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This is the author's manuscript

Original Citation:

Availability:

This version is available <http://hdl.handle.net/2318/85596> since

Published version:

DOI:10.1177/0959683610374885

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UNIVERSITÀ DEGLI STUDI DI TORINO

This is an author version of the contribution published on:

Questa è la versione dell'autore dell'opera:

*M. Gobbi, M. Isaia, F. De Bernardi (2011) Arthropod colonisation of a debris-covered glacier.
The Holocene 21 (2): 343-349, DOI: [10.1177/0959683610374885](https://doi.org/10.1177/0959683610374885)*

The definitive version is available at:

La versione definitiva è disponibile alla URL:

<http://hol.sagepub.com/content/21/2/343>

Arthropod colonisation of a debris-covered glacier

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Abstract

The largest debris covered glacier in the Alps (Miage Glacier, Western Italian Alps) has been studied to explore the effects of debris cover extent and depth, on the spatial distribution of ground-dwelling arthropods. A multi-taxa approach has been used to compare taxa richness and distribution to the functional role (dietary habits) of each taxon along the glacier tongue. Spiders and ground beetles have been studied in detail. Taxa richness declines with distance from the wooded sites (in front of the glacier tongue) to those above the glacier tongue. At each of the supraglacial sites, spiders, ground beetles, aphids, springtails and flies were found. A change in the dominance of the different functional roles was observed along the tongue. Wooded sites are characterised by predatory (e.g. spiders, beetles), detritivore (e.g. springtails and certain flies), phytophagous (e.g. aphids, certain beetles) and parasitoid (e.g. certain wasps) communities, whereas, at the debris-covered sites, aphids, flies and springtails become prey of spiders and beetles. The species richness of the predominant predators (spiders and beetles) shows a positive relationship with vegetation cover and debris thickness. Two mutually exclusive spider and ground beetle communities were found; one within the debris cover and one within the wooded sites. In our view, debris covered glacier are acting as refuge area for the cryophil stenotherm species living at higher altitudes and descending the glacial tongue to lower elevation. A similar hypothesis is at the base of the biogeographical interpretation of the distribution of many boreo-alpine relict species in the Alps. We discuss our results in the light of possible future scenarios which suggest an increase in debris cover with global warming.

Key-words: black glacier, Miage Glacier, Alps, climate change, spiders, carabid beetles.

Introduction

The alpine biome is currently characterized by the glacial retreat (Paul et al. 2007). During the last 150 years the largest Italian glaciers have lost almost fifty percent of their mass while the loss of smaller may reach ninety percent; many of which have been transformed into glacierets (Citterio *et al.*, 2007). Reduction in ice volume is not the only visible indicator of the effects of the climate warming; the glaciers are progressively suffering the covering of their surface with supraglacial debris, transforming themselves into partial debris covered glaciers and debris-covered glaciers, also referred to as “black glaciers” (Paul et al., 2003). The cover and the depth of deposits on the surface depends on the movement of the glacier, the type of substratum on which it resides and the formation and geological characteristic of the overhanging walls. Some rock types are sensitive to processes of alteration or affected by frequent slipping and castings of deposits. They can create large quantities of stony material which covers the glacier surface. Debris-covered glaciers, in comparison to ‘clean’ (uncovered) glaciers, are likely to experience: (i) a smaller amplitude of frontal fluctuations; (ii) a tongue descending to lower elevations; (iii) less negative mass balance during retreat periods and (iv) highly developed moraine complexes. If the thickness of the debris is above 1-2 cm, the mean ice ablation is reported to decrease logarithmically (Mattson and Gardner, 1989; Nakawo and Rana, 1999; Mihalcea et al., 2007).

Debris-covered glaciers belong to a meaningful fraction of the global population of glaciers (Nakawo et al., 2000). They are well represented on the Asian mountainous (e.g Karakorum group), the Himalaya, the Tien Shan (New Zealand) and in the Andes (Moribayashi and Higuchi, 1977). In the Alps their population and distribution is less significant. The Miage glacier is the most well known Italian debris-covered glacier which is notable for its mantle of supraglacial rock debris, probably caused by rare, but important cryoclastics and landslide events, covering the lower 4 Km² of the glacier.

Many authors have demonstrated how glacier retreat triggers plants and invertebrate succession on glacier forelands (e.g. Matthews 1992; Kaufmann 2001; Hodkinson et al. 2004; Bardgett et al. 2005; Caccianiga et al. 2006; Gobbi et al. 2006a). Invertebrates (mainly spiders and ground beetles) are also colonising the glacier surface where debris offers a favourable substrate for colonisation (Gobbi et al. 2006b; Gobbi et al., 2007); however this topic has been less well considered and studied. A debris-covered glacier can be considered as a good example of a study model to better understand how the colonisation of new areas at high altitude by biocoenoses will occur in the light of climate warming. Ground beetle (Coleoptera: Carabidae) and spiders (Arachnida: Araneae) can be used as key-taxa in monitoring habitat changes and may show clear responses to environmental disturbances (Thaler 2003; Hodkinson and Jackson 2005; Pearce and Venier, 2006, Gobbi et al. 2007; Pizzolotto et al. 2009; Negro et al., 2009, 2010).

The aims of our research were to show, using a multi-taxa approach, the arthropod coenoses colonising a debris covered glacier and to discuss, with a single taxon approach, the relationships of ground beetles and spiders with vegetation cover and debris thickness. The research also focuses on the role played by this kind of glacier on driving cool-living stenotherm species at lower elevation. To our knowledge no papers have, to date, been published on this topic in the Alps, but also for other world mountain chains. This study represents a first contribution to a new approach to primary invertebrate succession, which has not been researched previously and therefore provides a glimpse into the likely processes occurring along the glacial tongue from the top to the front of the glacier.

Study Area

Geographical location

Miage Glacier is a 13 km² compound valley glacier belonging to the Mont Blanc massif (Val d'Aosta, Western Italian Alps, 46°48'15''N – 6°50'26''E) fed by four steep tributaries. The lower glacier is 8 km long, has a gently sloping tongue and is partly entrenched in a deep, straight valley. When reaching the Val Veny it's bent its course is canalised by huge lateral moraines (up to 200 m high), before forming three divergent moraine-bounded lobes (the lowest terminating at 1730 m a.s.l.). Only the distal part (5.5 km long and 4 km² in area) of the glacier is debris-covered and together with Unteraargletscher in the Bernese Oberland (Switzerland), the Miage Glacier is the largest debris-covered glacier in the Alps and the largest in the Italian Alps (Fig. 1).

The glacier's history

A detailed description of the changes to the debris surface of the Miage Glacier is reported in Deline (2005). In summary, Miage Glacier exhibited discontinuous debris coverage during the last few decades of the Little Ice Age (LIA). The frontal area initially became debris-covered towards the end of the LIA (1860-1880) and further debris encroachment proceeded over the next fifty years (1880-1930), continuing to develop into its present state.

Debris thickness and vegetation cover

The debris thickness covering the glacier surface is not uniform. At the terminal end of the glacier tongue, the debris thickness is limited and determined by three small longitudinal median moraines, throughout which the ice appears at the surface. Deposits of debris can be observed on the surface of the glacier in Val Veny, at 2100 m a.s.l. and on the slopes of the nearby glacier of Monte Bianco at 2350 m.a.s.l.. Mihalcea et al. (2007) report that the debris covering the Miage Glacier

ranges from 55 (at 1839 m a.s.l.) to 4 centimetres (at 2365 m a.s.l.) These results in particular, show a general increase in debris thickness at the lowest altitudes.

About the vegetation, in front of the glacier tongue (Fig. 1, site F) woodlands dominated by *Picea abies* and *Pinus cembra-Larix decidua* are found (Fig. 1, site E, D). The terminal lobe of the Miage Glacier tongue is colonized by grassy vegetation and scattered larches (*Larix decidua*), spruces (*Picea excelsa*), willows (*Salix* spp.), poplars (*Populus tremula*) and silver birches (*Betula pendula*) (Fig. 1, site C). Among these, larches and willows are the most abundant

Materials and methods

Sampling stations

Sampling stations were selected to encompass a) different depths of debris cover on the glacier foreland and different degrees of vegetation cover (Tab. I). Seven stations were located on a transect along the glacier tongue (Fig. 1).

Sampling techniques

Arthropods were sampled during snow free periods (June-September 2006) using pitfall and sticky traps. Each trap was collected and re-set every 20 days. Pitfall trapping is a standardised method of qualitative and quantitative investigation (Brandmayr et al. 2005) with the ability to sample ground dwelling arthropods (Southwood 1978). The traps consist of a plastic cup (10 cm height, 7cm upper diameter, 4.5 cm lower diameter) buried up to the edge and filled with approximately 20 ml with a vinegar and salt solution (being both an attractive and preservative agent). Two small holes were pierced into the side of the cups (at approximately 7 cm height) to allow spillage in the event of rainfall. Sticky traps are a technique of qualitative sampling that traps flying arthropods (which can also be transported by the wind) when they hit the adhesive ribbon (Southwood 1978). The use of sticky traps as method of harvesting flying fauna above the surface of a glacier has been used for the first time in this study. The sticky traps consisted of a 1 m length stake (diameter of 1.5 cm) vertically inserted between the supraglacial deposit. A panel, measuring 30 x 30 cm and covered with adhesive ribbon, was attached to the top of the stake (Coulson et al. 2003). At each sampling station, six pitfall traps (positioned 10 m apart) and one sticky trap were used.

Data analysis

Environmental variables including altitude (metres), vegetation cover (percentage), debris thickness (centimetres) and debris cover (percentage) were recorded and used to analyse the differences

between sites. The majority of taxa were only identified to the Order level. In order to define functional roles beetles (Insecta: Coleoptera) and bees (Insecta: Hymenoptera) were identified at the Family level. Both ground beetles and spiders were determined to species level. Nomenclature refers to the checklist of the European Carabid beetles Fauna (Vigna Taglianti 2009) and to the World Spider Catalogue (Platnick 2010).

Taxa richness and functional groups. Dietary habits (e.g. predatory and parasitic) were used to characterise functional traits. The variation of taxa richness in each trap was compared using an ANOVA test (Sokal & Rohlf 1995). Spearman's correlation was also used to test the influence of environmental variables on taxa richness.

Ground beetle and spider species richness and abundance are given respectively as total number of species and specimens collected at each sampling station. The effect of environmental variables on species richness and abundance has been tested using linear regression (Sokal & Rohlf 1995).

Taxa turnover. The occurrence of taxa turnover along the glacier was performed with a meta-community analysis computed using a Macro of Excel developed by Leibold and Mikkelsen (2002). The probability of obtaining the observed spatial turnover between species and communities was calculated using a Monte Carlo simulation, where species (lines) and sites (columns) are ordered by Reciprocal Averaging (RA). The significance of differences in the number of species replacements among communities was tested using a two-tailed Z -test (observed vs. expected matrices). Significantly lower rates of species replacements (EA) than expected are represent as nested structures (representing low spatial turnover), with hierarchical structures present among communities. When rates are higher than expected are known as anti-nested structures, and provide an evidence of groups of species that are mutually exclusive. This analysis is also applied to test the turnover of ground beetles and spiders.

Results

Taxa richness and functional groups. Nine traps out of 45 contained no specimens. In the remaining thirty-six traps 23 different taxa were found. Only sticky traps placed above the glacier surface successfully trapped arthropods, notably trapping springtails (Collembola), flies (Diptera) and aphids (Homoptera). The taxa sampled by pitfall traps belonged to 4 functional groups: predators, phytophagous, detritivores and parasitoids (Tab. III a).

Taxa richness decreased consistently from the wooded sites to the glacier tongue. Vegetation cover shows a positive influence on the taxa richness (Spearman's $\rho = 0.535$, $P = 0.01$). On the contrary, an inverse relation was found in respect to altitude (Spearman's $\rho = -0.986$, $P = 0.001$). We thus observed an increase in taxa richness correlated with an increase in vegetation cover which decreases with altitude. Vegetation cover and altitude are negatively correlated (Tab. II) due to the distribution of the sampling sites along the transect. Taxa richness decreases along the transect from the sites located at the lowest altitude to those located to the highest altitude (ANOVA test: $F_{5,35} = 3,233$, $P = 0.019$) (Tab. III a).

Taxa turnover and number of functional group. The analysis of meta-community data shows a significant, but low taxa turnover ($P = 0.002$) (Tab. III a, b). The number of functional groups also changed, decreasing from 4 (in the stations D, E, F) to 3 (in the stations A, B, C), due to the absence of parasitoid wasps.

Spiders, ground beetles, aphids (Aphodoidea), springtails and flies occur constantly across the glacier surface (Tab. III a).

Ground beetles and spider richness

Sixteen species of spiders and 9 species of ground beetles were sampled. All species were collected in the pitfall traps, while the nocturnal dweller *Drassodex heeri* (Arachnida: Araneae) was also recovered on sticky traps.

The effect of elevation, vegetation cover, debris cover and debris thickness on predator species richness (ground beetles and spiders) was tested with a linear regression analyses (ANOVA test: $F_{3, 79}$, $P=0.012$). Elevation ($t=-0.58$, $P=0.661$) and debris cover ($t=-8.00$, $P=0.15$) may be ruled out as explanatory factors while vegetation cover ($t=-4.620$, $P=0.04$) and debris thickness ($t=-6.673$, $P=0.02$) are the most important factors influencing species richness. Abundance varied significantly (ANOVA test: $F_{3, 26} = 12.69$; $P<0.0001$) between each sampling station, but anybody environmental variables determine this change (P -values = n.s. for each variables).

The analysis of meta-community data shows a meaningful turnover of communities along the succession ($P = 0.035$) (Tab. IV a, b). This data shows there are mutually exclusive communities at some of the sampling stations, it is possible to distinguish two exclusive communities: the community found in the supraglacial detritus (stations A, B and C) composed of spiders (*Aculepeira ceropegia*, *Drassodex heeri*, *Pardosa saturator*, *Pisaura mirabilis*, *Rugathodes bellicosus*, *Xysticus lanio*) and one ground beetle (*Nebria angusticollis*). Secondly we find a distinctive forest community (stations E and F) composed of spiders (*Amaurobius fenestralis*, *Gnaphosa badia*, *Pardosa gr. lugubris*, *Zelotes devotus*, *Xerolycosa nemoralis*, *Xysticus cristatus*) and ground beetle (*Amara erratica*, *Calathus melanocephalus*, *Calathus micropterus*, *Cychrus attenuatus*, *Leistus nitidus*, *Platycarabus depressus*, *Pterostichus multipunctatus*). Station D acts as a boundary site where there is a mutual presence of species belonging to the forest and to the supraglacial environment (Tab. IV a).

Discussion

Taxa richness (and number of functional groups) of arthropods on Miage glacier resulted highly correlated to vegetation cover, attesting the important role of this variable on arthropod colonization.

As seen in Table III a, the taxa sampled in woody stations E and F, are those that conform to an above-ground life cycle (or within the first few centimetres of the grassy or shrubby layers) owing to their links with trees and mushrooms, for example earwigs (Dermaptera: Forficulidae), millipedes (Diplopoda: Glomeridae) and ants (Hymenoptera: Formicidae). It is interesting to observe the exclusive presence of flying parasitoids wasp (Hymenoptera: Ichneumonidae), in the stations D, E, F. The absence of vegetation above the glacier limited the presence of this icneumon wasp due to the absence of phytophagous insects to prey.

The only taxa associated with glacier surface (stations A, B, C, D) were carabid beetles, spiders, and flying taxa.

Previous literature has recorded and confirmed the presence of spiders and beetles above the glacier surface (Gobbi et al., 2006a). This study therefore provides additional evidence regarding these taxa and their presence on debris-covered glaciers in the Italian Alps.

The presence of springtails (detritivores) and aphids (insects that live sucking plant lymph) was also notable. However, these taxa also occur on the glacier surface, transported upwards and downwards by winds crossing the glacier and became prey for the predatory taxa. Many authors report that carabid beetles and spiders live at high altitudes thanks to the nutritive contribution coming from aeroplankton (Antor, 1994; Polis and Hurd 1995; Coulson et al., 2003; Hunchbacked et al., 2006). By using the sticky traps we have increased the existing knowledge about this method and its usefulness on and around alpine glaciers (Coulson et al., 2003). We conclude that these aerial arthropods (incidental and/or flying) provide an important food source for other invertebrates living on the glacier surface in the debris.

Ants and centipedes were also collected (Station D). These results support data collected by Gobbi et al. (2006a) along the Forni glacier foreland (Central Italian Alps), where ants and centipedes were collected from mature forest soils. These two taxa may therefore be regarded as indicators of evolution to a forest environment, which suggest that this station is likely to evolve to a forest in the recent future.

Analysis of the spider and carabid communities shows that vegetation cover has a positive influence on species richness differently to debris cover that has but a negative influence. Higher values of species richness are therefore highly associated with the more stable ecosystems, like prairies and forests. A similar trend for ground beetles (increasing in forests) and spiders (increasing in open habitats) was observed by Negro et al. (2009) in the montane belt (below the treeline). Above the treeline, the same authors (Negro et al., 2010) recorded a positive correlation of species richness and abundance of spiders and ground beetles along with grass coverage attesting the important role played by vegetation cover.

As shown by Correspondence Analyses (Tab. IV a), the community turnover is characterised by the succession of forest, prairie and glacier communities. Sites E and F are characterized by species that are generally found in forest habitat, such as the ground beetles *Calathus micropterus*, *Leistus nitidus*, *Platycarabus depressus* and *Pterostichus multipunctatus* (Brandmayr et al. 1988).

Station D, with small scattered larches and spruces, is characterized by the carabid beetle *Nebria picea* and the spiders *Ozyptila rauda*, characteristic of the forest-glacier boundary zone (Thaler, 2003; Zingerle, 1998, 1999).

Stations A and B are characterised by carabid species typical of stony cold environments and by spider species that colonise the glacier from nearby habitats: *Pisaura mirabilis* and *Aculepeira ceropegia* (see Thaler, 1991) are found at lower altitudes while *Drassodex heeri* is generally found in rocky habitats at medium- high altitudes (Hervè et al., 2009) as also observed by Negro et al., 2010. The result is a “mixed” spider coenoses with species colonising the tongue coming from habitats at the same elevation (forests and prairies) and species coming from higher altitudes “via”

glacier. The movement of *D. heeri* along the tongue is also tested by the sticky traps sampling, this was in fact the only species of spider caught by such method. Species found at lower altitudes, like the orb-web weaver *A. ceropegia* are found among the rocks due to their reliance on this substrate to build their webs. Debris-covered glaciers therefore provide a suitable habitat, both for high-alpine cryophilic species, colonizing the glacier tongue from higher altitudes and for the ones coming from nearby habitats. This is also true of the criss-cross web builder *Rugathodes bellicosus* referred by Ruzicka & Zacharda (1994) as inhabitant of “glacial wreckages” (rock blocks).

It is interesting to observe that two typical species of stony high altitude and glacial habitats like *Nebria angusticollis* and *Drassodex heeri* find a way to extend their altitudinal range to lower altitudes (e.g. Station C, 1870 m. a.s.l) thanks to the presence of debris on the glacier and its associated cold microclimate, that may represent a suitable habitat for cool-living stenotherm species. *Nebria angusticollis*, for example, normally live in nival alpine areas, therefore a debris covered glacier can be considered a refuge area for this species more sensible to climate warming.

Proposed theory and predictions

Considering the temperature changes predicted in the next years, an increase in debris thickness and vegetation on the glacier surface will favour arthropod colonisation. Kaufmann (2002) proposed a model linked to the rate of invertebrate successional evolution in relation to temperature changes. This model suggests that climate effect would be severe and act most strongly on the early colonising communities. In our case these communities are those living between the debris cover (sites A, B and C) including species coming from higher altitudes. These communities show low diversity and rapidly changing species composition. Kaufmann (2002) reports that an increase of 0.6°C in summer temperature approximately doubled the speed of colonization. In the Miage Glacier, the spatial distribution of forests species will increase after the shift in the treeline above the glacier. On the other hand the species living between the debris covering the glacier, therefore linked to cold and wet microclimate, will have two choices: the first is to shift to higher elevations

(Gobbi et al., 2007), and the second one that we hypothesize after our observations, is to move downwards into the debris where they can find suitable cold microclimate conditions. This hypothesis is in accordance with Ruzicka and Zacharda (1994), who observed that the underground cavities in the stony debris represent a refuge islet for many cool-living invertebrates due to the microclimate conditions similar to those in cool and wet sites of the nival zone. Those species with higher mobility will be likely to follow the first process, whereas those with low dispersal ability are likely to follow the latter.

During the last glaciation, the fauna of the periglacial and proglacial zone between the boreal and alpine continental glacier was composed by boreal (tundra) and mountain (alpine and nival zone) species (Lattin, 1967). Later, during the postglacial periods, this fauna followed the retreating continental glaciers and moved shifting at the highest elevation or to cavities between the debris. In our opinion, this will replicate similar dynamics that were triggered during the Pleistocene and Holocene period. During mass glacier retreat, the cool-living stenotherm species found refuge in cooler habitats, like for example subterranean environments, where they could find cold and stable micro-climatic conditions. This process is regarded as a driving force in the origin of Alpine endemisms, in particular in the Western alps, like for example the case of many species of subterranean cholevid beetles and carabid beetles (Casale and Vigna Taglianti 1993; Casale and Giachino 2010 in press; Focarile 1987). Debris-covered glaciers provide, in this sense, a glimpse on the early stages of this process, acting as ways of expansion of the altitudinal range of high altitude species.

Acknowledgements

No specific funding was received for this research. The authors would like to thank P. Sala and F. Casali for their field work and taxonomists M. Pavesi and C. Pesarini (Museo Civico di Storia Naturale of Milan) for their support in species identification. We are also grateful to A. Vater (UK-Environmental Observation Framework) for English revision and comments and to P. Brandmayr

(University of Calabria, Italy) for fruitful discussion to the manuscript. MG dedicates this article to his uncle Gianbattista Casarino, journalist and fan of climatology, who was always interested in understanding the effects of global warming.

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