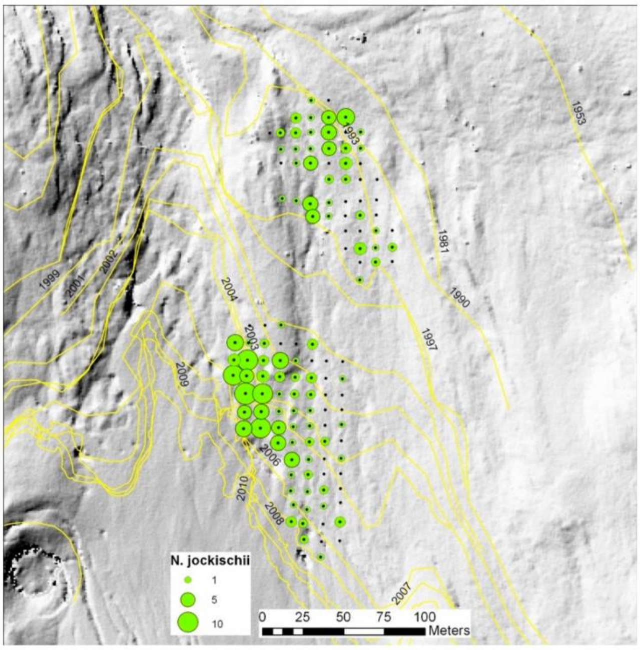


Figure 6. Occurrence of the carabid beetle *Nebria jockischii* in the Rotmoos foreland. Position of the glacier front in different years is indicated. Local conditions are decisive, not only site age.

Factors like these can create local successional pathways, finally leading to specific occurrence patterns for carabids and other arthropods on the landscape scale [33]. In Norway, dry and wet patches have been shown to be colonized by different arthropods and to develop different succession patterns [34].

2.3. *Ability to Find Food*

To a certain degree, airborne arthropods will act as food for early predators and contribute to energy flow in early food webs, but prey like Collembola and chironomid midges can also be produced locally [17,27]. Chlorophyll may appear surprisingly early, for instance as biofilm with diatom algae or cyanobacteria, or as tiny pioneer mosses [11,20]. Furthermore, bacteria and fungi may be food sources on pioneer ground. This topic will be further explored in a later section using two case studies to compare pioneer food webs. The case study from Hardangerjøkulen glacier in Norway documented a variety of food sources on 3-6 years old ground, and different pioneer arthropods selected among these options (Table 1). Studies on the Austrian Alps have described a high intraguild predation as well as a heavy predation on Collembola [17,35].

Table 1. Food sources of surface-active arthropods on 3–6 year old ground, based on gut content analyses. Data from Hardangerjøkulen glacier, Norway [11].

Species	Group	Bio-Film	Fungal Hyphae	Bryo-Phytes	Vascular Plants	Arthro-Pods	Ancient Carbon via Chironomidae
Agrenia bidenticulata	Collembola	x					
Desoria olivacea	Collembola	x					
Isotoma viridis	Collembola	x	x				
Lepidocyrtus lignorum	Collembola		x				
Bourletiella hortensis	Collembola		x	x			
Simplocaria metallica	Coleoptera			x			
Amara alpina	Coleoptera			x	x	x	
Amara quenseli	Coleoptera			x		x	
Nebria nivalis	Coleoptera					x	x
Bembidion hastii	Coleoptera					x	x
Mitopus morio	Opiliones					x	x

2.4. Ability to Reproduce

Both adults and young stages of Acari and Collembola were found on pioneer ground near Hardangerjøkulen in Norway, indicating reproduction. Young stages may, however, have been transported by wind. On a six year old Norwegian moraine, a larva of the beetle *Simplocaria metallica* (Byrrhidae) was recorded in a small patch of pioneer moss (Figure 7, [30]). Since carabid larvae may have a cryptic life between gravel and stones, we assume that *Nebria nivalis* and *Bembidion hastii* reproduced close to the glacier. Adults of both species were trapped on three year old ground, the later in large numbers [36]. From the Rotmoos glacier foreland in Austria, larvae, and juvenile stages within the first years of deglaciation have been identified for carabid beetles of the genera *Nebria* and *Oreonebria*, the spiders *Pardosa nigra* and *Erigone tirolensis*, as well as the harvestman *Mitopus glacialis* [31]. *Nebria* and *Oreonebria* seem to have a two year larval development [33] and long-lived adults (at least three years according to mark-recapture results (Kaufmann, unpublished)). Prolonged life-cycles are typical for high altitude species and/or populations [37], but their role in glacier forelands is unclear. Juvenile stages of species belonging to the genera *Nebria* and *Oreonebria* were also found in early successional stages and on supraglacial debris of Forni glacier in the Central Italian Alps [38], Amola glacier in the Central Eastern Italian Alps [39], and the Agola glacier of the Western-Dolomites [40]. From the Alps, the carabid *Pterostichus jurinei* is an example of a predator that by some reason is unable to reproduce on pioneer ground. It was found occasionally in single spots in the pioneer zone, but never established populations there (Kaufmann, unpublished) [41,42]. In later stages it was common [43].

On nunataks in Iceland, *Amara quenseli* larvae were caught in pitfall traps on land less than three years old and on 10–35 years old land. Further, Diptera larvae (Cyclorrapha) were occasionally caught in non-baited pitfall traps on a debris-covered glacier and on land younger than 10 years (Ingimarsdóttir, unpublished).

Along the Amola glacier foreland (Italian Alps), there is evidence of a trend in population sex-ratio of *Nebria germari* in relation to time since deglaciation, and thus distance from the glacier [29]. The sex-ratio of *Nebria germari* was female-biased on the debris-covered glacier and in front of the glacier snout. Probably, the initial colonization from the early successional stages (source habitat) to the glacier surface was favored by founder females (i.e., females arrived already fertilized and laid their eggs between the stones), which had a tendency to disperse. In Rotmoos, *Mitopus glacialis* seems to be parthenogenetic on the glacier foreland (Kaufmann, unpublished).

Figure 7. Larva and newly hatched adult of the moss-eating beetle *Simplocaria metallica* (Byrrhidae), extracted from a pioneer moss turf. From [30].

2.5. Different Filters for Different Successional Stages

Later successional stages will have other filters. An herbivore will, for instance, depend on the presence of its food plant, and a specialized predator or parasite must find its prey or host. Even if suitable food is present, the microclimate or habitat structure may be unacceptable. In an Icelandic study, dispersal ability and colonization success were studied in combination [19]. Microarthropods arriving more or less randomly on isolated nunataks (Figure 8) only survived on ground with a suitable age for each species, and a successional pattern was established similar to that seen in non-isolated forelands.

Figure 8. Nunataks on the Vatnajökull glacier, Iceland. The two nunataks in the central part of the photo are Brædrasker (**left**) and Kárasker (**right**). Photo: Oddur Sigurðsson.

3. Which Arthropod Taxa are Present on Pioneer Ground? A Comparison between Northern Europe and the Alps

The following lists of pioneer species on recently deglaciated ground (Tables 2–5) are mainly based on pitfall trapping (Figure 9) but also on soil samples for microarthropods. Macroarthropod lists cover surface active beetles (Coleoptera), harvestmen (Opiliones), and spiders (Araneae, Figure 10). Flying insects are not included here. Sampling intensity, age of the ground, and taxonomic resolution varies but these lists still tell a lot about early arthropod communities in different European countries and sites. During the compilation, it became evident that both the micro- and macroarthropod fauna of the Alps differed from that of northern Europe. In addition to this latitudinal diversity, longitudinal differences in species composition have been demonstrated in the Alps [44]. In the following section, we treat northern Europe and the Alps separately. Within each area, we look for characteristic pioneer species and try to understand early succession. Afterwards, we will compare the two geographical areas in search of common traits.

Table 2. Microarthropods recorded in young glacier forelands in Iceland, southern Norway, and Svalbard.

Country and Locality	**Iceland, Nunataks**	**Southern Norway, Hardangerjøkulen**			**Svalbard**		
Altitude (m)	460–728	1400			50		
Reference	[19]	[23,30,45]			[14]		[46]
Age of ground (years)	<10	0	3	32–34	2	16	0
COLLEMBOLA							
SYMPHYPLEONA							
Bourletiella hortensis			X	X			
Heterosminthurus claviger	X						
Sminthurides inequalis					X	X	
Sminthurides malmgreni	X						
ENTOMOBRYOMORPHA							
Agrenia bidenticulata		X	X	X			X
Desoria infuscata		X	X	X			
Desoria olivacea	X		X	X			
Desoria tolya	X		X	X			
Folsomia brevicauda	X						
Folsomia quadrioculata	X				X	X	
Isotoma anglicana	X				X	X	
Isotoma viridis			X	X			
Lepidocyrtus lignorum	X		X	X			
Pseudisotoma sensibilis	X						
Tetracanthella arctica	X						
Tetracanthella wahlgreni				X			
PODUROMORPHA							
Ceratophysella sp.	X						
Ceratophysella scotica			X	X			
Hypogastrura tullbergi					X	X	
Hypogastrura concolor							X
Mesaphorura sp.	X						
Micranurida pygmaea	X						
Oligophorura groenlandica	X						
Oligophorura schoetti				X			
Protaphorura sp.	X						
ACARI							

Table 2. *Cont.*

Country and Locality	Iceland, Nunataks	Southern Norway, Hardangerjøkulen	Svalbard	
ORIBATIDA *Camisia anomia*			X	X
Liochthonius cf. *sellnicki*		X		
Liochthonius clavatus	X			
Liochthonius strenzkei	X			
Pantelozetes paolii	X			
Tectocepheus velatus	X	X		X
PROSTIGMATA	X	X		
GAMASIDA		X	X	X

Table 3. Collembola recorded in young glacier forelands in the Alps.

Country and Locality	W-Sorapiss, Italy			C-Sorapiss, Italy		Agola Glacier, Italy			Amola Glacier, Italy		Rotmoos Glacier, Austria		Hintereis Glacier, Austria	
Altitude (m)	2300–2400			2200–2300		2500–2600			2500–2680		2450		2400	
Reference	Valle et al. (unpublished data)					Valle et al. (unpublished data)			Valle et al. (unpublished data)		[47]	[25]	[42]	
Age of ground (years)	**On ice**	**<50**	**50**	**On ice**	**40**	**On ice**	**<25**	**<50**	**On ice**	**<18**	**<40**	**0–3**	**0–1**	**2–4**
SYMPHYPLEONA														
Symphypleona indet.	X	X	X			X	X	X						
Heterosminthurus diffusus	X					X				X		X		
Sminthurinus trinotatus	X													
Bourletiella repanda													X	X
ENTOMOBRYO-MORPHA														
Orchesella cf. *alticola*	X	X	X	X	X	X	X	X		X			X	X
Orchesella bifasciata											X			X
Orchesella sp.												X		
Entomobryanivalis														X
Isotomidae indet.	X	X		X	X		X	X						
Folsomia manolachei											X			
Isotoma viridis											X			
Desoria saltans													X	
Parisotoma notabilis											X			
Proisotoma schoetti													X	X
Proisotoma crassicauda													X	X
Tetracanthella specifica											X			
Desoria nivalis										X				
Pachyotoma crassicauda							X			X				
Pachyotoma pseudorecta												X		
Isotomurus pseudopalustris								X						
Isotomurus maculatus							X							
Isotomurus palliceps										X		X		
Isotomurus alticolus												X		
Lepidocyrtus curvicollis gr.												X		
Lepidocyrtus sp.	X		X				X	X	X					
Tomocerus cf. *minor*					X		X	X						
PODUROMORPHA														
Pseudachorudina alpina			X					X						
Ceratophysella tuberculata				X										
Micranurida pygmaea											X			
Mesaphorura critica											X			
Hypogastrura cf. *socialis*										X				
Hypogastrura parva											X			
Hypogastruridae indet.												X		

Table 4. Macroarthropods sampled from young glacier forelands of Norway, Sweden, Iceland, and Svalbard. The data are restricted to ground-dwelling beetles (Coleoptera), harvestmen (Opiliones), and spiders (Araneae). Only few of the Staphylinidae from Jostedalen and Jotunheimen were identified. Flying insects, as Diptera and Hymenoptera, are not included, as they may be casual visitors.

Country and Locality	**Jostedalen, Norway**				**Jotunheimen, Norway**				**Hardanger-Vidda, Norway**		**North-Ern Swe-Den**	**Ice-Land**	**Sval-Bard**	
Glacier name	Aus-ter -dals-breen	Berg-set-breen	Fåberg-støls -breen	Bø-dals-breen	Stygge-dals-breen	Bøver-breen	Stor-breen	Vesle-juv-breen	Hardanger-jøkulen		Ålma-jallo -jeknaglacier	Nu-na-taks	MidtreLovén-bre	
Altitude (m)	320–390	400–500	480–620	560–600	1270	1400	1400	1860	1400		1180–1344	460–728	50	
Reference [numbers]	[48]	[48]	[48]	[48]	[48]	[48]	[48]	[48]	[36]		[49]	[19]	[14]	
Climatic zone	Sub-alpine	Sub-alpine	Sub-alpine	Sub-alpine	Low alpine	Low/mid-alpine	Low/mid-alpine	High alpine	Mid-alpine		Low/mid-alpine	Arctic	High arctic	
Age of ground (years)	<20	<20	<20	<20	<20	<20	<20	<20	3	40	<40	<10	2	16
COLEOPTERA, CARABIDAE														
Amara alpina		x	x	x		x	x		x	x				
Amara quenseli			x				x		x	x		x		
Nebria sp.	sp.		sp.	sp.	*N. nivalis*	sp.	sp.		*N. nivalis*	*N. nivalis* *N. rufescens*	*N. nivalis* *N. rufescens*			
Bembidion sp.			*B. fellmanni*		*B. fellmanni*		*B. fellmanni*		*B. hastii*	*B. hastii*	*B. hastii*			
Patrobus septentrionis										x				
Notiophilus aquaticus					x	x								
Miscodera arctica					x		x	x						
COLEOPTERA, BYRRHIDAE														
Simplocaria metallica									x	x				
Byrrhus arietinus						x	x							
COLEOPTERA, CURCULIONIDAE														
Otiorhynchus nodosus										x				
Otiorhynchus arcticus												x		
COLEOPTERA, STAPHYLINIDAE														
Oxypoda annularis										x				
Boreaphilus henningianus										x				
Geodromicus longipes									x	x				
Acidota crenata			x											
Anthophagus alpinus											x			
Arpedium quadrum									x		x			
Coryphiomorphus hyperboreus											x			
Olophrum boreale											x			
Tachinus elongatus											x			
Quedius sp.			x					x						
COLEOPTERA, HYDROPHILIDAE														
Helophorus glacialis										x				
COLEOPTERA, DYTISCIDAE														
Agabus bipustulatus									x					
Agabus thomsoni/lapponicus											x			
COLEOPTERA, CHRYSOMELIDAE														

Table 4. *Cont.*

Country and Locality	Jostedalen, Norway				Jotunheimen, Norway				Hardanger-Vidda, Norway		North-Ern Swe-Den	Ice-Land	Sval-Bard	
Phratora polaris											x			
COLEOPTERA, NITIDULIDAE														
Meligethes aeneus											x			
COLEOPTERA, SILPHIDAE														
Thanatophilus lapponicus											x			
COLEOPTERA, LEIODIDAE														
Catops tristis			x				x							
OPILIONES, PHALANGIIDAE														
Mitopus morio	x	x	x	x	x	x	x		x	x	x	x		
ARANEAE, LYCOSIDAE														
Pardosa trailli						x	x		x	x				
Pardosa palustris											x	x		
Pardosa pullata			x											
ARANEAE, GNAPHOSIDAE														
Zelotes subterraneus		x												
Gnaphosa leporina											x			
Micaria alpina											x			
ARANEAE, LINYPHIIDAE														
Gonatium rubellum								x						
Oedothorax retusus											x			
Erigone longipalpis			x			x	x	x						
Erigone tirolensis									x			x		
Erigone psychrophila													x	x
Erigone arctica									x		x			x
Meioneta nigripes											x	x	x	x
Collinsia spetsbergensis												x	x	x
Collinsia holmgreni									x		x	x		
Islandiana princeps												x		
Improphantes complicatus												x		

Table 5. Macroarthropods sampled from young glacier forelands of the Alps (Italy and Austria). The data are restricted to ground-dwelling beetles (Coleoptera), harvestmen (Opiliones), and spiders (Araneae). Flying insects, as Diptera and Hymenoptera, are not included, as they may be casual visitors. All data are from the Alpine zone, above the tree line.

Country and Glacier Name	Rotmoos-tal, Austria	Cedec Glacier, Italy	Forni Valley, Italy	Forni Valley, Italy		Trobio Glacier, Italy	W-Sorapiss Glacier, Italy			C-Sorapiss Glacier, Italy		D'Agola Glacier, Italy				Amola Glacier, Italy		Hintereis, Austria		Hornkees, Austria	
Altitude (m)	2500	2700	2500	2500		2500	2300–2400			2200–2300		2500–2600				2500–2680		2400		2200	
Reference	[31] and Kauf-mann, unpubl.	[50]	[38]	[51–53]		[10]	[43]			[43]		Gobbi et al. unpubl.				[39]		[42]		[41]	
Age of ground (years)	<10	<20	<5	On ice	24	<30	On ice	<50	50	On ice	40	On ice	<20	<50	50	On ice	<18	0–1	2–4	2	6–10
COLEOPTERA, CARABIDAE																					
Nebria germari	X						X	X	X	X	X	X	X	X	X	X	X			X	X
Nebria jockischii	X		X														X	X		X	X
Nebria hellwigi																					X
Nebria rufescens	X																				X
Oreonebria castanea	X	X	X	X																	
Oreonebria diaphana							X	X	X	X	X										
Oreonebria soror						X											X				
Amara quenseli	X	X			X													X			
Amara erratica																					X
Pterostichus jurinei	X																				
Carabus sylvestris		X			X																
Carabus adamellicola													X	X	X						
Trechus dolomitanus									X		X										
Sinechostichus doderoi			X																		
Princidium bipunctatum					X																
Bembidion geniculatum																		X			
COLEOPTERA, BYRRHIDAE																					
Simplocaria semistriata	X																				
COLEOPTERA, ELATERIDAE																					
Fleutiauxellus maritimus	X			X														X	X		
COLEOPTERA, HYDROPHILIDAE																					
Helophorus glacialis	X																				
COLEOPTERA, STAPHYLINIDAE																					
Eusphalerum anale	X																				
OPILIONES, PHALANGIIDAE																					
Dicranopalpus gasteinensis	X																				

Table 5. *Cont.*

Country and Glacier Name	Rotmoos-tal, Austria	Cedec Glacier, Italy	Forni Valley, Italy	Forni Valley, Italy		Trobio Glacier, Italy	W-Sorapiss Glacier, Italy			C-Sorapiss Glacier, Italy		D'Agola Glacier, Italy			Amola Glacier, Italy		Hintereis, Austria		Hornkees, Austria
Mitopus glacialis	X																X		
Gyas annulatus																	X		
ARANEAE, LYCOSIDAE																			
Pardosa nigra	X														X	X	X	X	
Acantholycosa pedestris							X	X	X	X	X	X							
Pardosa saturatior	X			X															
ARANEAE, GNAPHOSIDAE																			
Drassodex heeri									X				X	X					
ARANEAE, ERIGONIDAE																			
Erigone atra												X							
Erigone tirolensis	X																		
Mecynargus paetulus	X																		
Entelecara media	X					X													
Walckenaeria vigilax	X																		
ARANEAE, THERIDIIDAE																			
Robertus arundineti	X																		
ARANEAE, AGELENIDAE																			
Thanatus formicinus					X														
Coelotes mediocris					X														
Coelotes pickardiitirolensis													X	X					
ARANEAE, THOMISIDAE																			
Xysticus audax					X														
Xysticus alpinus									X	X	X								
ARANEAE, LINYPHIIDAE																			
Meioneta rurestris	X																		
Meioneta gulosa	X																		
Meioneta nigripes	X																		
Lepthyphantes variabilis	X																		
Agyneta rurestris						X	X	X				X			X				
Mughiphantes brunnerii							X			X									

Table 5. *Cont.*

Country and Glacier Name	Rotmoos-tal, Austria	Cedec Glacier, Italy	Forni Valley, Italy	Forni Valley, Italy	Trobio Glacier, Italy	W-Sorapiss Glacier, Italy	C-Sorapiss Glacier, Italy	D'Agola Glacier, Italy			Amola Glacier, Italy	Hintereis, Austria	Hornkees, Austria
Mughiphantes handschini								X	X	X			
Mughiphantes cf. *merretti*									X	X			
Mughiphantes pulcher					X								
Tenuiphanthes jacksonoides						X							
Diplocephalus helleri								X	X	X	X	X	X
Troglohyphantes fagei						X	X						
Erigone dentipalpis											X		
Oreonetides glacialis											X		
Janetschekia lesserti													X

Figure 9. Pitfall traps are efficient in collecting surface active arthropods. Here, the night-active carabid beetle, *Bembidion hastii*, has been trapped alive. From [30]. Photo: Sigmund Hågvar.

Figure 10. Wolf spiders (Lycosidae) belong to the typical pioneer predator fauna all over Europe, except for arctic and high alpine areas. Here, *Pardosa trailli* from Norway. The animal has a good camouflage and is difficult to discover when standing quietly. Photo: Sigmund Hågvar.

3.1. Microarthropods: The Super-Pioneers

3.1.1. Northern Europe

Microarthropods are probably the first animals to colonize deglaciated ground. A compilation of data from young forelands in Iceland, southern Norway and Svalbard illustrates their rapid presence (Table 2). Even a high Arctic foreland on Svalbard was inhabited by four species of Collembola, one Oribatida mite species, as well as Gamasida mites after two years. In southern Norway, eight Collembola species were recorded on 0–3 years old ground. One of them, the cold adapted *Agrenia bidenticulata*, followed the retreating ice edge closely and showed jumping activity on a melt water surface.

Among the long list of Icelandic pioneer Collembola, three were common to Hardangerjøkulen in southern Norway (*Desoria olivacea, Desoria tolya* and *Lepidocyrtus lignorum*), and two were common to Svalbard (*Folsomia quadrioculata* and *Isotoma anglicana*). Among Oribatida, *Tectocepheus velatus*, a well-known pioneer species, occurred in all three sites. Wind transport of this species was proved by sticky traps on a young moraine near Hardangerjøkulen in Norway [20]. On genus level, *Desoria, Lepidocyrtus, Folsomia*, and *Isotoma* are good North-European pioneer candidates among Collembola, and the very small *Liochthonius* species among Oribatida. Furthermore, Prostigmata and Gamasida mites were often observed in pioneer communities.

3.1.2. The Alps

In the Austrian Alps, a number of Collembola species have been recorded in the Rotmoos foreland on ground younger than 40 years [47] and from younger ages down to 0–3 years [25]. Older Austrian data exist from Hintereis nearby [42]. From Italy, unpublished data on pioneer Collembola are available from four different forelands, among them the glacier Amola (Figure 11). Table 3 shows that several of the Collembola recorded in the Alps belong to other genera than in northern Europe. Some species were observed on the glacier surface, often on debris-covered glaciers. Furthermore, the species list reveals only few common species to Austria and Italy: *Heterosminthurus diffusus, Orchesella* cf. *alticola*, and *Isotomurus palliceps*. Even within the Italian Alps, some species change along a longitudinal gradient, suggesting local variation in species composition. Acari commonly occur on recently deglaciated terrains of the Italian Alps but have not yet been studied in-depth.

Figure 11. The debris-covered glacier Vedretta d'Amola (Presanella Mountain Group, Italy) and its glacier foreland. Photo: Mauro Gobbi.

3.2. *Macroarthropods: The Early Predators*

3.2.1. Northern Europe

Most early macroarthropods are predators. They are typically a mixture of harvestmen, carabid beetles, and various spiders, usually Lycosidae and Linyphiidae (Table 4). The high arctic site on Svalbard had only linyphiid spiders in addition to microarthropods.

Eight forelands younger than 20 years in Jostedalen and Jotunheimen in Norway had a rather predictable pioneer community [48]. Several of these species were common to a three year old site at Hardangervidda. A foreland near Veslejuvbreen glacier in the high alpine zone, however, contained only two beetles and two linyphiid spiders. Some predator species within the genera *Nebria, Bembidion, Mitopus, Erigone*, and *Collinsia* were common to Norway and Sweden. Icelandic forelands younger than ten years contained linyphiid spiders. However, a very old and partly vegetated nunatak contained three of the "classic" pioneers of Norway: *Mitopus morio*, *Amara quenseli*, and a *Pardosa* wolf spider [15].

3.2.2. The Alps

Pioneer macroarthropods from the Alps are listed in Table 5. Many of the species are noted only from either Austria or Italy, and several are endemic and/or cold adapted. Pioneer macroarthropods are typically a mixture of harvestmen, carabid beetles and various spiders, usually Lycosidae and

Linyphiidae. Centipedes (Chilopoda) were sometimes caught by pitfall traps on supraglacial debris and pioneer grounds of Italian Alps (*Lithobius lucifugus* on Sorapiss glaciers) but usually they are associated with older sites [31,51]. Lepidoptera larvae have been found abundantly on Rotmoos foreland after 34 years of deglaciation [47]. These data are consistent with the hypothesis that they are the initial humus formers [42].

Younger sites of Alpine glacier foreland and supraglacial debris host endemic cold-adapted species, for instance *Nebria germari* [39,40], *Oreonebria soror tresignore* [10], and *Mughiphanthes brunneri* [43].

3.3. Comparing Pioneer Communities in Northern Europe and the Alps

On genus level, young glacier forelands in the Alps contain a macroarthropod fauna that has much in common with forelands in Norway and Sweden (Tables 4 and 5). Common genera for the two areas are *Nebria* and *Amara* among Carabidae beetles, *Simplocaria* among Byrrhidae beetles, *Mitopus* among Opiliones, and *Pardosa*, *Erigone, Meioneta*, and *Collinsia* among Aranea. Table 5 also illustrates how the genera *Nebria*, *Oreonebria*, *Amara*, and *Pardosa* occurred in different localities of the Alps. On species level, however, few are common to Northern Europe (e.g., Norway and Sweden) and the Alps: *Amara quenseli, Erigone tirolensis*, and *Meioneta nigripes.* Among pioneer Collembola, northern Europe and the Alps have several genera in common but only *Isotoma viridis* and *Micranurida pygmaea* on species level according to Tables 2 and 3. In general, Isotomidae and Hypogastruridae were two characteristic pioneer families for northern Europe and the Alps. Surface active Symphypleona may also be early colonizers, present after only two years on Svalbard, after 1–3 years in Austria, and after three years in Norway. Certain Symphypleona were found on supraglacial debris in certain Italian sites (Table 3). Oribatida mites have been documented among pioneers in northern Europe, but information from the Alps are missing. Data from Rotmoos foreland in Austria indicate that Oribatida become abundant in the >30 year stages.

The faunal difference between northern Europe and the Alps can be related to Pleistocene glaciations. While the fauna in Norway, Sweden, Iceland, and Svalbard had to recolonize after the last glaciation, glacial and interglacial refuge areas located in the Alps during the Pleistocene drove speciation. A number of cold adapted arthropods and plant evolved in the Alps [54].

Moreover, Tables 2–5 reveal great difference in both macro- and microarthropod fauna within the Alps, between the Austrian and Italian study sites. For example, some species belonging to the *Oreonebria* genus (e.g., *Oreonebria soror*), as well as several species of spiders, are steno-endemic of restricted geographic areas. It is also possible that Collembola underwent similar speciation trends during the Pleistocene; this is suggested by the variability that is observed along the southern Alps. The percentage of cryptic species of Collembola has been calculated as very high [55]. For example, in Rotmoos valley, two cryptic species of *Isotomurus alticolus* were recorded [25]. This may indicate ongoing speciation, and biodiversity should be analyzed on a molecular level.

We are led to the conclusion that only glacier forelands within a restricted geographical area have a rather predictable fauna of pioneer arthropods. Examples on such restricted areas are Norway/Sweden/Iceland, closely situated foreland valleys in Austria, and forelands in northern Italy belonging to the same biogeographical area. On the genus level, however, there are some common traits across Europe.

3.4. Effects of Altitude and Latitude on Pioneer Fauna

Up to about 1400 m altitude in Norway and Sweden, the pioneer fauna in glacier forelands is rather characteristic, containing both Opiliones (*Mitopus morio*), certain carabid beetles and various Lycosidae and Linyphiidae spiders. However, at the high alpine site Veslejuvbreen in Norway, at 1860 m altitude, the only macroarthropods recorded were two beetles and two Linyphiidae spiders (Table 4). Furthermore, succession is slower at high altitudes [12,49,56].

With increasing latitude, there was a gradual "thinning" of pioneer species. In Iceland, young forelands (less than ten years old) contained few macroarthropod species. However, on a large and old, partly vegetated nunatak, certain "classic" pioneer taxa were present on young soil: the harvestman *Mitopus morio*, the carabid beetle *Amara quenseli*, and Lycosidae and Linyphiidae spiders. In the high Arctic on Svalbard, Opiliones, beetles, and Lycosidae were absent, but certain Acari and "ballooning" Linyphiidae spiders still joined Collembola in colonizing during the first two years [14].

In the Alps, the investigated areas deglaciated less than 20 years ago (Tables 3 and 5) were located at an average altitude of 2500 m, thus usually above the treeline. The Alps lack large plateau glaciers that provide the ice masses needed for a glacier tongue to reach far down into the valleys; however, there are a few big debris-covered glaciers that reach very low altitude (e.g., Miage glacier and Belvedere glacier that reaches the coniferous forest at 1800 m asl). Thus, the differences in species composition among the investigated glacier forelands can be explained by different biogeographic patterns and not only by habitat filtering [24]. On higher taxonomic level, the pioneer fauna in Alpine glacier forelands is rather similar to those of northern Europe, with Opiliones (*Mitopus* sp.), certain carabid beetles (*Nebria* spp.), springtails, and various Lycosidae and Linyphiidae spiders.

In summary, the harsher climate related to altitude or latitude gradually excludes most carabid beetles, Lycosidae, and Opiliones in Europe. Collembola, however, seem to thrive and reproduce on pioneer ground both under arctic and high alpine conditions.

4. From Structure to Function: A Comparison between Two Well-studied Pioneer Food Webs

Having described variations in the taxonomical structure of pioneer arthropod communities, this section focuses on function, i.e., food choice and food web architecture. Two thorough studies exist on pioneer food webs close to receding glaciers, one in Norway [57] and one in Austria [17]. These two forelands are comparable as they are both above the tree line, the actual terrain was deglaciated less than eight years ago, and they have a similar arthropod fauna on higher taxonomic level. We are interested in the following aspects:

- If the two food webs are different: why are they different, and can the difference illustrate flexibility in pioneer arthropod communities?
- Can these well-studied pioneer food webs shed new light on the "predator first paradox"?

4.1. Study Sites and Methods

The Norwegian study was performed close to the receding Hardangerjøkulen glacier in the southern, alpine part of the country [57]. Gut contents of three predators were studied in the microscope: the carabid beetles *Nebria nivalis* and *Bembidion hastii* and the harvestman *Mitopus morio*. Good knowledge of the anatomy of potential prey at the site allowed for identification of chitinous prey fragments in crop and gut. Early herbivory on pioneer mosses or biofilm was documented through gut content studies of certain Collembola, the Byrrhidae beetle *Simplocaria metallica*, and two omnivore carabid beetles, *Amara quenseli* and *A. alpina*. Species or genus of moss could often be identified from the cell structure in moss leaf fragments, even in Collembola guts [11].

The Austrian case was a DNA-based presence/absence study of prey items in gut contents of several predators [17]. The importance of a certain taxon, for instance Collembola, as prey was indicated by the percentage of predator guts that contained the actual taxon. Two early age stages (0–8 and 13–20 years old) were investigated in three glacier forelands in neighboring valleys in Tyrol, among them Rotmoos valley with a long research history (Figures 2 and 12). Extensive DNA analyses of gut contents made it possible to construct food webs.

Figure 12. Pioneer ground in the Rotmoos foreland, Austria, where food web studies were performed. Photo: Rüdiger Kaufmann.

4.2. Main Similarities and Differences

The Austrian study found great similarities in the food webs of the three valleys, and also between the two age classes of the ground. The overall conclusion was as follows: the three food sources, Collembola, other predators, and flying insects, contributed with approximately one third each, to the food consumed by predators. The Norwegian study concluded the opposite, with few Collembola eaten, and few other predators on the menu. Instead, chironomid midges belonging to local decomposers, were the dominant prey (Table 6).

Table 6. Main food items for pioneer predators in the Norwegian and the Austrian study, based on gut contents.

Country and Reference	Method	Collembola	Chironomid Midges	Other Predators	Foreign Prey?	Locally Produced Prey?
Norway [57]	Microscope study of gut content	Rare	Common	Rare	Yes, but rare?	Yes, locally produced chironomid midges
Austria [17]	DNA study of gut content	Common	Rare	Common	Yes, Mostly Dipterans and aphids	Yes, locally produced Collembola, and maybe other predators

Certain conclusions were, however, common in the Austrian and Norwegian study:

- Typical macroarthropod predators in the pioneer community were Carabidae beetles, Opiliones and Lycosidae, and Linyphiidae among spiders.
- The main food for pioneer predators was considered to be produced locally and not transported to the pioneer ground by air.
- Collembola seemed to be among the very first animal colonizers of newly exposed ground.

4.3. Special Observations in the Austrian Case

All predators were flexible generalists. This led to rather complicated food webs. Still, the main web structure was surprisingly similar between sites and ages. Intraguild predation (predators eating other predators) was documented to be high, Collembola was often a favored prey, and several groups of airborne, winged insects were also eaten. The situation can be visualized as a hunting ground rich in predators, Collembola and landed, winged insects. Assuming to be resident, with reproducing populations on pioneer ground, Collembola were probably key organisms for rapid establishment of predators. Remarkable was a pronounced maximum of *Heterosminthurus diffusus* immediately at the glacier front (Table 7) [25]. Most of the Collembola analyzed had guts filled with various fungal material, mineral particles, and airborne pollen. A Symphypleona maximum at glacier edge was confirmed by [18]. In contrast to the Norwegian case, chironomids were not abundantly available. In all three valleys, there were only few and small spring fed brooks hosting insect larvae. The glacial stream is hostile for insects due to its silt load. Non-biting midges are the main colonizers of glacier-fed streams, with some species belonging almost exclusively to the genus *Diamesa* [28,58].

Table 7. Quantitative data on Collembola in Rotmoos glacier foreland at three sites with different age [25]. Totals from all sampling methods.

Family	Genus/Species	0–3 Years	9–14 Years	18–25 Years	On Glacier	Total Numbers
Bourletiellidae	*Heterosminthurus diffusus*	1927	320	32	5	2284
Entomobryidae	*Orchesella* sp.	375	61	9	2	447
	Lepidocyrtus cf. *curvicollis*	10	104	114	2	230
Isotomidae	*Pachyotoma pseudorecta*	33	1	3	0	37
	Isotomurus cf. *alticolus*	57	1	41	1	100
	Isotomurus palliceps	1	24	11	0	36
	Agrenia bidenticulata	0	0	1	1	2
	Desoria sp.	0	0	0	2	2
	Isotomidae indet.	0	0	9	0	9
Hypogastruridae	Hypogastruridae sp. 1	6	4	0	0	10
	Hypogastruridae sp. 2	0	0	0	3	3
	Hypogastruridae sp. 3	0	0	1	0	1
	Hypogastrura sp.	0	0	0	1	1

Despite being all generalists, the predators differed in their usage of prey items, and they responded positively to periodic high availability of specific prey, for instance a pulse of airborne aphids. There were some predator specific diet shifts from the glacier front to the following stage with the first pioneer plants, most notably that the consumption of collembolans decreased in one of the carabids and in both wolf spider species [17]. Over longer successional times, however, such diet shifts can become much more pronounced as shown by analyses of stable isotopes [59].

4.4. Special Observations in the Norwegian Case

The Norwegian study revealed a surprisingly early presence of chlorophyll. The very start of a community was terrestrial biofilm with photosynthesizing diatom algae. The cold-loving, very active Collembola species, *Agrenia bidenticulata*, grazed on the biofilm and was able to follow the retreating ice edge closely. The species was absent in later successional stages (Table 8). Tiny pioneer mosses were established after four years and was grazed upon by the large Collembola *Bourletiella hortensis*, the Byrrhidae beetle *Simplocaria metallica*, as well as the omnivore Carabidae beetles *Amara alpina* and *A. quenseli*.

Table 8. Collembola succession on barren ground close to a Norwegian receding glacier: Percentage dominance of each species at different ages of the ground. From [30].

Age (Year)	**0**	**3**	**32–36**	**41–47**
Sampling method	Flotation	Pitfall	Pitfall	Pitfall
Agrenia bidenticulata	84.6	24.7		
Desoria infuscata	15.4	1.5	6.5	
Bourletiella hortensis		59.9	1.1	
Isotoma viridis		5.2	28.3	21.3
Lepidocyrtus lignorum		0.4	50.0	65.3
Desoria olivacea		8.0	8.7	4.5
Desoria tolya		0.2	4.3	3.0
Ceratophysella scotica		0.1	1.1	6.1
Number of animals sampled	26	1465	92	66

The local production of chironomid midges in the Norwegian site had a surprising explanation. Chironomid larvae developed in the sediment of small, young ponds, where they ate and assimilated bioavailable, ancient carbon released by the glacier. The ancient carbon compounds were assumed to be long-transported aerosols resulting from incomplete combustion of fossil fuels [60]. Chironomid larvae, with ancient carbon embedded in their tissue, had a radiocarbon age of 3270 years. Adult chironomids with a radiocarbon age of 1400 years transported the ancient carbon to terrestrial predators, which achieved radiocarbon ages between 340 and 1100 years [27,57].

Isotoma viridis and *Lepidocyrtus lignorum* are two well-known generalists among Collembola. They colonized early and remained for a long time. Table 9 illustrates their ability to adjust their food choice according to what is available. On three year old ground, mineral particles dominated their gut content, and biofilm feeding is probably a good guess. On 30–40 years old ground, some fungal hyphae and spores were seen in guts, and on 63 years old ground, both species had become typical fungal feeders. Clearly, pioneer ground is open for both specialists and generalists among Collembola [11].

Table 9. Changes in visible gut content during succession in two Collembola species. Relative amounts of different elements are roughly indicated by + (very little) up to ++++ (dominant gut content). Simplified from [11].

Species	**Gut Content**	**3 Years**	**30–40 Years**	**63 Years**
Isotoma viridis	Mineral particles	++++	++++	+
	Diatom algae	+	-	-
	Fungal hyphae	+	++	++++
	Fungal spores	+	++	-
Lepidocyrtus lignorum	Mineral particles	++++	++++	+
	Diatom algae	-	-	-
	Fungal hyphae	+	++	+++
	Fungal spores	-	++	+++

4.5. Discussion of the Two Studies

4.5.1. Flexibility in Pioneer Food Webs

This comparison between the two forelands illustrates flexibility in food webs on newly deglaciated ground. Based on the same main groups of arthropods (Carabidae, Lycosidae, Linyphiidae, Opiliones, and Collembola), two different food webs were established, taking advantage of different local resources. In both sites, generalist predators adjusted their food according to what was available. While the Norwegian site was favored by local production of chironomid midges as prey, the Austrian case illustrated a mixed diet: resident Collembola and other predators, as well as airborne prey, including pulses of aphids.

Flexibility also characterized the Collembola fauna, both in succession pattern (Tables 7 and 8) and in the food choice of single species (Table 9). The Norwegian study documented early chlorophyll by terrestrial diatom algae and tiny pioneer mosses, and pioneer Collembola fed on these sources. The food webs described from Austria did not include chlorophyll of any kind. However, diatom algae, pollen, and fungal hyphae were seen in collembolan guts [25]. A diverse fungal community can exist close to glaciers, more resembling cryoconite and glacier surface than typical soil communities [61]. Furthermore, unpublished studies of Collembola guts from the Italian Dolomites have indicated the presence of cyanobacteria. In summary, pioneer ground may contain a variety of food options for Collembola.

4.5.2. The Predator first Paradox Resolved?

The paradox relies on two assumptions: That predatory macroarthropods are first, and that their food is transported into the pioneer ground through the air [13]. Studies from both Austria and Norway indicated that Collembola, and not predators, are the real pioneers. Moreover, both studies documented that an important part of the available prey can probably be produced locally—either as resident Collembola or as chironomid midges hatching from young ponds or rivers. Future studies in other forelands may well document cases where prey is mainly airborne, so we shall not exclude that the "paradox" may be explained in that way. Anyhow, for an external observer, the presence of predators on pioneer ground without visible plants or herbivores, will spontaneously appear as a biological paradox.

5. General Discussion

5.1. Driving Forces in Early Succession: A Geoecological View

In early succession theory, the concepts of facilitation, inhibition, and tolerance were introduced to illustrate how species favored or inhibited each other [5]. This view was purely biotic. Later, a more fruitful geoecological perspective was introduced, taking abiotic factors into consideration. One aspect is that certain soil parameters gradually change with deglaciation age: reduced pH values and calcium content, and increased organic matter content [10,45,47]. Another aspect is that several abiotic parameters may be patchily distributed within the same age zone. Local factors like topography, exposition, substrate type, and moisture can modify the succession pattern from the very start [8–10,12,31,34,48,49,56,62]. For instance, an open sand and silt substrate without shelter can be unsuitable for carabid beetles. A young pond created by local topography may produce chironomid midges to serve as food for local predators and boost early succession. Unfortunately, arthropod studies in places with many ponds for comparison are lacking in the Alps, due to bedrock characteristics.

We should also add wind as a driving force. In principle, all organisms present on pioneer ground, including algae and mosses, are favored by wind transport. Such transport is episodic, depending on wind strength and direction. Furthermore, shelter from wind may be important for local survival.

A cold and open habitat near the retreating glacier facilitates the establishment of cold adapted and open-ground species among Collembola, spiders, and Coleoptera. Certain competition-weak plants are known to thrive on pioneer ground until vegetation closes [4,6–8]. Such negative interactions are, however, little understood in the arthropod communities. Among plants, competition has been assumed to become the driving force for species turnover in later successional stages [5]. There is a species turnover in arthropod succession, but is it driven by competition, or by other inhibiting interactions? Are the generalist predators also competing in the early stages? Is food really limiting, or can they avoid competition by using different microhabitats? These factors are more difficult to study among mobile arthropods than among immobile plants.

5.2. How to Quantify Food Choice?

Many potential prey groups can disperse to the pioneer ground by air, either by wind or active flight [19–21]. Various field observations and trapping systems in the Austrian case indicated strongly that flying insects were of allochthonous origin. A better quantification between allochthonous and autochthonous prey would improve our understanding of how pioneer food webs are fueled.

Regarding gut analyses, both DNA and direct observations in the microscope are methods with differing strengths and weaknesses. DNA is an elegant method to identify prey taxa but only records presence/absence and does not distinguish between a gut containing, for instance, few Collembola and one containing many. Quantification of a certain prey is therefore by the percentage of stomachs containing the actual sample. A high percentage of Collembola prey can be achieved even if few Collembola were eaten by each predator. The Norwegian microscopic study of gut contents illustrated that. While the percentage of guts containing Collembola was considerable (34% in *Mitopus morio*, 17% in *Bembidion hastii*, and 13% in *Nebria nivalis)*, the mean number per gut was less than one in all predators. As biomass, Collembola prey was insignificant. All three predators also consumed spiders, but always in very low numbers [57].

5.3. Pristine Ground—Both a Sink and a New Ecosystem

Pioneer ground functions more or less as an ecological sink. For instance, aphids arriving without any host plant available, will soon die but can represent valuable prey [17]. Certain arthropods found in fallout or on sticky traps near Hardangervidda glacier in Norway clearly did not belong to the pioneer community and died soon after arrival [20]. There are also several examples of arthropods trapped in pitfall traps on Icelandic nunataks that were non-survivors [63]. Dead arthropods may, however, contribute to soil fertilization and facilitate the establishment of plants [22]. If the transport of arthropods is continuous, for instance by ballooning Linyphiids, species may be wrongly recorded as a "resident" even if individuals die shortly after landing. Truly resident, reproductive species may be difficult to identify. However, the presence of larvae and juveniles (which are less mobile), several gravid females, and newly hatched adults, all indicate a reproducing population.

The new ecosystem starts to function as soon as sufficient food sources are present and the population size as well as the sex-ratio of the resident populations is favorable [29]. Collembola, the super-pioneers, evidently have a great ability to find food on newly exposed ground. Most authors have assumed that early Collembola are detritivores, decomposing blown-in dead organic material [13,59,63]. In the Norwegian study of their gut contents, pioneer Collembola were revealed to be mainly herbivores, grazing on diatom algae in biofilm or on tiny pioneer mosses. Only later in succession did certain species shift to a diet of fungal hyphae, typical for decomposers (Table 9) [11,57]. None of the other studies referred to contradict the possibility that pioneer Collembola can be herbivores. For instance, the two Collembola species *Isotoma viridis* and *Orchesella bifasciata* were placed close to the moss-eating beetle *Simplocaria semistriata* in a study of stable ^{15}N isotopes [59]. This result was considered a support for Collembola as plant litter decomposers, but an alternative explanation is herbivory. In Iceland, the ^{13}C isotopes of Collembola resembled that of plants and lichens [63]. In the DNA-based documentation of an Austrian pioneer food web with Collembola as an important prey, it was concluded, "A logical next step would now be to investigate the food sources of collembolans in more detail as it is not clear how important allochthonous input (detritus) is for these springtails compared to local production by algae and microbes" [17].

5.4. The Pioneer Community Enigma: A Mix of Different Life Forms

Within a certain geographical area, the community structure of arthropods on freshly deglaciated ground is rather predictable, at least on higher taxonomic level. But why do certain specific arthropods colonize pioneer ground, while other taxa present in the surroundings do not? One might expect that the ecological filters would result in pioneer species with strong similarities in their ecology. If so, are they specialists or generalists? If specialist, in what way? The key to understand their common success as pioneers is what we have called, "The pioneer community enigma".

To be a good disperser and find advantageous shelter are obvious favorable properties. However, to understand why they thrive (reproduce and survive), we must look at the ecology of each species. Can species with quite different ecologies live together in a pioneer community? If so, what is the key factor for each of them? And which parameters do not impact colonization?

As a case study, we have chosen to look at ecological parameters for a number of pioneer arthropods near Hardangerjøkulen glacier in Norway. Here, both micro- and macroarthropods have been studied and gut contents analyzed. Furthermore, early chlorophyll was detected.

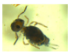
In Table 10, species from this locality are listed with the earliest colonizers on top, followed by an approximate succession of species downwards. Algae and mosses are included in the list of colonizers. For each organism, we ask whether it is a specialist or a generalist concerning three parameters: climate, habitat, and food. This presentation is rather schematic, but still tells us something about the species' suitability as pioneers. Two very early species are cold-adapted and probably prefer open space: the Collembola *Agrenia bidenticulata* and the Carabidae *Nebria nivalis.* Both are specialists in climate and habitat, and *Agrenia* also as a biofilm-eater. Their key is their specializations, and they follow the retreating ice edge closely. However, their specializations have a cost: they belong to the near-glacier fauna community, which in the long term is threatened by glacier retreat. Cold-adapted carabid species and other arthropods is also a characteristic feature of pioneer communities in Austrian and Italian Alps. Several carabid species belonging to the genera *Nebria* and *Oreonebria* depend on glaciers [38,39]. Interestingly, until forty years ago, the species *Nebria germari* was particularly abundant in front of the glacier, on scree slopes and on alpine prairies of the southern Alps. Recent studies demonstrated its extinction on alpine prairies and a consequently population contraction [40,64]. Large-sized populations can be still found only on recently deglaciated terrains and on some debris-covered glaciers [39,40]. Conversely, some cold-adapted steno-endemic species belonging to the genus *Oreonebria* (e.g., *Oreonebria lombarda*) were recorded also far from the glacier front, but only on glacier forelands located in peripheral mountain ranges with high winter precipitation rates [10].

A preference for open ground is a key also for the following species in Table 10: the Carabidae beetle *Bembidion hastii*, the Lycosidae spider *Pardosa trailli*, as well as various pioneer mosses, the Collembola *Bourletiella hortensis*, and probably the Byrrhidae beetle *Simplocaria metallica*. The most sensitive among these is probably *B. hastii* which disappears as soon as vegetation closes in. Furthermore, we have moss-eating specialists among the pioneers: *Bourletiella hortensis* and *Simplocaria metallica*, and two omnivore *Amara* species.

Four generalist predators are listed in Table 10. The tolerance for different prey types is their key. Three of them are specialists on open ground, and one is cold adapted. The super-generalist seems to be the Opiliones *Mitopus morio*, with a general high tolerance for variations in climate, habitat, and prey [26]. Likewise, in the Austrian Rotmoos valley, *M. morio* is widespread, apart from on the youngest site where *M. glacialis* takes over. Without looking at the ecology of each species, the enigma could not be solved.

Certain parameters seem to be less important when considering ability to colonize. Reproduction mode could theoretically be important: One might easily assume that parthenogenetic species would be favored as pioneers, since one individual would be sufficient for reproduction and establishment. Furthermore, species with short life cycle and ability to reproduce rapidly, might thought to be favored. It has been shown, however, that pioneer microarthropods are a mix of parthenogenic and sexual species, as well as species with short and long life-cycle [23,30,45]. Why it is so, remains unclear. Furthermore, among pioneer macroarthropods, we find variation in reproduction mode and life cycle length. In Austria, *Mitopus glacialis* is a parthenogenetic species with an annual life cycle. Wolf spiders are sexual with an annual life cycle. The actual carabids have a sexual reproduction and extended life cycles which include an astonishing longevity of adults covering three reproducing seasons (Kaufmann, unpublished) [40].

Table 10. This Table illustrates how various specialists and generalists together can shape a pioneer arthropod community. Data from 0 to 7 year old foreland of Hardangerjøkulen glacier, Norway. Illustrations from [11,27].

	Species	**Group**	**Climate**		**Habitat**		**Food**	
	TERRESTRIAL		**Specialist**	**Generalist**	**Specialist**	**Generalist**	**Specialist**	**Generalist**
	Diatom algaein biofilm	Algae			Open			
	*Agrenia bidenticulata*	Collem-bola	Cold adapted		(Open)		Biofilm	
	*Nebria nivalis*	Cara-bidae	Cold adapted		(Open)			Generalist predator
	*Bembidion hastii*	Cara-bidae			Open			Generalist predator
	*Pardosa trailli*	Lyco-sidae			Open			Generalist predator
	*Mitopus morio*	Opili-ones		Generalist		Generalist		Generalist predator
	Pioneer mosses	Moss			Open			
	*Bourletiella hortensis*	Collem-bola			Open		Moss	
	*Simplocaria metallica*	Byrr-hidae			(Open)		Moss	
	*Amara alpina*	Cara-bidae	(Alpine)				(Moss)	Omnivore
	*Amara quenseli*	Cara-bidae					(Moss)	Omnivore
	*Isotoma viridis*	Collem-bola					Biofilm and fungal hyphae	
AQUATIC								
	Chironomidae larvae	Diptera			Young ponds		Bio-available ancient carbon	
	Tipulidae larvae	Diptera			Young ponds		Bio-available ancient carbon	
	*Agabus bipustulatus*	Dytis-cidae			Young ponds		Predator on Chirono-mid larvae	

To summarize, the ecological filters allow quite different life forms to pass, and various types of specialists and generalists live together in pioneer communities. "The pioneer community enigma" can only be understood through close studies of each species' demands and tolerances.

5.5. Nature Conservation Aspects

Cold adapted pioneer arthropods living adjacent to glaciers are in danger of extinction due to rapid glacier melting [10,28,38,39,50–52]. Some may survive for a time, either along cold rivers and brooks or in subterranean, cold microhabitats among stones and gravel. Cold adapted species are both ecologically and physiologically interesting. They have adapted to low temperatures during long time periods. Because the Alps avoided a complete ice covering during the last glaciation, cold adapted species not only survived here, but developed new species, including endemic ones in the Alps. There are, for instance, many cold adapted species in the Alps of the carabid genera *Nebria* and *Oreonebria*. There are also a number of cold adapted spiders and Collembola present (Tables 3 and 5). Furthermore, certain brachypterous beetles with little dispersal capacity and dependent on stable, often cold, habitats, are clearly threatened when glaciers retreat rapidly [50,65]. Where glaciers reach lower altitude, for instance down to the forest line, cold adapted species may still survive in cool, supraglacial debris [66]. In that situation, the specialization of cold adapted species becomes very evident [24]. Protecting refugia that allowed the survival of such species during Holocene climatic optimum, could help such species during the current global warming [24,28].

Our view conforms well with a global meta-analysis of biodiversity change across three major glacier-influenced systems: glacier-fed fjords, glacier-fed freshwaters, and glacier forefields. The analysis concludes that there are both losers and winners following glacier retreat. Most of the losers are specialist species, uniquely adapted to glacial conditions, while winners are typically generalists, and often invasive species [67].

6. Conclusions

6.1. General Findings

- Arthropods colonize deglaciated ground in a rapid succession and may develop food webs within a few years, before higher plants establish or only occur sporadically.
- Pioneer species are fewer, and succession is slower at high altitudes and latitudes.
- Each pioneer species has to overcome certain obstacles, or “ecological filters”: It must travel, it must find an acceptable habitat with tolerable climate and shelter to avoid hostile conditions, it must be able to find food, and it must be able to reproduce.
- Microarthropods, especially Collembola, are “super-pioneers”. They colonize during the very first years, even in high alpine or high arctic conditions.
- Macroarthropod predators follow closely and are well represented after just a few years (1–5 years). Typical taxa in Europe are Carabidae among Coleoptera, Lycosidae, and Linyphiidae among Aranea, and *Mitopus* sp. among Opiliones.
- On species level, pioneer arthropods differ between northern Europe and the Alps, due to different glaciation and speciation history. However, certain genera are common to both.
- A pioneer arthropod community is a mixture of specialists and generalists.
- The pioneer community may include both parthenogenetic and sexually reproducing species, species with short or long life cycle, and small as well as large species.
- Certain specialists may disappear after a few decades (30–50 years). Examples are cold-adapted species and species preferring open ground.
- Melting of glaciers threaten several cold-adapted species within various groups as Carabidae, Araneae, and Collembola.
- Recent studies challenge the classic “predator first paradox”, which describe a heterotrophic pioneer community depending on airborne prey for predators and airborne dead organic material for decomposing Collembola. It has been shown that predators can be fed by locally produced food, and Collembola can be herbivores.
- Certain “invisible” carbon sources can contribute to the pioneer community: terrestrial biofilm with diatom algae or cyanobacteria, tiny pioneer mosses, pollen, and bioavailable ancient carbon released by the glacier.
- Two well-studied pioneer food webs, one from Norway and one from Austria, revealed similarities in arthropod families and genera, but the structure and function of the food webs differed.

- The pioneer ground can be surprisingly rich in microhabitats and food sources.
- For many arthropods, pioneer ground is a sink, but dead animals can contribute as prey or soil fertilizers.
- Definition of succession is a matter of scale. For instance, a small pioneer moss turf may harbor moss-eating Byrrhidae beetles. Moreover, patches with different microclimate or substrate may have different succession pathways.
- Terrestrial and aquatic environments can be connected in early succession. For instance, young ponds and glacial stream rivers may produce chironomid midges that serve as prey for terrestrial predators.

6.2. The Birth of an Ecosystem: Short Answers to the Two Main Questions

A. How "flexible" are arthropod communities in the early phase of primary succession?

We find from our comparative studies, that quite different pioneer arthropod communities are possible (Tables 2–5) reflecting that primary succession can be flexible and does not have a fixed driving force predicting the outcomes. Species with very different life strategies, including both specialists and generalists, may pass through the "ecological filters" and co-occur in a pioneer community (Table 10). The community structure will depend on available candidate species in surrounding source habitats, and their ability to disperse and establish. Altitude, latitude, climate, and local conditions are important parameters. Prey can be transported by air but may also be produced in situ (for instance Collembola and chironomid midges). Pioneer food webs may rely on different resources, for instance different prey items, early chlorophyll in biofilm or tiny pioneer mosses, or use of bioavailable ancient carbon released by the glacier.

B. Do pioneer arthropod communities under different conditions still have certain basic traits in common?

A common trait for pioneer communities throughout Europe, including high altitude and high Arctic forelands, is the role of Collembola as "super-pioneers". The "predator first paradox" could be substituted by "The Collembola first principle". At high altitudes and latitudes, ballooning Linyphiidae spiders represent the macroarthropods. In less extreme climate, pioneer communities of Europe are typically added a macroarthropod association of carabid beetles, Opiliones and Lycosidae, and Linyphiidae spiders. The pristine ground is a sink habitat for many arriving species. However, non-surviving arthropods may serve as prey and also fertilize virgin soils.

7. Suggestions for Further Studies

In order to understand "ecosystem birth", a higher number of young glacier forelands must be investigated. We must learn more about the ecology of pioneer species: Why can certain species act as pioneers, while others, perhaps closely related, cannot? This question is especially relevant for Collembola. Even under harsh conditions, as in high alpine areas and in the high Arctic, certain Collembola species are able to conquer pristine ground immediately. They are able to find shelter and food, and they reproduce. Moreover, they function as prey for early predators, contributing to the first food webs. The good dispersal ability of Collembola combined with a high species diversity is obviously a part of their success story. However, the ultimate question about these super-pioneers, is what do they eat? Do they graze on early chlorophyll rather than being fungal-feeding decomposers, or can they continuously adjust their food according to what is available? Are pioneer Collembola a mix of specialist feeders and/or generalist feeders?

Overlooked early chlorophyll should be searched for, as well as a possible release of bioavailable ancient carbon. It is, however, not only carbon that matters. Nitrogen is important and is commonly considered to be limiting in young ecosystems. It has been claimed that phosphorus may also be a limiting element [68]. On the glacier surface, there is limited primary production (algae and cyanobacteria) and decomposition of organic fall-out (cryoconite holes). This can wash down into the deglaciated ground and favor the upstart of a new ecosystem.

More detailed case studies are needed in order to understand the variation in which an ecosystem is established close to a melting glacier. Comparing cases with similar climate and fauna would illustrate how local conditions may affect food webs; for instance, the presence or absence of ponds. Cases with different climate and fauna from other regions in the world could reveal whether there are some quite general patterns, for instance whether Collembola are general super-pioneers.

Comparison between studies is often problematic due to varying taxonomic resolution. Species-rich but "difficult" groups like Staphylinidae beetles, Collembola, or Acari may not be identified to species level. Furthermore, sample size, type, and number of traps, as well as trapping period, can be critical factors when species number shall be compared between sites. Carabids, for instance, may have their main activity period early in the snow-free season, and trap numbers should be large enough to stabilize the cumulative species number. During soil sampling, local variation should be covered through many small samples rather than a few large ones. Certain large and active, surface-living Collembola easily escape sampling with a soil corer, so pitfall catches represent a valuable supplement.

In order to understand energy flows in pioneer communities, more quantitative data are needed. How large is the contribution of aerial transport of prey compared to local prey production, and how do predators select between the two sources?

Certain neglected invertebrate groups may shortly be mentioned here: Testate amoebae (Protista) are known as early colonizers of high latitudes [14,69]. In four-year-old soil at Hardangerjøkulen glacier in Norway, both Nematoda, Tardigrada, and Rotifera have been documented (Magnusson, Willassen and Hågvar, unpublished). Nematoda and Rotifera have been studied on supraglacial debris of two Alpine debris-covered glacier [70].

Future studies on early animal and plant succession should follow up the geo-ecological perspective, which has been well exemplified in a 33-year chronosequence on the Storbreen glacier foreland, Jotunheimen, southern Norway. It was documented that physical environmental changes, soil development and spatial heterogeneity markedly influenced animal colonization and successional trajectories [71].

Our review represents a mix of conclusions and questions, in a field of increasing attention. The present global shrinking of glaciers gives unique possibilities to reveal both variations, and basic principles, when new ecosystems evolve during primary succession. Such knowledge could shed new light on our ecological understanding.

Author Contributions: S.H. prepared and revised the manuscript draft with extensive inputs from the other authors. All authors have reviewed and approved the manuscript for publication.

Funding: This review received no external funding.

Acknowledgments: We are grateful for being allowed to reuse Figures and Tables from Arctic, Antarctic, and Alpine Research (copyright by the Regents of the University of Colorado). Thanks to Oddur Sigurðsson for use of picture of nunataks.

Conflicts of Interest: The authors declare no conflict of interest.

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Chapter 5

Conclusions and perspectives

5.1 CONCLUSIONS AND PERSPECTIVES

This PhD project contributed to the knowledge of glacial and periglacial biological communities with a multi-taxa approach, following two different and complementary approaches: analysis and synthesis, fundamental for understanding both specific variability and global trends, in a monitoring perspective. The obtained knowledge on biological communities by analysing their occurrence and distribution in relation to environmental parameters constituted a powerful tool for finding global trends and predicting glacial and periglacial biodiversity responses to climate change. In this perspective, an important feature of this PhD consisted in the collaboration with Natural, Regional and National Parks (Ampezzo Dolomites Natural Park, Natural Park of Maritime Alps, Adamello-Brenta Natural Park) in investigating all this biological and geological diversity.

An important part of glacial biodiversity is still taxonomically unknown, especially in the peripheral mountains (Gobbi et al., 2021). Thus, the descriptive effort focused especially on these areas, currently already very close to a complete loss of the existing glaciers, that represent a hotspot of biodiversity because of their biogeographic position during glacial and/or interglacial periods. Studying these glacial sites, I highlighted how part of this high-altitude biodiversity is cold-adapted and strictly linked to ice which, probably, acts as a local refugium for these species. In the future it will be necessary to apply these information for monitoring projects and, possibly, for conservation projects that are difficult to plan at global scale but can be planned at more local scale (e.g *ex situ* breeding, reduction of human mountain activities impact).

Another important result of this PhD project regards the contribute to the knowledge of ice-dwelling cryophilic springtails (Collembola: Isotomidae), a taxonomically almost neglected taxon on European Alps. Nevertheless, their ecological and trophic importance in pioneer glacial communities was evident in the last years and also the urgency of describe and monitor these organisms as biological indicators of these vanishing habitats. I described with a great detail ice-dwelling cryophilic springtails from all the Alps and the Apennines, giving the basis for the first biogeographic consideration on this taxon (paper 3.3, 3.4). To the two known taxa of ice-dwelling springtails, three new species have been discovered and described with integrative taxonomy and one previously described have been suggested as invalid name. A first record of a genus of debris-dwelling springtail has been reported for European Alps. The distribution of ice-dwelling species reflects the most important biogeographic classification of the Alps (Western Alps and Eastern Alps) and responds to potential local isolation of some glacier and, maybe, other glacial dynamics that still need to be clarified in relation to ice-fluxes during Pleistocene glaciations and to glacier fluctuations occurred throughout the Holocene. Springtails, thanks to their sensitivity to microhabitats and cold biomes are good candidates for becoming biological indicators for glacial and periglacial habitat monitoring.

In conclusion, from this PhD project it emerges how is important to combine small and large scale sampling plans, traditional and molecular approaches - being integrative taxonomy, by now, the only complete way for clarifying springtail diversity and distribution (Potapov et al. 2020)- and a multitaxa, multidisciplinary approach for studying glaciers and rock glaciers ecology. These habitats are a good test field for combine all these disciplines, having a relatively reduced biodiversity, but extremely specialised and threatened.

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Chapter 6

Curriculum vitae of the PhD

Activities of the PhD

Barbara Valle

Study stays in other institutions

2022	Pavol Jozef Šafárik University in **Košice** (Slovakia), in ÚBEV - Institute of Biology and Ecology, for collaborating on the project of supraglacial springtails (two months).
2021	University of **Siena** (Italy**),** in Evolutionary and Systematic Zoology Laboratory, for collaborating on the project of supraglacial springtails (two months, in different periods)

Conference attendances and organization

16-18 Jun. 2022	**Member of scientific and organization committee** of the 55th Congress of SISV - Vegetation science and global changes: scenarios, challenges and innovation. **Oral presentation**: Valle B, Di Musciano M, Gobbi M, Invernizzi A, Caccianiga M: "Not only plants: multi-taxa approach to plant community studies in harsh environments"
20-23 Sep. 2021	63° International Association for Vegetation Sciences (IAVS) Symposium. **Poster:** Gigante D, Angelini F, Angiolini C, S. Bagella S, Bonini F, Caccianiga M, De Simone N, Gabellini A, Rivieccio G, Valle B, Garabini M: "Natural Intelligence for robotic monitoring of Annex I Habitats: first steps in an unexplored world"
26-27 Mar. 2021	Congresso Botanica Sudalpina 2020 (Società Botanica Ticinese) **Poster:** Valle B, Gobbi M, Seppi R, Borgatti M Tognetti M, Bernasconi M, Caccianiga M: Primary succession on carbonate glacier forelands : the case study of three dolomitic glaciers"
9 Oct. 2020	**Member of scientific and organization committee** Workshop of Società Italiana di Scienze della Vegetazione (SISV): "Dalla fitosociologia al monitoraggio degli Habitat: specie caratteristiche, specie diagnostiche, specie tipiche
6-7 Feb. 2020	CYBO: Congress of young Botanists **Oral presentation:** Valle B, Tognetti M, Caccianiga M "Ecological features of supraglacial plant communities along the Alps and the role of Debris-covered glaciers as refugia for cold-stenotherm species"
16-20 Sep. 2019	19° European Carabidologist Meeting **Poster**: Valle. B, Ambrosini R., Caccianiga M, Gobbi M.: "Nebria germari Heer, 1837 – insight about the distribution and ecology of a climate-sensitive species of the Eastern Alps"

Grants application and project cooperation

2021-present	Collaborator for the project **H2020** "Natural Intelligence for robotic monitoring of habitats (NI)" – Code H20_RIA21MCACC_01
2022	Speaker and organizer of **EMBO Practical Course** "Integrating traditional and molecular approaches in ecology of glacial habitats (ICME11)" https://icme11-embo.readthedocs.io/en/latest/index.html
2022	Participation as springtail expert to a project for PRIN financing grant ("projects of significant national interest" of Italian Ministry of University and Research). Title of the project "Cold Case: structure and functioning of the disappearing glacier biodiversity - (project under review)
2021	Participation as springtail expert to a project for Biodiversa+ financing grant. Title of the project: "Vanishing habitats: conservation priorities for glacier-related biodiversity threatened by climate change" (PrioritIce). (project under review)
2020	Partecipation as springtail expert to a grant proposal for Polish National Science Centre entitled "Unrecognized HOtspots for gLacial MEtazoanS – effects of physicochemistry, thermal regime and climate on animals assemblages across glacier zones and habitats (HOLMES)" (not founded)
2019-2020	Collaboration at MUSE- Museum of Trento for the project "azioni volte alla valorizzazione degli elementi geomorfologici, della flora e fauna degli ambienti glaciali e proglaciali del gruppo del Sorapiss", for dissemination actions about glacial and proglacial environments of Sorapiss glaciers (Dolomites)
2019-2020	Collaboration at University of Milano for studying plant and arthropod proglacial communities in Maritime Alps (Clapier e Peirabroc).
2019	Application for National Geographic Exploration Grants ~ NGS Grantee Community (not founded). Title of project: "Alpine springtails on the last glaciers: almost unknown but already threatened"

Awards

2022	**Prize Sandro Ruffo 2022**, Museo di Storia Naturale di Verona. Project: Taxonomic identification, computerized cataloging and logistical reorganization of the Collembola collection of the Natural History Museum
2019	**Best poster prize** at the 19° European Carabidologist Meeting: Valle. B, Ambrosini R., Caccianiga M, Gobbi M.: "*Nebria germari Heer, 1837 – insight about the distribution and ecology of a climate-sensitive species of the Eastern Alps*"

Published papers

2022 Valle B, Gobbi M, Tognetti M, Borgatti MS, Compostella C, Pantini P, Caccianiga M (2022) *Glacial biodiversity of the southernmost glaciers of the European Alps (Clapier and Peirabroc, Italy)*. Journal of Mountain Science 19(8). https://doi.org/10.1007/s11629-022-7331-8

2022 Valle B, Di Musciano M, Gobbi M, (2022*) Biodiversity and ecology of plants and arthropods on the last preserved glacier of the Apennines mountain chain (Italy)*. The Holocene. 32 (8): 853-865. https://doi.org/10.1177/09596836221096292

2022 Lunghi E, Valle B, Guerrieri A, Bonin A, Cianferoni F, Manenti R, Ficetola GF (2022) *Environmental DNA of insects and springtails from caves reveals complex processes of eDNA transfer in soils***,** STOTEN, DOI: 10.2139/ssrn.3989492

2021 Valle B, Cucini C, Nardi F, Caccianiga M, Gobbi M, Di Musciano M, Carapelli A, Ficetola GF, Guerrieri A, Fanciulli PP (2021) Desoria calderonis *sp. nov., a new species of alpine cryophilic springtail (Collembola: Isotomidae) from the Apennines (Italy), with phylogenetic and ecological considerations*. European Journal of Taxonomy, 787(1): 32-52. https://doi.org/10.5852/ejt.2021.787.1599

2021 Bonari G, Fantinato E, Lazzaro L, Sperandii MG, Acosta ATR, Allegrezza M, Assini S, Caccianiga M, Di Cecco V, Frattaroli A, Gigante D, Rivieccio G, Tesei G, Valle B (* corresponding author) et al, (2021) *Shedding light on typical species: implications for habitat monitoring*, Plant Sociology, DOI 10.3897/pls2020581/08

2021 Gobbi M, Ambrosini R, Casarotto C, Diolaiuti G, Ficetola GF, Lencioni V, Seppi R, Smiraglia C, Tampucci D., Valle B, Caccianiga M, (2021) *Vanishing permanent glaciers: climate change is threatening a European Union habitat (Code 8340) and its poorly known biodiversity*, Biodiversity and Conservation,

2020 Valle B., Ambrosini R, Caccianiga M, Gobbi M (2020) *Ecology of the cold-adapted species Nebria germari (Coleoptera: Carabidae): the role of supraglacial stony debris as refugium during the current interglacial period***,** Acta Zoologica Academiae Scientiarum Hungaricae 66 (Suppl.), pp. 199–220, 2020, DOI: 10.17109/AZH.66.Suppl.199.2020

2020 Hågvar, S.; Gobbi, M.; Kaufmann, R.; Ingimarsdóttir, M.; Caccianiga, M.; Valle, B.; Pantini, P.; Fanciulli, P.P.; Vater, A. (2020) *Ecosystem Birth Near Melting Glaciers: A Review on the Pioneer Role of Ground-Dwelling Arthropods*. Insects 2020, 11, 644

2019 Valle B., Ambrosini R, Caccianiga M, Gobbi M (2019) Nebria germari *Heer, 1837 – insight about the distribution and ecology of a climate-sensitive species of the Eastern Alps*, ARPHA Conference Abstracts 2: e37074. https://doi.org/10.3897/aca.2.e37074

2019 Bernasconi M, Borgatti M.S., Tognetti M., Valle B., Caccianiga M., Gobbi M., Casarotto C., (2019) *Checklist ragionata della flora e degli artropodi (Coleoptera: Carabidae e Arachnida: Araneae) dei ghiacciai Centrale e Occidentale del Sorapiss (Dolomiti d'Ampezzo),* Frammenti, Parco Nazionale delle Dolomiti Bellunesi. (non-ISI journal)

Paper submitted and in submission

2022 Ornaghi S, Valle B. (* corresponding author), Caccianiga M, Seppi R, Gobbi M *Sex-ratio and body size plasticity in two cold-adapted ground beetles (Coleoptera: Carabidae) co-occurring in a periglacial area of the European Alps.*. Fragmenta Entomologica - submitted

2022 Fugazza D., Valle B., Caccianiga M., Gobbi M., Traversa G., Tognetti M., Senese A. *An empirical melt model of a small Alpine debris-covered glacier: the case study of the Amola Glacier* (Italy). Cold Regions Science and Technology – in submission

Paper in preparation

- Valle B, Gobbi M, Boschi S, Cucini C, Nardi F, Barbon G, Ficetola GF, Kovač L, Ambrosini R, Buda J, Franzetti A, Zimmer A, Caccianiga M. *Glacier fleas" (Hexapoda: Collembola) from supraglacial environment of European Alps: taxonomy, ecology and biogeography*
- Gobbi M, Brambilla M, Tampucci D, Caccianiga M. *Global scenario, local approach: challenges for alpine plants, insects and spiders in a warming world*
- Valle B, Skarżyński D, Porco D, Zeni M, Caccianiga M, Rodriguez Prieto A, Gobbi M. *Alpine "blooming" of collembola: a focus on snow-active species and description of a new species of* Hypogastrura *Bourlet, 1839*
- Valle B, Gobbi M, Caccianiga M, *Comparison among different sampling methods for studying springtails in glacial lithosols*
- Valle B, Gobbi M, Di Musciano M, Dalle Fratte M, Cerabolini BEL, Caccianiga M. *Functional characterization of glacial and periglacial plant and arthropod communities*
- Valle B, Gobbi M, Invernizzi A., Ligi O, Ornaghi S., Caccianiga M. *Plant and arthropod communities (Vascular plants, bryophytes, ground beetles, spiders and springtails) of two Alpine rock glaciers with contrasting lithology (Cima Uomo and Lazaun, Eastern Alps)*

Contribution to scientific volumes

2022 Preparation of the chapter "*Cave Collembola of Italy*" for the international Encyclopaedia Biospeologica

Teaching activity

2022 **Speaker and organizer of EMBO Practical Course** "Integrating traditional and molecular approaches in ecology of glacial habitats (ICME11)" https://icme11-embo.readthedocs.io/en/latest/index.html English

2022 **Teacher of Botanic for the course** “Fauna and Flora of Orobian meadow-pastures”organized by the Orobie bergamasche Park for the project C.ORO - CAPITALE OROBIE founded by Cariplo

2022 **Seminar “ life in harsh environments: studying glacial and periglacial habitats”**
For the Institute of Biology and Ecology (Pavol Jozef Šafárik University in Košice, Slovakia). English

2020 and 2021 **Seminar “Botanical sampling”**
For the course Approaches to the Study of Ecological Systems for the Master in Environmental Science and Policies (University of Milan, Italy). English

2022 and 2021 **Teaching assistant** for Systematic Botany for Bachelor course in Natural sciences (University of Milan, Italy). Italian

2021 **Teaching assistant** for Botany for Bachelor course in Natural sciences (University of Milan, Italy). Italian

Theses supervised

		Graduated:
Anna Invernizzi, Master Thesis	Caratterizzazione tassonomica e funzionale di una comunità vegetale di rock glacier Alpino/*Taxonomic and functional characterization of an Alpine rock glacier plant community*	11 Apr. 2022
Simone Ornaghi, Master Thesis	Comunità di Carabidi (Coleoptera: Carabidae) di due rock glacier alpini/ *Community of Carabidae (Coleoptera: Carabidae) of two alpine rock glaciers*	Graduated 19 Oct. 2021
Olga Ligi, Master Thesis	Comunità briofitiche di due rock glacier alpini di differente litologia/ *Bryophyte communities of two alpine rock glaciers of different lithology*	(Apr. 2023)
Asia Biassoni, Bachelor Thesis	Flora muscinale del debris-covered glacier di Cima Uomo (Dolomiti, TN)/*Bryoflora of the debris-covered glacier of Cima Uomo (Dolomites, TN)*	Graduated 18. Oct. 2022
Brian Villa, Bachelor Thesis	Intelligenza artificiale per il monitoraggio degli habitat/*Artificial intelligence for habitat monitoring*	(Apr. 2023)
Matteo Valentini, Bachelor Thesis	Flora muscinale di un rock glacier dolomitico*/ Bryoflora of a dolomitic rock glacier*	(Apr. 2023)

Dissemination papers and seminar

2022 Article for Bollettino del Club Alpino Italiano (CAI): Gobbi M, Ambrosini R, Casarotto C, Diolaiuti G, Ficetola GF, Lencioni V, Seppi R, Smiraglia C, Tampucci D., Valle B, Caccianiga M., *Ghiacciai in estinzione e crisi della biodiversità I cambiamenti climatici minacciano la criosfera Alpina, habitat*

	protetto dall'Unione Europea/ “retreating glaciers and biodiversity crisis: climate change threaten Alpine cryosphere, a habitat protected by EU” – (Italian)
2021	Seminar for Flora Alpina Bergamasca (FAB) on “Plant and arthropod communities of Dolomitic glaciers” (Italian)
2019 - 2020	Preparation of the “naturalistic trail of Sorapiss glacier” for a joined project among Ampezzo Dolomite Park, MUSE -Science Museum of Trento and University of Milan. Is a thematic trail along proglacial habitat of Sorapiss glacier (BL, Italy), guided by panels and a brochure. (Italian)
2019	Article for Gardenia (in collaboration with Rete Orti Botanici Lombardia): *Là dove osano… le piante*!”/there… where plants dare!” – (Italian)
2018	Article for Strenna del MUSE - Museo delle Scienze di Trento: *Un inaspettato colore per la biodiversità: il significato ecologico dei ghiacciai neri*./”an unexpected colour for biodiversity: the ecological meaning of debris-covered(black) glaciers” – (Italian)

ACKNOWLEDGMENTS

First of all, I would like to thank Marco Caccianiga and Mauro Gobbi for introducing me to their research projects on glacial and periglacial habitats, for supervising my work and for helping me to concretize many projects and ideas with friendship and professionalism.

This PhD project has been realized also thanks to the collaboration of many expert from different Institutes: I would like to thank Pietro Paolo Fanciulli (University of Siena), that showed me for the first time springtail taxonomy and beauty and Claudio Cucini, Francesco Nardi and Sara Boschi (University of Siena) for teaching me molecular approaches. Thank to Roberto Ambrosini, Davide Fugazza and Giacomo Traversa (University of Milano) for sharing glaciological interest and a lot of hard field work all along the Alps. Gentile Francesco Ficetola, Mattia Brambilla (University of Milano) for collaborating in project planning and data analysis. Thanks to Michele di Musciano (University of L'Aquila) for the scientific enthusiasm and for the wonderful exploration and discovery of Calderone glacier. Thanks to Ľubomír Kováč (Univeristy of Košice) for showing me for the first time cave habitat and cave springtails and thanks also to all floor mates in the Institute of Biology and Ecology in Košice that made my stay in Slovakia wonderful. Thanks to Roberto Seppi (University of Pavia) for showing me and studying together some very peculiar periglacial areas of Alps. I would like to thank Paolo Pantini (Natural science Museum of Bergamo) for the great taxonomic support for studying spiders and all taxonomist that support multitaxa studies. Thanks to Andrea Franzetti (University of Milano-Bicocca), Krzysztof Zawierucha and Jacub Buda (University of Poznań) for sharing interest, projects and samples of glacial habitats.

Thanks to thesis students, for their decisive support in field sampling and laboratory work: Anna Invernizzi, Simone Ornaghi, Olga Ligi, Asia Biassoni, Brian Villa e Matteo Valentini

I would like to thank Marina Serena Borgatti and Marta Tognetti for their friendship and their collaboration in studying high altitude habitats since our common Master Thesis, for the many mountain trips done together and the heavy samples we took several time down from the glaciers.

Thanks to my father Marco Valle for being such a good scientist and for accompanying me to Pyrenées in one of the most beautiful sampling trip I have ever done.

And then, thanks to my family and to all my friends that support my work making me feel good.

Viva il collembolo
bestia ideale,
il più simpatico d'ogni animale!

Il podurino
vive tranquillo nella foresta:
viva il collembolo,
bestia modesta!

L'onychiurino
passeggia placido col bianco manto:
viva il collembolo,
bestia di vanto!

L'isotomino
per ritrovarlo ti basta un niente:
viva il collembolo,
bestia frequente!

L'entomobryno
saltella allegro, snello e svettante:
viva il collembolo,
bestia elegante!

Lo sminthurino
sui prati in fiore forma il suo regno:
viva il collembolo,
bestia d'ingegno!

Viva il collembolo
bestia ideale,
il più simpatico d'ogni animale!

Ermanno Malatesta