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Periglacial and glacial landforms as warm-stage refugia for cold-adapted plant and arthropod species

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Introduction

Climate changes and warm-stage refugia for cold-adapted species

The effects of climate changes

Quaternary climate variations as the cyclical alternation of cold- and warm-climatic stages (e.g. glacial and interglacial periods) highly affected the evolution and distribution of plant and animal species on Earth. The effects include adaptation, speciation and extinction processes (Merila et al., 2013; Schilthuizen et al., 2013; Steven et al., 2013; Bellard et al., 2014), migrations toward southern/northern latitude or lower/higher altitude and areal expansion/contraction (Birks and Willis, 2008; Rull, 2009; Stewart et al., 2010; Bellard et al., 2014). A refugium is defined as the geographical region that a species inhabits during the period of a glacial/interglacial cycle that represents the species minimum areal extension (Stewart et al., 2010). The refugium condition over a glacial/interglacial cycle occurs depending on species ecological requirements: the distribution range of species adapted to the relatively warm climates of lower latitude/altitude tend to reach its minimum during cold-climatic stages (cold-stage refugia), while that of species adapted to the relatively cold climates of higher latitude/altitude tend to reach its minimum during warm-climatic stages (warm-stage refugia). Warm-stage refugia are thus defined as sites able to preserve suitable climate conditions for cold-adapted species (see page 5 for definition) in spite of the climate warming (Birks and Willis, 2008; Rull, 2009; Stewart et al., 2010).

Since 1880 air temperature at global scale rapidly increased of c. 0.85 °C likely due to the increasing amount of anthropogenic greenhouse gas and is forecast to increase over the 21st century as well (IPCC, 2014); cold-adapted species are thus the first to be threatened due to the progressive reduction of their suitable areas (Dullinger et al., 2012; Bellard et al., 2014). To prevent the extinction risk, cold-adapted species can react in three main ways: 1) adapting to the new environmental conditions; 2) migrating toward suitable areas following the shift of latitudinal/altitudinal belts; 3) persist in the same areas seeking for warm-stage refugia (Theurillat and Guisan, 2001; Dobrowski, 2011; Keppel et al., 2012, 2015; Bellard et al., 2014). Since the first two strategies likely need too much time with respect to the extraordinarily fast anthropogenic climate change (Jump and Peñuelas, 2005), the third is drawing more attention in ecological and biogeographical research.

The role of microclimatic heterogeneity

Geomorphic and microclimatic heterogeneity at landscape level is supposed to play an important role in providing warm-stage refugia for cold-adapted species (Dobrowski, 2011; Scherrer and Körner, 2011; Ashcroft et al., 2012; Keppel et al., 2012, 2015). The microclimatic heterogeneity of many mountain regions can be enhanced by periglacial and glacial landforms characterized by debris with underlying ice, like active rock glaciers and debris-covered glaciers (Fickert et al., 2007; Millar et al., 2010, 2013; Caccianiga et al., 2011; Gobbi et al., 2011; Gentili et al., 2015).

Active rock glaciers are periglacial landforms consisting of coarse debris with interstitial ice or ice core, characterized by creeping due to ice deformation (Haeberli et al., 1985; Barsch, 1996; Janke et al., 2013). Active rock glaciers are the most evident expressions of permafrost in mountain landscapes; they show a certain thermal inertia toward the climate variations due to the insulation effect of the debris fraction (Clark et al., 1996; Frauenfelder and Kääb, 2000). Debris-covered glaciers are glaciers with the ablation zone covered by a debris layer. Such landforms are relatively decoupled from air temperature, since a debris layer thick enough (above c. 1-2 cm) acts as thermal insulator and protects the underlying ice from ablation (Mattson et al., 1993; Nakawo and Rana, 1999). Debris-covered glaciers differ from debris-free ones for less negative mass balance, smaller amplitude of frontal fluctuations and tongue descending to lower altitudes (Kirkbride, 2000; Diolaiuti et al., 2003; Deline, 2005).

Active rock glaciers and debris-covered glaciers count some important difference which in turns affect their ecological features: 1) active rock glaciers occur at the highest elevation being theoretically included between the lower limit of permafrost and the equilibrium line of glaciers (Haeberli, 1985), while debris-covered glaciers can extend their tongues through a wider altitudinal range due to their peculiar mass balance (Deline, 2005); 2) the surfaces of active rock glaciers are mainly characterized by large blocks with scarce fine matrix (Barsch, 1996), while the supraglacial debris includes a wider range of grain size distribution (Diolaiuti et al., 2003); 3) active rock glaciers are characterized by relatively slow movements (generally < 1 m/y) (Barsch, 1996), while debris-covered glaciers can reach much more higher flow velocity (up to 16 m/y) (Caccianiga et al., 2011).

Despite such differences, active rock glaciers and debris-covered glaciers are ecologically comparable as habitat at least for the presence of debris with underlying ice. Both plants and arthropods were observed on such landforms in spite of the harsh environmental condition, especially pioneer and cold-adapted species. Debris-covered glaciers and active rock glaciers were thus proposed as potential warm-stage refugia for cold-adapted species, due to the microclimate features provided by the underlying ice and the thermal inertia provided by the debris insulation (Fickert et al., 2007; Caccianiga et al., 2011; Gobbi et al., 2011; Millar et al., 2013).

Studies about geomorphological (e.g. Diolaiuti et al., 2003; Deline, 2005; Humlum, 1998, 2000), botanical (e.g. Fickert et al., 2007; Caccianiga et al., 2011; Cannone and Gerdol, 2003; Burga et al., 2004) and zoological features (e.g. Gobbi et al., 2011; Millar et al., 2010, 2013, Azzoni et al., 2015) of active rock glaciers and debris-covered glaciers were already performed, but the ecological features of such landforms can be understood only through multidisciplinary approaches. To our knowledge, no studies integrated climate, soil, plants and arthropods data at the same time.

The ecological variability within active rock glaciers and debris-covered glaciers was already analyzed especially for plants (e.g. Cannone and Gerold, 2003; Burga et al., 2004; Fickert et al., 2007; Caccianiga et al., 2011; Rieg et al., 2012), but a clear contextualization of such landforms at landscape level is needed to infer their potentiality as warm-stage refugia. To our knowledge: 1) no studies compared active rock glaciers and debris-covered glaciers with the surrounding iceless landforms in order to infer the thermal effect of underlying ice on plant and arthropod communities, and 2) no study analyzed the arrangement of such landforms with respect to the altitudinal zonation of mountain ecosystems (e.g. with respect to the climatic treeline), in order to infer their ability to host cold-adapted species in adverse bioclimatic contexts.

The role of macroclimatic heterogeneity

Besides microclimatic heterogeneity at landscape level, macroclimate heterogeneity at regional scale should be considered in the framework of the current climate change. Particularly interesting are the macroclimate contexts able to limit the effects of climate change themselves on high mountain landscapes and ecosystems, thus preventing the extinction risk for cold-adapted species.

The most evident effects of climate change on high alpine landscapes and ecosystems are glaciers retreat (Citterio et al., 2007) and primary successions on glacier forelands (terrain ice-free by glacier retreats) and on recent moraines (terrain deposed by recent temporary glacier advances) (e.g. Kaufmann, 2001; Caccianiga and Andreis, 2004). In a chronosequence of glacier retreat, pioneer species are progressively replaced by mid- and late-successional ones, until the ultimate establishment of the "climax" communities. Among pioneer species, the cold-adapted ones are the first to be threatened by such process, since (as pioneer) they are forced to follow the glacier retreat to avoid the competition with mid- and late-successional species, and (as cold-adapted) they are unable to withdraw on other habitats if not at higher elevation. Such scenario suggests a local extinction of pioneer cold-adapted species once glaciers will disappear. However, the temporal patterns of both glaciers retreat and primary successions on glacial landforms can be highly affected by the macroclimate at regional scale.

One of the most remarkable example of macroclimate heterogeneity of any mountain system is the contrast between the cold-dry continental climates of inner ranges and the cold-wet oceanic climates of peripheral ones (Körner 2003; Beniston, 2005). The geographical arrangement of peripheral mountain ranges toward the atmospheric circulation results in high winter precipitations and long-lasting snow cover, which in turn allow the long-lasting persistence of glaciers at relatively low altitude (Scotti et al., 2014) and suggest a slow biological colonization of glacial landforms (Caccianiga and Andreis, 2004). Glacier forelands and recent moraines of peripheral mountain ranges may thus act as temporary warm-stage refugia for pioneer cold-adapted species, allowing them to persist along the chronosequences of glaciers retreat much longer than on those of the inner mountain ranges at the same elevation.

Primary succession on glacial landforms were widely investigated on the inner massifs of the Alps both for plants (e.g. Burga, 1999; Marcante et al., 2009; Gobbi et al., 2010) and arthropods (e.g. Kaufmann, 2001; Schlegel and Riesen, 2012; Gobbi et al., 2010), while the knowledge about peripheral mountain range is still scarce (Caccianiga et al., 1993; Caccianiga and Andreis, 2004); a multidisciplinary study is thus needed to analyze the features of a primary succession in such context and to compare its temporal pattern with those of the glacial landforms of inner mountain ranges.

The scientific interest of peripheral mountain ranges concerns not only their ecological peculiarities, but also their biodiversity and its related biogeographical implications. Peripheral mountain ranges of many mountain systems are currently characterized by the highest number of species and endemism (Pauli et al., 2003), many of which are cold-adapted. The isolation due to the ice-sheets expansion in cold-climatic stages (e.g. the Last Glacial Maximum, c. 22000 years BP, Antonioli and Vai, 2004) was traditionally involved to explain the present biogeographical features of these areas, both for plants (e.g. Martini et al. 2012; Schönswetter et al. 2005) and arthropods (e.g. Latella et al., 2012; Lohse et al., 2011). By contrast, the areal contraction of cold-adapted species in warm-climatic stages (e.g. the Holocene Climate Optimum, c. 8000 years BP, Antonioli and Vai, 2004) was less considered.

Since glacial landforms of peripheral mountain ranges could act as warm-stage refugia, their occurrence could explain part of the present distribution of cold-adapted species. A biogeographical study which compare the distributional pattern of cold-adapted species with the putative position of cold- and warm-stage refugia is thus needed to shade light on the present biogeographical arrangement of peripheral mountain ranges.

Aims and methods of the PhD project

General aims

Aim of this study was to analyze the ecological features of periglacial and glacial landforms (active rock glaciers and debris-covered glaciers on inner mountain ranges, glacier forelands and recent moraines on peripheral mountain ranges) to test whether they have the main requirements to act as potential warm-stage refugia for cold-adapted species. A multidisciplinary approach was followed, considering both the abiotic (ground surface temperature and humidity, soil physical and chemical parameters) and biotic variables (plant and arthropod communities).

Concerning active rock glaciers and debris-covered glaciers on inner mountain ranges, we considered as key-requirements to act as potential warm-stage refugia: 1) a cold-wet microclimate due to the underlying ice able to support cold-adapted species and, 2) the ability to cross the altitudinal zonation of mountain ecosystems, thus to support cold-adapted species in adverse climate contexts.

Concerning glacier forelands and recent moraines on peripheral mountain ranges, we considered as main key-requirement to act as potential warm-stage refugia a relatively slow colonization pattern, able to long-lasting support pioneer cold-adapted species in spite of their replacement with mid- and late-successional ones.

Definition of cold-adapted species

With the term "cold-adapted species" we refer to the species strictly linked to the alpine-nival belt, thus characterized by a limited range of tolerance in altitudinal distribution.

We defined the main thermal requirement of species on the basis of their normal altitudinal distribution, as the present study is focused on high mountain ecosystems of the Alps and altitude is the main factor driving air temperature in mountain regions (Rolland, 2013). Since the climatic treeline represents the lower bioclimatic threshold of the alpine belt (Körner, 2003), we assumed its elevation as the minimum value below which cold-adapted species should be considered below their normal altitudinal distribution, thus in adverse climate context. Concerning plants, we consider as cold-adapted all 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 based on the available descriptive literature on the altitudinal distribution of each taxa (e.g. Casale et al., 1982; Pantini and Isaia, 2016).

However, air temperature altitudinal lapse rate can differently affect ground surface temperature below and above the treeline: while below such threshold the microclimate variability due to topography tends to be levelled off by the tree canopy, above the treeline the topography becomes the main driver of microclimates distributional pattern. The alpine-nival belt thus results in a complex mosaic of microclimates depending on topography rather than air altitudinal temperature lapse rate (Körner, 2003; Scherrer and Körner, 2011). We are aware of that defining cold-adapted species only on the basis of their altitudinal distribution we inevitably gather alpine-nival species with quite different microclimate requirements, like those adapted to cold-wet microclimates and long-lasting snow cover of the hollows, those adapted to cold-dry microclimates and brief-lasting snow cover of the humps and all the transitions between each other. In our study we take account of such intrinsic environmental variability referring to the specialized literature on single species ecological requirements (e.g. Casale et al., 1982; Oberdorfer, 1998; Grabherr and Mucina, 1993; Pantini and Isaia, 2016).

Study areas

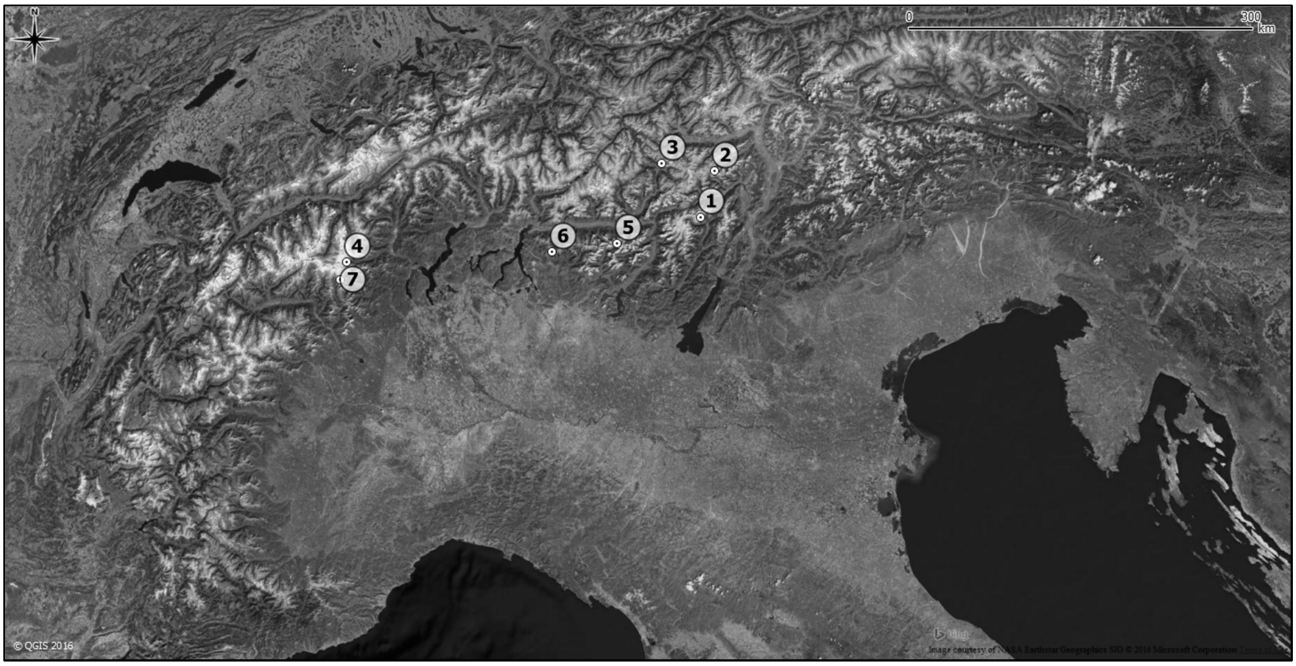
The PhD project was carried out in five main study areas of the Italian Alps (Fig. 1).

The ecological studies on active rock glaciers and debris-covered glaciers as habitat and potential warm-stage refugia were carried out in the inner Alps, where such landforms are currently well expressed.

Active rock glaciers are widespread on the whole Alpine chain, embracing a wide range of geographical and geological contexts. In order to perform an overview as complete as possible on the ecological features of such landforms, three areas with contrasting lithology were selected: one on igneous silicate substrate (Val d'Amola, Adamello-Presanella), one on metamorphic silicate substrate (Val d'Ultimo, Ortles-Cevedale) and one on sedimentary carbonate substrate (Valle del Braulio, Ortles-Cevedale). Debris-covered glaciers are few and mainly located in the highest massifs of the western sector of the Alps; we analyzed Belvedere glacier (Valle Anzasca, Monte Rosa) as one of the largest Alpine debris-covered glaciers (e.g. Monterin, 1923; Haeberli et al., 2002; Diolaiuti et al., 2003).

The ecological and biogeographical studies on peripheral mountain ranges as a location of warm-stage refugia were carried out on Orobian Alps (Lombardy), as one of the best known peripheral mountain ranges of the Alpine chain by the geomorphological (Jadoul et al., 2000; Bini and Tognini, 2001; Bini et al., 2009; Scotti et al., 2013, 2014), botanical (Pirola and Credaro, 1977; Caccianiga et al., 1993, 2008; Martini et al., 2012; Bona et al., 2013) and zoological viewpoints (Lohse et al., 2011). Trobio glacier foreland (Val Seriana) was selected to analyze a chronosequence of glacier retreat in such context, since its Holocene dynamic is one of the best known of the area (Caccianiga et al., 1993; Bonardi et al., 2012). Finally, the whole Orobian Alps was considered as a study area in a biogeographical study aimed to compare the distribution of cold-adapted species with the putative position of cold- and warm-stage refugia.

Besides these main study areas, data were collected in other areas to create a dataset aimed to perform a first synthesis at Alpine scale on periglacial and glacial landforms as habitat and warm-stage refugia for cold-adapted species (Fig. 1). Such areas were selected in order to increase the range of geographical, geological and climatical variability of the investigated landforms. In particular: the active rock glacier of Col d'Olen (Valle del Lys, Monte Rosa) was included as active rock glacier on serpentine substrate; the active rock glacier of Valmorta (Val Seriana, Orobian Alps) was included as example of active rock glacier located in the extreme climate condition of peripheral mountain ranges; the Coca glacieret was included, in contraposition to Trobio glacier, as one of the Orobian glaciers less subjected to retreat; the scree slopes of Pizzo Tre Signori were included as examples of debris-featured landforms in an area of Orobian Alps not involved in recent periglacial and glacial processes.



ID	Valley	Area	Landforms
1*	Val d'Amola	Amola	Debris-covered glacier, glacier foreland, rock glacier, control slope, scree slope
2*	Val d'Ultimo	Lago Lungo	Rock glacier, control slope, scree slope
3*	Valle del Braulio	Vedrettino	Rock glacier, control slope, scree slope
4*	Valle Anzasca	Belvedere	Debris-covered glacier, control slope, iceless moraine
5*	Val Seriana	Trobio	Glacier foreland, control slope
5	Val Seriana	Coca	Glacier foreland, control slope, scree slope
5	Val Seriana	Valmorta	Rock glacier, scree slope
6	Val Brembana	Tre Signori (BG)	Scree slopes
6	Val Gerola	Tre Signori (SO)	Scree slopes
7	Valle del Lys	Col d'Olen	Rock glacier, control slope, scree slope

Fig. 1. Study areas (* = main area) with their location (valley) and investigated landforms.

General methods

For each area, different landforms were analyzed and compared. The same integrated methods were applied to collect multidisciplinary data about climate, soil, plant and arthropod on these landforms (fig. 2): data-loggers were used to analyze ground surface temperature and humidity during a one-year period; soil samples were taken at the surface for physical (grain size distribution) and chemical analyses (soil pH, organic matter content and calcium carbonate content); plant species surveys of 25m^2 were performed to estimate the percentage of bare soil surface and the cover of each plant species with a resolution of 5%; arthropod species sampling was performed through pitfall traps (plastic cups buried up to the edge and filled with approximately 20 ml of wine-vinegar and salt solution) collected and re-set every 20 days during the snow-free season.

A stratified sampling design based on a number of "sampling points" as pseudo-replicas gathered in a number of "plots" as replicas was followed, with slight differences depending on the study area.

Regression methods (e.g. Quantile Regression Model and Generalized Linear Model) and Indicator Species Analysis were used to analyze the differences among sampling units in terms of abiotic and biotic variables; multivariate methods (e.g. Cluster Analysis, Principal Component Analysis and Canonical Correspondence Analysis) were used for community's classification, species ordination and to analyze the association among abiotic and biotic variables. All the analyses were performed with the R software (R Core Team 2015).

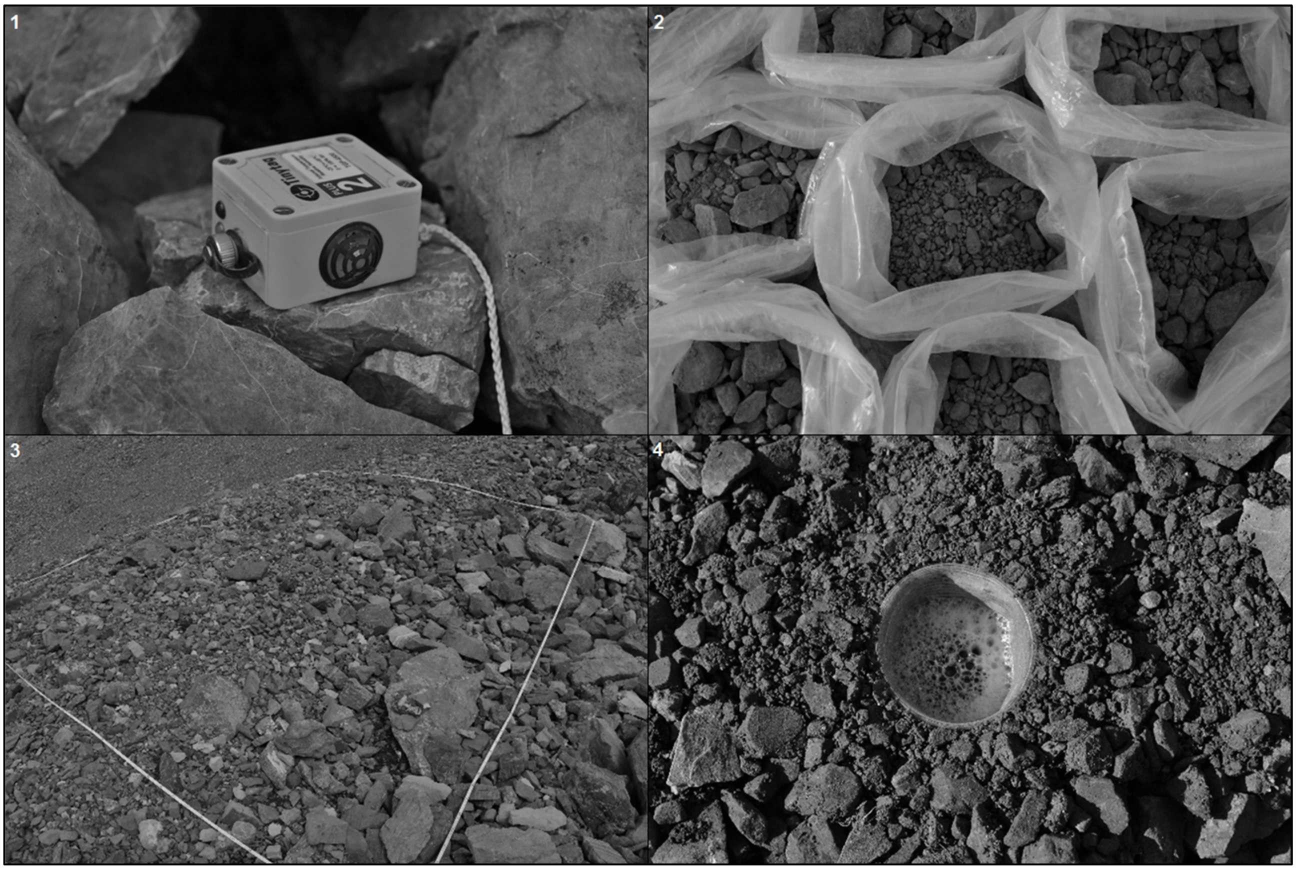


Fig. 2. Methods for the multidisciplinary data collection: 1) data-logger to record ground surface temperature and humidity; 2) soil sampling for physical and chemical analyses; 3) vegetation survey area of 25 m^2; 4) pitfall trap for arthropod sampling.

Key taxa

Vascular plant species were selected as key taxa because are reliable bioindicators (Landolt et al., 2010) especially at high altitude, where the harsh abiotic factors (e.g. soil and climate) prevail on biotic ones (e.g. competition) (Pauli et al., 2003). Moreover, community data are easily collectable (Braun-Blanquet and Jenny, 1926) and species are well known by the ecological and biogeographical viewpoints (Aeschimann et al., 2004; Landolt et al., 2010). In strength of such features, vascular plants were extensively used in ecological studies about the effect of climate change on high latitude/altitude ecosystems (e.g. Theurillat and Guisan, 2001; Pauli et al., 2003; Thuiller et al., 2005; Dullinger, 2012).

Carabid beetles (Coleoptera: Carabidae) and spiders (Arachnida: Araneae) were selected as arthropod key taxa. The choice of predatory taxa allows to exclude a direct trophic relationships with vascular plants (Gobbi et al., 2010; Hodkinson et al., 2002), thus to focus the study on the ecological role of abiotic factors (e.g. climate and soil). Carabid beetles and spiders are the most abundant predatory taxa on periglacial and glacial landforms and were extensively used in ecological studies about the effects of climate change on high latitude/altitude ecosystems (e.g. Gobbi et al., 2006a, 2006b, 2007; Bråten et al., 2012; Pizzolotto et al., 2014). Indeed, such taxa are reliable bioindicators (Groppali, 1998; Brandmayr et al., 2005, 2013), easily collectable (Brandmayr, 2005) and well known by the ecological and biogeographical viewpoints (Brandmayr et al., 2003; Thaler, 2003).

Functional traits

Besides the taxonomical approach, which remains the main rationale of the PhD project, we characterized each plant and arthropod species found on the main study areas by the functional viewpoint. A functional approach was previously applied to analyze high alpine ecosystems for plants (e.g. Caccianiga et al., 2006), arthropods (e.g. Bråten et al., 2012) and even to compare plants and arthropods at the same time (Gobbi et al., 2010). This approach could be useful in the framework of our research to compare plants and arthropods of periglacial and glacial landforms at global scale, overtaking the taxonomical differences due to biogeography.

Plant species were characterized by the functional viewpoint following the CSR strategy scheme (Grime, 1977; Grime and Pierce, 2012). This theory proposes three main plant functional types as response to three different ecological conditions and selective forces. 1) C-selected plants (competitors) are adapted to survive in stable and productive environments by investing resources in vegetative growth and organ size for resource preemption; 2) S-selected plants (stress tolerators) protect metabolic performance in resource-poor environments by investing in capacity to retain resources and repair cellular components in dense and persistent tissues; 3) R-selected plants (ruderal) are adapted to environments characterized by periodical biomass destruction, investing resources not in the individual but in propagules from which the population can regenerate in the face of the disturbance.

The main plant functional trait spectra represent variation in organs size and resource economics (a trade-off between traits conferring internal conservation and resource acquisition). Leaf area (LA), which play a key role in intercepting light (typical of the C strategy), can be considered as a function of the organ size spectrum. Leaf dry matter content (LDMC) and specific leaf area (SLA) can be considered as indicators of the opposite extremes of the resource economics spectrum, representing internal conservation (typical of the S strategy) and resource acquisition (typical of the R strategy), respectively. The measurement of the three leaf parameters (LA, LDMC and SLA) can thus be used to outline the CSR strategy of each plant species (Pierce et al., 2013).

Plant species for which leaf parameters were not collected in previous studies were characterized by the functional viewpoint following the CSR theory, measuring leaf parameters on the basis of the standard sampling and analysis methods (Pierce et al., 2013). The obtained data were merged with a database which contributed to the elaboration of a global method for calculating plant CSR ecological strategies.

Also arthropod species can be analyzed by the functional viewpoint (e.g. Gobbi et al., 2010; Bråten et al., 2012; Schirmel et al., 2012). Even though a standardized method based on the measurement of quantitative biological parameters (like leaf parameters for plant species) and a categorization in functional types based on a scheme of adaptative strategy (like the CSR scheme for plant species) are not available yet, both carabid beetles and spiders shows adaptation useful to outline the ecological strategy of each species.

Two main criteria were generally followed to characterize arthropod species by the functional viewpoint. 1) Dispersal ability can be used as indicator of the ability to face periodical disturbances: high-dispersal arthropods (e.g. winged carabid beetles and ballooner spiders) have more chance to escape from disturbances and to recolonize a recently disturbed habitat; by contrast, low-dispersal arthropods (e.g. wingless carabid beetles and runner spiders), have less chance to persist in such condition and generally need for more stable ecosystems (Brandmayr, 1991; Bell et al., 2005). 2) Diet and hunt strategy can be used as indicators of the habitat maturity: the occurrence of some traits (e.g. carnivorous carabid beetles and ground hunters spiders) rather than others (e.g. omnivorous carabid beetles and web weavers spiders) is strictly linked to the trophic availability of the habitat and the complexity of the ecosystem (Hodkinson, 2001, 2002; Gobbi et al., 2010; Bråten et al., 2012).

Data about arthropod functional traits were obtained on the basis of the specialized carabid beetles (Hůrka 1996; Brandmayr et al. 2005; Homburg et al. 2014) and spiders literature (Cardoso et al., 2011; Nentwig et al., 2016). The functional approach to analyze arthropod species was tested on an Alpine glacier foreland to infer the variation of functional traits along a chronosequence of glacier retreat.

Results organization

The results of the PhD project were reported as a collection of fourteen scientific products: the first nine are papers representing the main core of the research results, while the other five are contribution to side-projects coherent with the main theme of the research. The scientific products were organized in chapters as follows.

Chapter 2. Five papers concerning active rock glaciers and debris-covered glaciers on inner mountain ranges. Three of these papers (one published, one accepted, one ready for submission) consist of multidisciplinary studies on the ecology of such landforms as habitat and potential warm-stage refugia for cold-adapted species (active rock glaciers of Adamello-Presanella and Ortles-Cevedale, debris-covered glacier of Belvedere). The other two papers (both published) consist of descriptive outlines of climate and vegetation features of the investigated areas and landforms (active rock glaciers of Ortles-Cevedale, debris-covered glacier of Belvedere).

Chapter 3. Two papers concerning peripheral mountain ranges (Orobian Alps) as a location of warm-stage refugia for cold-adapted species. The first paper (published) consist of a multidisciplinary study of the primary succession along a glacier foreland in this context (Trobio glacier, Val Seriana); the second paper (in preparation) consist of a biogeographical study which compare the distribution of cold-adapted species with respect to the putative position of cold- and warm-stage refugia on Orobian Alps.

Chapter 4. Two papers (one accepted and one submitted) concerning the functional approach to high alpine plant and arthropod analyses: the one on the CSR theory for plant species (with an application to active rock glaciers of Ortles-Cevedale and debris-covered glacier of Belvedere), the other on arthropod functional traits along a glacier foreland (Val d'Amola, Adamello Presanella).

Chapter 5. Preliminary analysis of a dataset including all the study areas investigated in the PhD project. The dataset aimed to provide a basis also for further synthesis works at Alpine scale on plants and arthropods of periglacial and glacial landforms.

Chapter 6. Conclusions and perspectives.

Chapter 7. Five contributions (four published and one accepted) to the ecological and biogeographical knowledge on some endemic, rare or threatened Alpine plant species. Two contributions consist of assessments for the IUCN Italian Red List about two plant species endemic of Lombardy (*Androsace brevis* and *Viola comollia*); three contributions consist of updates of the regional distribution of rare plant species (*Botrychium multifidum* and *Saxifraga presolanensis* in Lombardy and *Galium megalospermum* in Val d'Aosta).

Chapter 8. Summary of the PhD products.

Supervision, collaborations and funding

This PhD research project was carried out under the supervision of the tutors Dr. Marco Caccianiga [1] and Dr. Mauro Gobbi [2]. Datalogger programming and soil analyses were performed under the supervision of Dr. Chiara Compostella [3]. Vegetation survey were managed independently. Plant species functional traits analyses were performed under the supervision of Dr. Marco Caccianiga and Dr. Simon Pierce [4]. Pitfall traps placement, arthropod taxa sorting, carabid beetles identification and functional traits analyses were performed under the supervision of Dr. Mauro Gobbi. Spider species identification and functional traits analyses were performed with the collaboration of Dr. Francesco Ballarin [5], Dr. Marco Isaia [6], and Dr. Paolo Pantini [7], depending on the study area. Statistical analyses were performed under the supervision of Dr. Giuseppe Marano [8] and Prof. Patrizia Boracchi [8]. This PhD project was supported by UNIMI - Università degli Studi di Milano and MUSE - Museo delle Scienze di Trento and co-financed by Stelvio National Park and Orobie Bergamasche Regional Park.

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Physical and biological features of an active rock glacier in the Italian Alps

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Abstract

We report on the key physical features of an active rock glacier that influence the distribution of plants and arthropods. We also perform a comparison with neighboring scree slope and alpine grassland to test whether the environmental features of the rock glacier drive the presence of specific species assemblages. Compared with scree slope and grassland, the studied rock glacier provides particular physical features that determine the presence of unique species. Plant distribution is mainly driven by grain size. Arthropod distribution is linked to grain size, with cold-adapted species found on areas with coarse-grained deep debris, which also shows a distinctive temperature regime with very low values throughout the year. On the basis of these findings, we advance the hypothesis that rock glaciers provide specific ecological conditions creating potential refugia for cold-demanding species during warm climatic periods.

Keywords

Alps, arthropods, climate change, cold-adapted species, flora, periglacial, permafrost, refugia

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Introduction

The importance of geomorphological heterogeneity for enhancing biodiversity in Alpine ecosystems has often been acknowledged, as well as its important ecological and biogeographical role in response to climatic fluctuations (Baroni et al., 2007; Caccianiga et al., 2011; Gobbi et al., 2011; Matthews, 1992). A specific landform with its distinctive environmental conditions may promote the survival of plant and animal taxa when the surrounding habitats become climatically unfavorable and may thus act as a refugium (Stewart et al., 2010). Therefore, environmental heterogeneity within high-altitude landscape could make the difference between expected survival and extinction of both animal and plant taxa (Birks and Willis, 2008; Essl et al., 2011).

Rock glaciers are a periglacial landform characterized by distinctive environmental conditions because of the occurrence of subsurface ice (permafrost). Previous studies outlined the occurrence of plant cover on their surface (Burga et al., 2004; Rieg et al., 2012); a recent paper reports arthropod assemblages associated with rock glaciers on Californian mountains (Millar et al., 2014). To our knowledge, no data on the presence of arthropod assemblages on Alpine rock glaciers are presently available. Furthermore, so far no study has tried to address the relationship between environmental conditions and plant and arthropod assemblages on these landforms. Rock glaciers, with respect to their surrounding habitats, offer a unique environment, and we test their suitability for the survival of high-altitude plant and arthropod taxa for the first time.

The research aims to describe plant and ground-dwelling arthropod (spiders and ground beetles) assemblages on an active rock glacier of the Alps and to compare them with those of neighboring habitats (scree slope and grassland). We also discuss the role of active rock glaciers as potential refugia for high alpine taxa during warm climatic phases.

Materials and methods

Study area

The Amola Rock Glacier (Central-Eastern Italian Alps, 46°12′–10°42′, Figure 1) is mostly composed of matrix-free, angular boulders up to some meters in diameter, while fine-grained material locally outcrops on the lateral and frontal slopes and on the top of the ridges (Seppi et al., 2011, 2012).

Sampling design and environmental variables

To detect the displacement of the rock glacier, topographic surveys were conducted annually since 2001 with a total station

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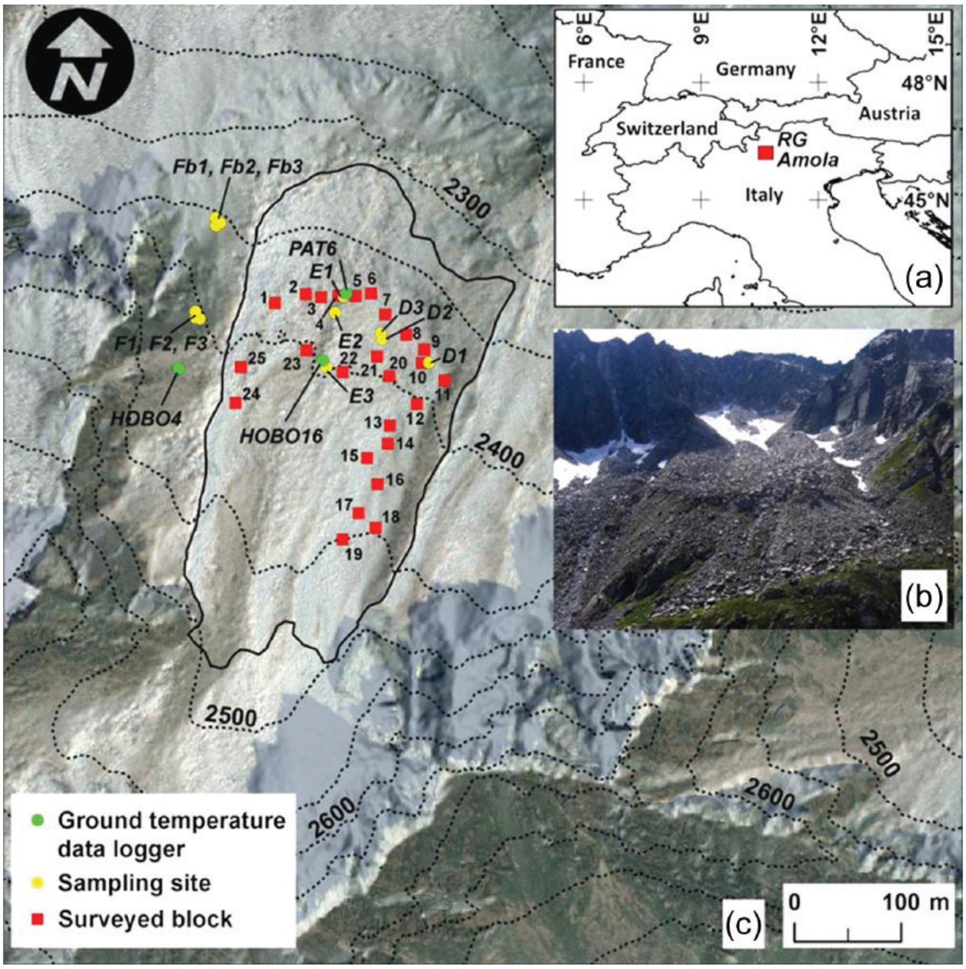

Figure 1. (a) Geographic setting and (b) general view of the Amola Rock Glacier (Central-Eastern Italian Alps). The elevation ranges from 2280 to 2500 m a.s.l., and the area is about 9.7 ha. The bedrock consists of biotitic–amphibolic tonalite. (c) Sampling sites, ground temperature data logger, and surveyed boulders on the rock glacier and in the surrounding area.

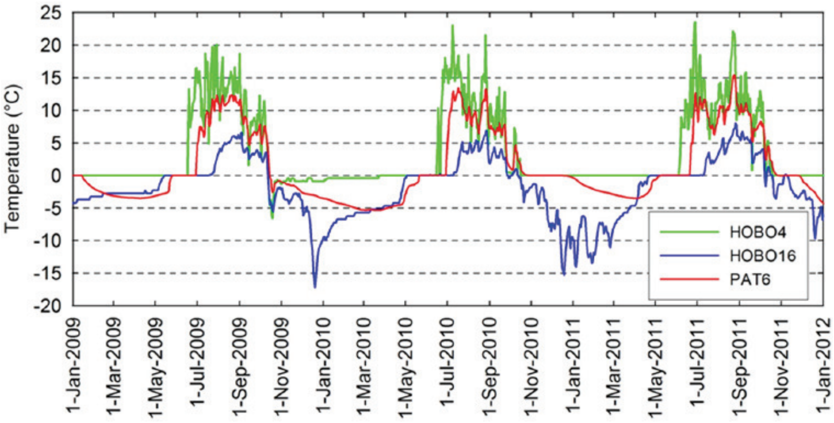

Figure 2. Thermal regime of the monitoring sites located on the rock glacier (PAT6 and HOBO16) and on a nearby scree slope (HOBO4). The data logger PAT6 was installed on the top of a ridge in fine-grained material, at about 10 cm below the surface to avoid direct solar radiation. The data logger HOBO16 was placed between large boulders few meters below the surface and measured the air temperature in the voids between the boulders. The data logger HOBO4 was installed in fine-grained material about 5 cm below the surface.

(LEICA TCA 2003), measuring a network of 25 large boulders (Figure 1). The maximum measurement uncertainty can be estimated at ±2.5 cm. The velocity of the frontal area of the rock glacier, where the plant and arthropod sampling points are located, was interpolated in a GIS by an inverse distance weighted (IDW) method, obtaining a raster surface. The velocity of the sample points was then estimated by intersecting them with the raster surface.

Near-surface ground temperature was continuously measured at two sites on the rock glacier and on a nearby scree slope (Figures 1 and 2). Data were collected for 3 years (2009–2012) with hourly resolution using data loggers Tinytag TGP-4020 with an external probe (measurement range: −40° to +125°C; accuracy: ±0.35°C) and HOBO H8 Temp (measurement range: −20°C to + 70°C; accuracy: ±0.7°C). The mean annual ground surface temperature (MAGST) was then calculated for each measuring site, and the thermal regime was analyzed.

For plant and arthropod sampling, two sampling sites were randomly placed on the rock glacier (sites D and E) and two others, as a control, on an undisturbed surface within an alpine grassland community (site F) and on a scree slope (site Fb) (Figure 1). Each sampling site included three randomly placed pitfall traps, the same utilized in similar habitats (see Gobbi et al., 2011), surrounded by four plots for vegetation sampling; each trap was distanced at least 10 m to avoid any spatial autocorrelation. The traps were emptied about every 20 days during the snow-free season (July–September 2010 and 2011).

Two milieu souterrain superficiel (MSS) traps (Juberthie, 1979) were located at different depths on the rock glacier, one within fine grain size at 60 cm (MSS_1) and the other between metric boulders at 6 m of depth (MSS_2). These traps were used to evaluate the presence of endogean fauna and were located in July 2011 and emptied in late August 2011.

Plots for the sampling of plant cover consisted of a metal circle of 40 cm diameter placed at the four opposite sides of the pitfall trap. Vascular plants, bryophytes, and ground lichens occurring within the plot were recorded; the overall vegetation cover and that of every species were visually estimated with a resolution of 5%. The mean values from the four plots were calculated to obtain a single value associated with each trap. Collected data in such a small area may not be representative of the whole plant cover but could be strictly associated with substrate and arthropod sampling.

A substrate sample of 1–2 kg for particle size distribution analysis was taken at every sampling site. An amount of 200 g of substrate was sampled at each pitfall trap for pH (in 1:2.5 soil:water) and organic matter content (Walkley–Black method) analysis. All the soil samples were taken at the surface.

Statistical analyses

The differences in the analyzed variables between each sampling site were evaluated by the analysis of variance (ANOVA) and post hoc Tukey's HSD test. The relationships between environmental variables and species were outlined through a direct gradient analysis. According to the gradient length (Podani, 2000), a redundancy analysis (RDA) (length <2.5 cm) was performed for plants and a canonical correspondence analysis (CCA) (length >2.5 cm) for arthropods. A forward selection within the CCA and RDA was performed to select the significant explanatory predictor variables. Statistical significance ($p < 0.01$) of each environmental factor was assessed independently by means of an unrestricted Monte Carlo permutation test (999 permutations). For multiple simultaneous testing, the Bonferroni correction was considered. The significance of the total model, after deleting the non-significant environmental factors, was also tested by Monte Carlo permutation test (999 permutations).

> *Plants*. Four environmental variables (silt–clay, gravel–sand, soil pH, and soil organic matter) and 63 species were included in the analysis. From the analyses, 27 plant species occurring in only one site were eliminated.
> *Arthropods*. We analyzed spider (Arachnida: Araneae) and ground beetle (Coleoptera: Carabidae) assemblages as they are the most abundant ground-dwelling arthropods with well-known ecology and spatial patterns (Brandmayr et al., 2003; Thaler, 2003) and have been found to clearly react to climate warming in the Italian Alps (Brambilla and Gobbi, 2014; Gobbi et al., 2006). Six environmental variables (vegetation cover, vegetation richness, silt–clay, gravel–sand, soil pH, and soil organic matter) and 20 species were included in the analysis. Six rare (number of specimens <2) species were omitted from the analysis.

The statistical analyses were performed using IBM SPSS Statistics v. 20 and CANOCO v. 4.51 for Windows (Ter Braak and Smilauer, 1998).

Results

Environmental variables

From 2001 to 2011, the rock glacier showed mean velocities between 0.1 and 20.7 cm/yr and is therefore active. The velocity of the measuring points located on frontal sector ($n = 14$) ranged from 1 to 14 cm/yr, with the displacement direction following the maximum slope. The estimated velocities of the sampling sites ranged from more than 2 cm/yr (point D3) to about 10 cm/yr (points E1 and E2; Table 1).

Soil organic matter content was very low in both rock glacier sites (mean values: 46.03 ± 7.10 and 30.51 ± 12.38 g/kg for sites D and E, respectively) without any significant difference between them (Tukey's HSD test $p = 0.778$). Rock glacier sites, scree control sites, and grassland control sites were significantly different from each other (ANOVA test and post hoc Tukey's HSD test $F(3, 10) = 52.851$; $p < 0.001$), with grassland showing the highest values of organic matter (433.74 ± 15.03 and 211.22 ± 44.86 g/kg for grassland and scree, respectively). Soil pH did not show any significant variation among sites (ANOVA test and post hoc Tukey's HSD test $F(3, 10) = 1.612$; $p = 0.262$).

On the rock glacier, remarkably cold conditions were observed at HOBO16 site (Figure 2), where the MAGST was always negative (−1.4°C, −2.3°C, and −1.8°C in 2009, 2010, and 2011, respectively). Winter temperature was affected by wide, short-term fluctuations, suggesting a continuous air circulation in the pore space and an air exchange with the atmosphere due to the low insulating effect of the snow cover. At PAT6 site, the MAGST above zero was recorded in the same years (1.1°C, 0.7°C, and 1.9°C, respectively). Due to the effective thermal insulation of the snow layer, the temperature at this site constantly decreased during winter, reaching a stable period in late winter/early spring with values ranging from −5°C to −3°C (Figure 2). A different thermal behavior characterized the site located outside the rock glacier (HOBO4). MAGST was always above 3°C, and the temperature during the snow cover period was constantly at 0°C (Figure 2), suggesting the absence of permafrost (Hoelzle et al., 1999). The onset of the summer thermal regime (Figure 2) showed that the snow disappeared earlier on the scree slope than on the rock glacier.

Plants

In total, 63 plant species were recorded; total plant cover ranged from 15% (trap E2) to 86% (trap F2). The number of plant species ranged from 4 (trap E3) to 27 (trap F3) (Table 1). *Saxifraga bryoides, Oxyria digyna, Poa laxa, Veronica alpina, Adenostyles leucophylla, Cystopteris fragilis, Hedwigia ciliata*, and *Homalia besseri* were exclusive to the rock glacier surface.

Plant cover was correlated with plant species number ($r = 0.928$; $p < 0.001$) and was significantly higher on the grassland (site F) (ANOVA test and post hoc Tukey's HSD test $F(3, 10) = 11.518$; $p = 0.003$); plant species number varied significantly among sites (ANOVA test $F(3, 10) = 29.610$; $p < 0.001$) and was significantly higher on site F and lower on site E.

After forward selection (RDA), one environmental variable (grain size as gravel–sand) was extracted that significantly correlated with the distribution of the plant species, explaining 54.1% of the total variance (Figure 3a). The first axis was strongly correlated with grain size ($r = -0.85$ with gravel–sand) and separated the rock glacier sites (left) from control sites. Grain size was significantly correlated with soil organic matter content ($r = -0.97$

Table 1. Data of sampling sites. Total displacement and mean velocities of the sampling sites on the rock glacier estimated in the period 2001–2011; vascular plants (pl), bryophytes (br), lichens (li), carabid beetles (be), and spiders (sp) sampled in each site (values represent the average plant cover plots and the number of arthropod individuals). ID: acronyms for plant and arthropod names as reported in Figure 3. Nomenclature follows Pignatti (1982) for vascular plants, Cortini Pedrotti (2001) for bryophytes, and Nimis and Martellos (2008) for lichens.

			Rock glacier						Scree			Grassland		
			D1	D2	D3	E1	E2	E3	Fb1	Fb2	Fb3	F1	F2	F3
		Total horizontal displacement (cm)	41.0	53.5	25.8	100.8	103.2	44.8	–	–	–	–	–	–
		Mean velocity (cm/yr)	4.1	5.4	2.6	10.1	10.3	4.5	–	–	–	–	–	–
ID		Species												
Car_sem	pl	*Carex sempervirens*	0.00	0.00	0.00	0.00	0.00	0.00	5.00	0.00	0.00	13.75	21.25	15.00
Sax_bry	pl	*Saxifraga bryoides*	7.75	13.75	3.75	7.50	7.75	10.25	0.00	0.00	0.00	0.00	0.00	0.00
Sal_ser	pl	*Salix serpyllifolia*	0.00	0.00	0.00	0.00	0.00	0.00	27.50	3.50	0.00	0.00	1.25	6.25
Ely_myo	pl	*Elyna myosuroides*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	8.75	17.50	10.00
Oxy_dig	pl	*Oxyria digyna*	6.25	6.25	11.25	3.75	4.00	0.25	0.00	0.00	0.00	0.00	0.00	0.00
Dor_clu	pl	*Doronicum clusii*	2.75	5.00	6.50	4.25	0.00	0.00	2.00	6.67	0.00	0.00	0.00	0.00
Rho_fer	pl	*Rhododendron ferrugineum*	0.00	0.00	0.00	0.00	0.00	0.00	2.00	15.00	0.00	0.00	0.00	6.25
Leo_hel	pl	*Leontodon helveticus*	0.00	0.00	0.00	0.00	0.00	0.00	5.00	0.00	2.00	5.00	3.75	5.00
Agr_alp	pl	*Agrostis alpina*	0.00	0.00	0.00	0.00	0.00	0.00	13.33	0.00	7.25	0.00	0.00	0.00
Agr_rup	pl	*Agrostis rupestris*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	13.75	2.75	3.75
Hom_alp	pl	*Homogyne alpina*	0.00	0.00	0.00	0.00	0.00	0.00	5.00	3.00	0.00	5.25	5.00	1.50
Ant_alp	pl	*Anthoxanthum alpinum*	0.00	0.00	0.00	0.00	0.00	0.00	10.00	5.67	0.00	0.00	2.50	0.25
Fes_nig	pl	*Festuca nigrescens*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.50	2.50	12.50
Vac_gau	pl	*Vaccinium gaultherioides*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.75	2.75	10.00
Pol_viv	pl	*Polygonum viviparum*	0.00	0.00	0.00	0.00	0.00	0.00	6.67	0.00	0.00	3.00	5.00	1.50
Agr_sch	pl	*Agrostis schraderana*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	9.25	0.00	0.00	5.00	1.50
Poa_alp	pl	*Poa alpina*	0.00	0.00	0.00	0.00	0.00	0.00	5.67	0.00	6.00	0.00	3.75	0.00
Pul_alp	pl	*Pulsatilla alpina*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.50	5.00	6.25
Luz_lut	pl	*Luzula lutea*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	10.00	0.00	2.50	0.00
Jun_tri	pl	*Juncus trifidus*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	5.00	6.25	0.00
Poa_lax	pl	*Poa laxa*	0.50	1.25	0.00	1.50	2.00	3.00	0.00	0.00	0.00	0.00	0.00	0.00
Lig_mut	pl	*Ligusticum mutellina*	0.00	0.00	0.00	0.00	0.00	0.00	3.50	0.00	0.00	0.00	2.75	2.00
Ran_mon	pl	*Ranunculus montanus*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.50	5.00	1.25
Pot_aur	pl	*Potentilla aurea*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.50	2.50	2.50
Hup_sel	pl	*Huperzia selago*	0.00	0.00	0.00	0.00	0.00	0.00	3.50	3.50	0.00	0.00	0.00	0.00
Sol_pus	pl	*Soldanella pusilla*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.50	0.00	1.50	0.00	1.25
Phy_hem	pl	*Phyteuma hemisphaericum*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.00	2.00	0.00	0.25	0.25
Vio_bif	pl	*Viola biflora*	0.00	0.00	0.00	0.00	0.00	0.00	4.00	0.00	0.00	0.00	0.00	0.00
Emp_her	pl	*Empetrum hermaphroditum*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.75
Leu_alp	pl	*Leucanthemopsis alpina*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.00	0.25	0.00	1.25
Lot_alp	pl	*Lotus alpinus*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.50	1.25
Ave_ver	pl	*Avenula versicolor*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.50	0.00
Eup_min	pl	*Euphrasia minima*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.25	0.25	0.50
Sal_her	pl	*Salix herbacea*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.00	0.00	0.00	0.00
Sed_alp	pl	*Sedum alpestre*	0.00	0.00	0.00	0.00	0.00	0.00	2.00	0.00	0.00	0.00	0.00	0.00
Ara_alp	pl	*Arabis alpina*	0.00	0.00	0.00	0.00	0.00	0.00	2.00	0.00	0.00	0.00	0.00	0.00
Gen_pun	pl	*Gentiana punctata*	0.00	0.00	0.00	0.00	0.00	0.00	2.00	0.00	0.00	0.00	0.00	0.00
Hie_pil	pl	*Hieracium pilosella*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.00	0.00	0.00	0.00	0.00
Thy_sp.	pl	*Thymus* sp.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.00	0.00	0.00	0.00
Sib_pro	pl	*Sibbaldia procumbens*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.25	1.25	0.00
Car_cur	pl	*Carex curvula*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.25	0.00	0.00
Gen_ger	pl	*Gentianella germanica*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.25	0.00	0.00
Loi_pro	pl	*Loiseleria procumbens*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.25
Sel_sel	pl	*Selaginella selaginoides*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.25	0.00	0.00
Ver_alp	pl	*Veronica alpina*	0.25	0.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Cam_sch	pl	*Campanula scheuchzeri*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.25	0.25	0.00
Gen_koc	pl	*Gentiana kochiana*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.25	0.00	0.25
Ade_leu	pl	*Adenostyles leucophylla*	0.00	0.00	0.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Bar_alp	pl	*Bartsia alpina*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.25
Cys_fra	pl	*Cystopteris fragilis*	0.00	0.00	0.00	0.00	0.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Nar_str	pl	*Nardus stricta*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.25	0.00	0.00
Pyr_sp.	pl	*Pyrola* sp.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.25
Pri_dao	pl	*Primula daonensis*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.25
Sax_opp	pl	*Saxifraga oppositifolia*	0.00	0.00	0.00	0.00	0.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Vac_myr	pl	*Vaccinium myrtillus*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.25	0.00
Pol_alp	br	*Polytrichastrum alpinum*	1.00	7.50	27.50	0.25	1.50	5.25	0.00	0.00	0.00	1.25	0.00	0.00
Ste_alp	li	*Stereocaulon alpinum*	0.00	0.00	0.00	0.00	0.00	0.00	7.50	0.00	0.00	0.00	0.00	0.00
Dic_sub	br	*Dicranella subulata*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	6.00	0.00	0.00	0.00
Pol_jun	br	*Polytrichum juniperinum*	0.00	0.00	0.00	0.00	0.00	0.00	3.50	0.00	2.00	0.00	0.00	0.00
Amb_ten	br	*Amblystegium tenax*	0.00	0.00	0.00	0.00	0.00	0.00	5.50	0.00	0.00	0.00	0.00	0.00
Hed_cil	br	*Hedwigia ciliata*	0.00	0.00	2.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Hom_bes	br	*Homalia besseri*	0.00	0.00	2.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Hep_spp	br	*Hepaticae* spp.	0.00	0.00	0.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Table 1. (Continued)

			Rock glacier						Scree			Grassland		
			D1	D2	D3	E1	E2	E3	Fb1	Fb2	Fb3	F1	F2	F3
Ore_ang	be	*Oreonebria angustata*	5	5	42	17	3	71	1	4	0	0	0	0
Neb_ger	be	*Nebria germari*	0	2	0	0	6	108	0	0	0	0	0	0
Tre_tri	be	*Trechus tristiculus*	0	1	6	10	2	0	0	0	0	0	0	0
Bem_niv	be	*Bembidon bipunctatum nivale*	0	0	0	0	0	0	0	0	0	14	0	0
Car_ada	be	*Carabus adamellicola*	0	0	0	0	0	0	0	0	0	0	7	6
Ozy_tru	sp	*Ozyptila trux*	0	0	0	0	0	0	0	0	0	0	5	7
Pte_mul	be	*Pterostichus multipunctatus*	0	1	0	6	0	0	0	2	0	0	0	1
Coe_tir	sp	*Coelotes pickardi tirolensis*	0	0	0	0	0	0	3	2	0	0	0	1
Par_ore	sp	*Pardosa oreophila*	0	0	0	0	0	0	0	0	0	1	5	0
Mug_han	sp	*Mughiphantes handschini*	0	0	0	1	3	0	0	0	0	0	1	0
Ore_mon	sp	*Oreoneta montigena*	0	0	1	3	0	1	0	0	0	0	0	0
Car_dep	be	*Carabus depressus*	0	0	0	0	0	0	0	0	0	0	4	1
Dra_hee	sp	*Drassodex heeri*	0	0	0	0	0	0	2	0	0	0	2	0
Par_nig	sp	*Pardosa nigra*	0	0	0	0	0	0	0	4	0	0	0	0
Par_gie	sp	*Pardosa giebeli*	0	0	0	0	0	0	0	0	0	3	0	0
Sit_lon	sp	*Sitticus longipes*	0	0	0	0	0	0	0	0	0	3	0	0
Not_big	be	*Notiophilus biguttatus*	0	0	3	0	0	0	0	0	0	0	0	0
Cym_vap	be	*Cymindis vaporariorum*	0	0	0	1	0	0	0	0	0	0	1	0
Car_syl	be	*Carabus sylvestris*	0	0	0	0	0	0	0	0	0	2	0	0
Ore_gla	sp	*Oreonetides glacialis*	0	0	0	0	0	2	0	0	0	0	0	0
Pel_rad	sp	*Pelecopsis radiciola*	0	0	0	0	0	0	0	0	0	0	2	0
Ent_med	sp	*Entelecara media*	0	0	0	0	0	1	0	0	0	0	0	0
Mei_rur	sp	*Meioneta rurestris*	0	0	0	0	0	1	0	0	0	0	0	0
Xys_des	sp	*Xysticus desidiosus*	0	0	0	0	0	0	0	0	0	0	1	0
Tri_lae	be	*Trichotichnus laevicollins*	0	0	0	1	0	0	0	0	0	0	0	0
Pri_bip	be	*Princidium bipunctatum*	0	0	0	0	0	0	0	0	0	1	0	0
Cyc_att	be	*Cychrus attenuatus*	0	0	0	0	0	0	0	0	0	0	1	0
		Vascular plants cover (sum)	17.50	26.50	21.75	17.00	14.25	13.50	99.17	54.08	33.25	75.00	103.25	96.00
		Bryophytes cover (sum)	1.00	7.50	32.75	0.25	1.50	5.25	16.50	0.00	8.00	1.25	0.00	0.00
		Arthropod species richness	1	4	4	7	4	7	3	4	0	6	10	5
		Arthropods abundance	5	9	52	39	14	185	6	12	0	24	29	16

with gravel–sand); therefore, the first axis defines a gradient, with particle size and organic matter amount increasing from right to left. The second axis possibly indicated a moisture gradient probably linked to microtopography, with species of relatively wet sites (*Salix herbacea, Soldanella pusilla*) at the negative side of the axis and species of dryer sites (e.g. *Sedum alpestre*) at the positive side.

Arthropods

A total of 394 specimens (391 in the pitfall traps and 3 in the MSS traps) belonging to 27 species were sampled (Table 1). Of them, 13 species were carabid beetles, while 14 species were spiders. The most abundant species were *Oreonebria angustata* ($N = 148$, 2 specimens in the MSS traps) and *Nebria germari* ($N = 116$, 1 specimen in MSS_2); the latter was found only on the rock glacier together with *Trechus tristiculus* ($N = 19$) and *Oreoneta montigena* ($N = 5$).

Arthropod species richness and the number of individuals were not correlated to each other ($r = 0.40$; $p = 0.22$). Both species richness and abundance did not significantly change between rock glacier (sites D and E) and controls (sites F and Fb) (ANOVA test for species richness: $F(3, 10) = 2.77$; $p = 0.12$; ANOVA test for individuals: $F(3, 10) = 1.03$; $p = 0.43$).

After forward selection (CCA), one environmental variable (grain size as gravel–sand) was extracted that significantly correlated with the distribution of spiders and ground beetles, explaining 25.9% of the total variance (Figure 3b). The first axis was correlated strongly with grain size ($r = -0.99$ with gravel–sand). It separated the rock glacier sites (left), characterized by coarse grain size, from the control sites (right). Grain size was significantly correlated with soil organic matter amount ($r = -0.97$ with gravel–sand); therefore, the first axis defines a gradient, with particle size and organic matter content increasing from right to left.

CCA showed the main gradient evidencing the presence of specific assemblages from sites with the finest grain size and highest organic matter (site F) to sites with large grain size and low organic matter (sites D and E); Fb site showed intermediate position (Figure 3b). Four carabid beetles (*Oreonebria angustata, Nebria germari, Trechus tristiculus*, and *Notiophilus biguttatus*) and two spiders (*Oreonetides glacialis* and *Oreoneta montigena*) were linked to the sites on the rock glacier (sites D and E).

Discussion

Our data showed the uniqueness of the rock glacier environment, characterized by surface movement and thermal regimes indicating the occurrence of permafrost according to Hoelzle et al. (1999). Temperature regime differentiates rock glacier from the surrounding habitats but also emphasizes its heterogeneity as a function of grain size, with coarse-sized areas showing the 'negative thermal anomaly' that characterizes the blocky deposits (Harris and Pedersen, 1998; Juliussen and Humlum, 2008).

Plant cover was not observed on areas consisting of metric boulders or coarse gravel. The overall pattern of plant cover was that of scattered 'islands' where plant and moss cover could locally attain 50% cover. The effects of grain size could probably be due to both its direct effect and its role in determining the distinctive temperature regime characterized by very low values even during the growing season, when harsh winter climate and disturbance must be balanced by relatively favorable conditions to allow plant survival (Caccianiga et al., 2006; Körner, 1999).

Substrate velocity is not a limiting factor for plant survival; the maximum value recorded in our sampling sites (10.3 cm/yr) is

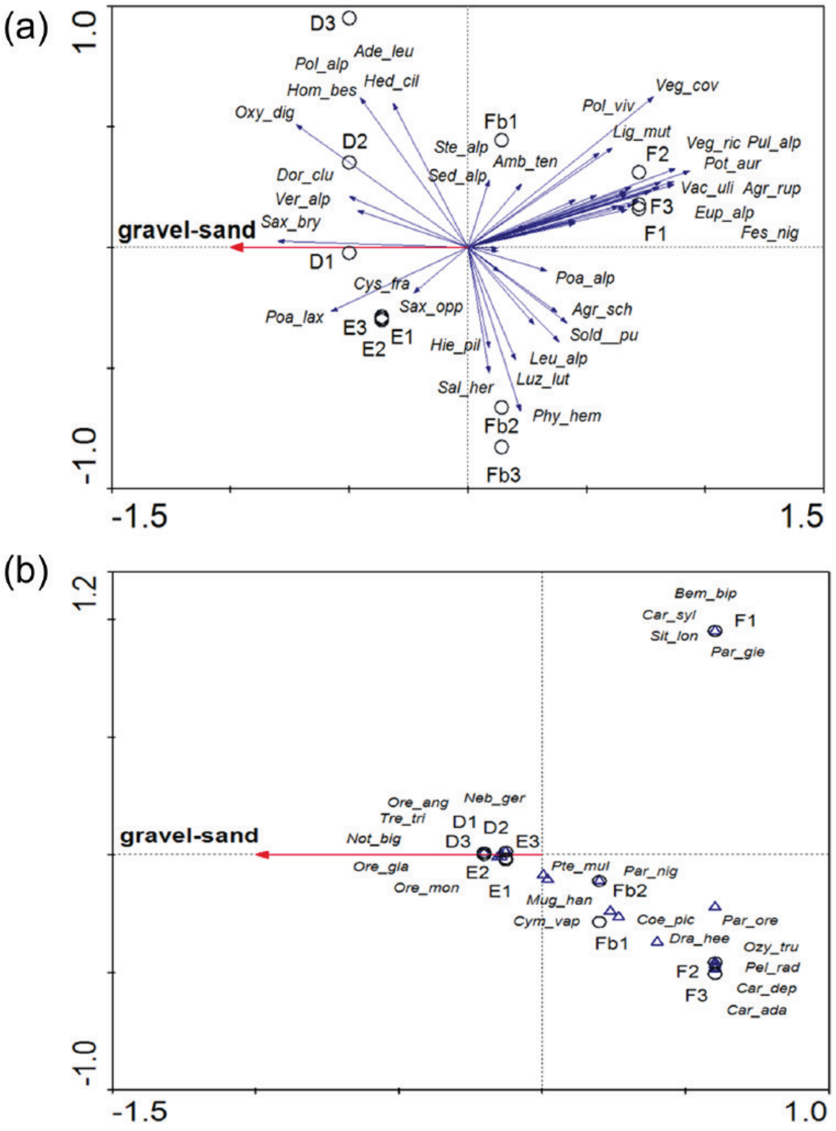

Figure 3. Direct gradient analysis indicating the relationship between the environmental variables and (a) plant and (b) arthropod species distribution. (a) Plants: four eigenvalues were extracted – first axis: 0.541; second axis: 0.287; third axis: 0.082; fourth axis: 0.032. Significance of all canonical axes was $p = 0.001$. (b) Arthropods: four eigenvalues were extracted – first axis: 0.923; second axis: 0.922; third axis: 0.532; fourth axis: 0.421. Significance of all canonical axes was $p = 0.001$.

lower than the limiting threshold for plant survival of 30 cm/yr reported by Burga et al. (2004) and the velocity recorded on debris-covered glaciers (up to *c*. 15 m/yr; Caccianiga et al., 2011). Our velocity values are lower than 1.5 m/yr, threshold below which grain size becomes the main factor affecting plant cover according to Rieg et al. (2012).

The overall plant species composition of the rock glacier surface could be considered similar to that of scree slopes and moraines (Caccianiga and Andreis, 2004), but lacking the local occurrence of demanding species that are able to colonize favorable microsites on gravitative deposits. Another feature separating rock glacier communities from those of gravitative scree is the higher frequency of some bryophytes, particularly *Polytrichastrum alpinum*, an indicator of long-lasting snow cover (Odland and Munkejord, 2008); moss abundance has already been indicated by Burga et al. (2004) as a likely indicator of permafrost occurrence.

Concerning the arthropod assemblages, our results indicate the presence of exclusive species to each landform (rock glacier, scree, and grassland). Specifically, the rock glacier hosts large populations of three carabids: *Nebria germari, Oreonebria angustata*, and *Trechus tristiculus*. These species are typical of cold and wet high-altitude environments (Ledoux and Roux, 2005): *Nebria germari* and *Oreonebria angustata* can be found near glacier fronts, on glacier surface, and on gravitative scree slopes (Brandmayr and Zetto Brandmayr, 1988; Gereben-Krenn et al., 2011). *Trechus tristiculus* is a cold-adapted species with endogean lifestyle, indicator of deep screes with macroporal system in rocky material (Lompe, 2004). Although these species are known in the literature to be able to live on high-altitude scree slopes, both *Nebria germari* and *Trechus tristiculus* could not be found on the studied scree slope. Only a small population of *Oreonebria angustata* occurred in the studied scree slope compared with that on the rock glacier (5 vs 143 specimens). These species suggest that the rock glacier offers more suitable microhabitat conditions than scree slope because of the distinctive grain size and the presence of subsurface ice. Moreover, the carabids belonging to genus *Trechus* are able to colonize only habitats with specific microthermal conditions like caves or deep screes (Lompe, 2004). The detritus depth of the rock glacier has been confirmed by the catch of *Nebria germari* and *Oreonebria angustata* with the MSS traps, thus suggesting the presence of an architecturally complex macroporal structure where ice ensures the occurrence of continuously low temperature throughout the year.

Rock glaciers as potential warm-stage refugia

Concerning the arthropod assemblages, it is possible to define a rock glacier as a superficial subterranean habitat represented by fissure network among boulders, human-sized caves included. Unlike other superficial subterranean habitats like scree slopes, where temperatures could reach relatively high values in summer (this paper; see also Růžička et al., 2013), rock glaciers are selected by cold-adapted species, which avoid scree slopes as they do not offer constantly low temperatures during summer. For example, the recent extinction of *Nebria germari* and *Trechus* sp. was demonstrated by Pizzolotto et al. (2014) in some scree slopes of the Dolomites where these species were dominant 30 years before, indicating that on this landform no refugia were available for these cold-demanding species.

It is possible to compare the proposed hypothesis of rock glaciers as refugia during interglacial period with a role similar to that of caves during quaternary climatic fluctuations. Such a role is less apparent for plant species, as the distinctive temperature regime of rock glacier surface could act as a limiting factor for plant survival; however, in a warming scenario, such regime could provide survival opportunities for cold-requiring species, as suggested for debris-covered glaciers (Caccianiga et al., 2011).

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Vegetation outlines of two active rock glaciers with contrasting lithology

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Abstract
Rock glaciers are periglacial landforms consisting of coarse debris with interstitial ice or ice core, characterized by creeping due to ice deformation. These landforms are drawing the attention of plant ecologist as harsh habitats and potential refugia in the global change context. Our aim was to describe the vegetation outlines of two active rock glaciers of the Ortles-Cevedale Massif (Central Italian Alps) on different substrates (silicate and carbonate) and compare them with the neighboring stable slopes and scree slopes. Two hypotheses were tested: 1) rock glaciers differ from the surrounding landforms for the presence of cold-adapted plant communities; 2) rock glacier plant communities indicate similar microclimatic conditions in spite of the contrasting lithology. Data were collected by phytosociological method performing 80 relevés of 25 m^2. Plant communities were compared by a cluster analysis based on the presence/absence species matrix and species relative frequencies for each landform were calculated. The cluster analysis separated first for all the two sites; afterwards, the landforms were differently discerned each other depending on the site. Despite the remarkable floristic differences due to the substrate, the vegetation of both rock glaciers suggest a general adjustment to cold-moist microclimate and long-lasting snow cover, differentiating more or less evidently from the adjacent scree slopes and enhancing the survival of nival entities at the elevation of alpine grasslands.

Key words: alpine flora, alpine vegetation, climate change, periglacial, permafrost, refugia, scree slope.

Introduction

Rock glaciers are periglacial landforms consisting of coarse debris with interstitial ice or ice core, characterized by creeping due to ice deformation (Barsch, 1996; Janke *et al*., 2013). These landforms are one of the most evident expressions of permafrost in mountain regions. They are theoretically located between the lower permafrost limit and the equilibrium line of the glaciers, an altitudinal belt well expressed in cold and dry climates that tends to shrink in response to temperature and precipitations increase (Barsch, 1996; Haeberli, 1985). Consequently, rock glaciers gravitate towards continental ranges like the inner Alps, even though the relative contribution of debris and snow at topoclimatic scale seems to have a major role in driving their distribution rather than regional climate itself (Humlum, 1998). Ice deformation gives rock glaciers a creep movement similar to that of glaciers but slower (generally less than 1 m/y). There are three types of rock glaciers depending on dynamic and ice presence: active (with ice and creeping, located in contexts compatible with permafrost); inactive (with ice, but static for climatic or geomorphological reasons); relict (iceless and static, found in conditions no more compatible with permafrost and linked to past climate conditions) (Barsch, 1996; Haeberli, 1985).

In the last decade, rock glaciers have drawn the attention of ecologists and botanists. Indeed, these landforms host communities adapted to harsh ecological conditions and are supposed to assume a biogeographical role in relation with climatic variations. In the matter of that, rock glaciers were proposed as potential refugia for high alpine plants and animals during the warm stages of the Holocene, as consequence of their microclimate and thermal inertia (Gentili *et al*., 2015; Gobbi *et al*., 2014; Millar & Westfall, 2010; Millar *et al*., 2013), a role similar to that already hypothesized for debris-covered glaciers (Caccianiga *et al*., 2011; Gentili *et al*., 2015; Gobbi *et al*., 2011).

Previous knowledge about the vegetation of alpine rock glaciers come from the studies of Cannone & Gerdol (2003) in the area of Livigno-Bormiese (Central Italian Alps) and Burga *et al*. (2004) in the area of Piz Corvatsch (Switzerland). These authors reported pioneer communities generally attributable to the order *Androsacetalia alpinae* (associations *Sieversio-Oxyrietum digynae* and *Androsacetum alpinae* following Burga *et al*., 2004), with plants adapted to mechanical disturbance also recurring on scree slopes, glacier forelands and recent moraines. Vegetation cover and floristic composition depend mainly on substrate particle-size and movement intensity. Active rock glaciers are almost unvegetated, with sporadic glareicolous plants concentrated overall in the peripheral zones, where the surface movement is slower

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and fine-grained material is available. Instead, inactive and relict rock glaciers tend to be colonized by the typical species of alpine grasslands and snow-patches communities, or even by subalpine shrubs and trees at lower elevations. Rieg *et al.* (2012), analyzing four active rock glaciers in Stubai and Ötztal Alps (Tyrol, Austria), found a threshold of 1,5 m/y for surface velocity: below this value plants cover depends on fine-grain availability, while over that limit the vegetation is heavily affected by ground instability. Coherently, Gobbi *et al.* (2014) identify grain-size as main driver of species distribution, highlighting the correlation with organic matter availability. In the same paper, the thermal regime of rock glacier was analyzed and evaluated as further limiting factor in plant colonization.

However, the vegetation features of alpine rock glaciers deserve further researches, since the few available studies concern only silicate substrates and the comparison with other high alpine landforms were not always in-depth analyzed. Our aim was to describe the vegetation of two active rock glaciers on different substrates (silicate and carbonate) and compare them with the neighboring stable slopes and scree slopes. Two hypothesis were tested: 1) rock glaciers differ from the surrounding landforms for the presence of cold-adapted plant communities; 2) rock glacier plant communities indicate similar microclimatic conditions in spite of the contrasting lithology.

Study area

The analyzed rock glaciers are located in two valleys belonging to the Ortles-Cevedale Massif (II/C-28.I-A in Marazzi, 2005), within the area of Stelvio National Park (Italy): Val d'Ultimo and Valle del Braulio. The sites are less than 32 km apart and no geographical barriers occurs between them, so they can be considered part of the same floristic context (Northeastern Alps subsection in Blasi *et al.*, 2015).

Val d'Ultimo (South Tyrol) is a NE-SW oriented valley extended from the basin of Merano to the Giogo Nero pass. The examined rock glacier ("Lago Lungo"; 46° 27.435' N, 10° 48.985' E) (fig. 1a) is located in the Group of Gioveretto-Sternai (II/C-28.I-A.3.c in Marazzi, 2005). It is a multilobe tongue-shaped rock glacier fed by acid silicate debris (micaschist and ortogneiss of "Unità di Pejo") that leans against a NW-facing slope between 2350 and 2550 m a.s.l. The surrounding areas are characterized by widespread and well-expressed periglacial landforms, while the glacial masses are few and small. (Artoni, 1992; Martin *et al.*, 2009; Seppi *et al.*, 2005).

Valle del Braulio (Lombardy) is a SW-NE oriented valley extended from the basin of Bormio to the Stelvio Pass. The examined rock glacier ("Vedrettino"; 46° 30.025' N, 10° 24.050' E) (fig. 1b) is located in the Group of Cristallo (II/C-28.I-A.1.a in Marazzi, 2005). It is a multilobe tongue-shaped rock glacier fed by carbonate debris (dolomite limestones of "Dolomia Principale") that lies in a NW-facing glacial cirque, between 2500 and 2650 m a.s.l. The site is surrounded by imposing talus and until the first decades of 20th century was occupied by the namesake glacier, now reduced to a little mass of dead-ice completely debris-covered (Artoni, 1992; Bonardi *et al.*, 2012; Montrasio *et al.*, 2012).

Since the examined landforms stand at comparable elevation with similar values of aspect and slope, the main ecological difference between them lies in the bedrock. Temperatures and precipitations within the period 1983-2012 were analyzed using the records provided by Meteo Service of the Province of Bolzano for Val d'Ultimo (station of Fontana Bianca, 1900 m a.s.l.) (fig. 2a) and ARPA Lombardia for Valle del Braulio (station of Bormio, 1225 m a.s.l.) (fig. 2b). Calculating the Rivas-Martinez Index of thermal continentality (Rivas-Martínez & Rivas-Saenz, 1996-2009) and the Gams Index of hygric continentality (Ozenda, 1985), both areas results characterized by the typical continental climate of the inner Alps (respectively: 27,37 and 60,96° for Val d'Ultimo and 25,41 and 58,00° for Valle del Braulio).

Methods

Data were collected between July and August 2014. 80 vegetation relevés were performed by phytosociological method with the Braun-Blanquet scale as modified by Pignatti (1952) on three landforms for each area: stable slope (soil without ice), scree slope (debris without ice) and rock glacier (debris with ice). All the relevés were performed on 25 m^2 surfaces. Such value allows a homogeneous and representative sampling of the main object of our research, glareicolous vegetation of rock glaciers and scree slopes. On alpine grasslands, the micro-topographic pattern causes floristic variability at small (few centimeters) scale. Such variability, intrinsic of these communities, could be overlooked by our sampling strategy: for this reason, we performed a high-rank phytosociological outline of these communities. Relevés were compared by a cluster analysis based on the presence/absence species matrix, using the UPGMA method with Jaccard dissimilarity index. The conventional dissimilarity value of 0,75 was assumed as lower threshold for the admission of an association, according to Mueller-Dombois & Ellenberg (1974). Species relative frequencies for each landform, regardless the clustering, were calculated and gathered in 5 frequency classes with resolution of 20%. We also compared our data with that collected in the previous studies (Burga *et al.*, 2004; Cannone & Gerdol, 2003; Gobbi *et al.*, 2014; Rieg *et al.*, 2012).

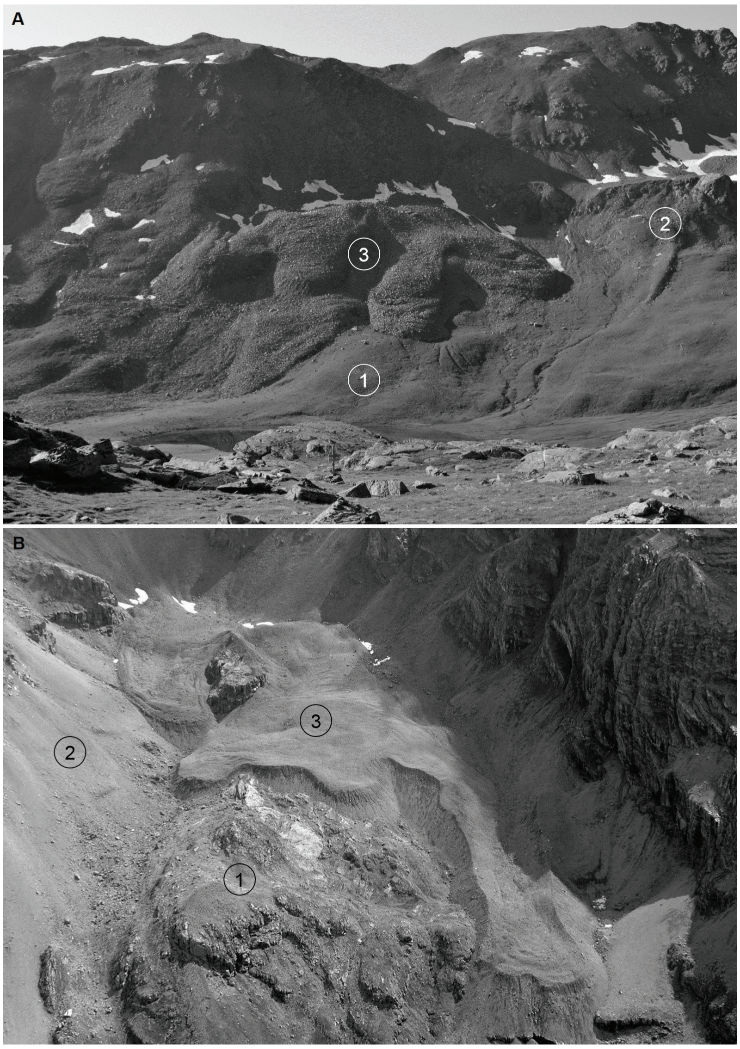

Fig. 1 - Rock glaciers “Lago Lungo” in Val d’Ultimo (A) and “Vedrettino” in Valle del Braulio (B). The landforms are indicated as follows: 1) stable slope, 2) scree slope, 3) rock glacier.

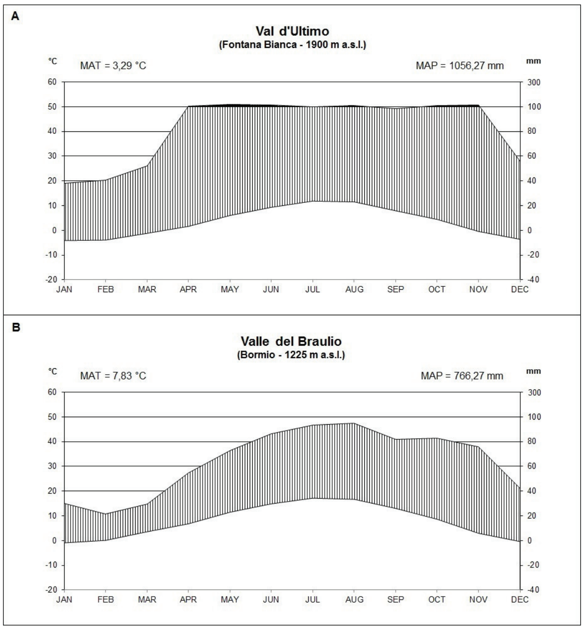

Fig. 2 - Climograms of Fontana Bianca for Val d’Ultimo (A) and Bormio for Valle del Braulio (B).

The nomenclature follows Landolt *et al*. (2010) for species and Grabherr & Mucina (1993) for syntaxa. The phytosociological interpretation generally agrees with Grabherr & Mucina (1993) and Oberdorfer (1977), adjusted for some local peculiarities following Giacomini & Pignatti (1955).

Results

We identified 118 vascular plant species in total. 71 plant species were found both in Val d’Ultimo and Valle del Braulio (47 mutually exclusive and 24 shared). It was possible to describe five clusters with dissimilarity index > 0,75 (fig. 3). The main dichotomy detected by cluster analysis was the one between the two investigated sites, afterwards the landforms were differently discerned each other depending on the site. Concerning Val d’Ultimo, the dendrogram separated at first the stable slope from the remaining landforms, but inside the latter group another partition between rock glacier and scree slope was well recognizable. Concerning Valle del Braulio, the cluster analysis distinguished only stable slopes, without a clear split between rock glacier

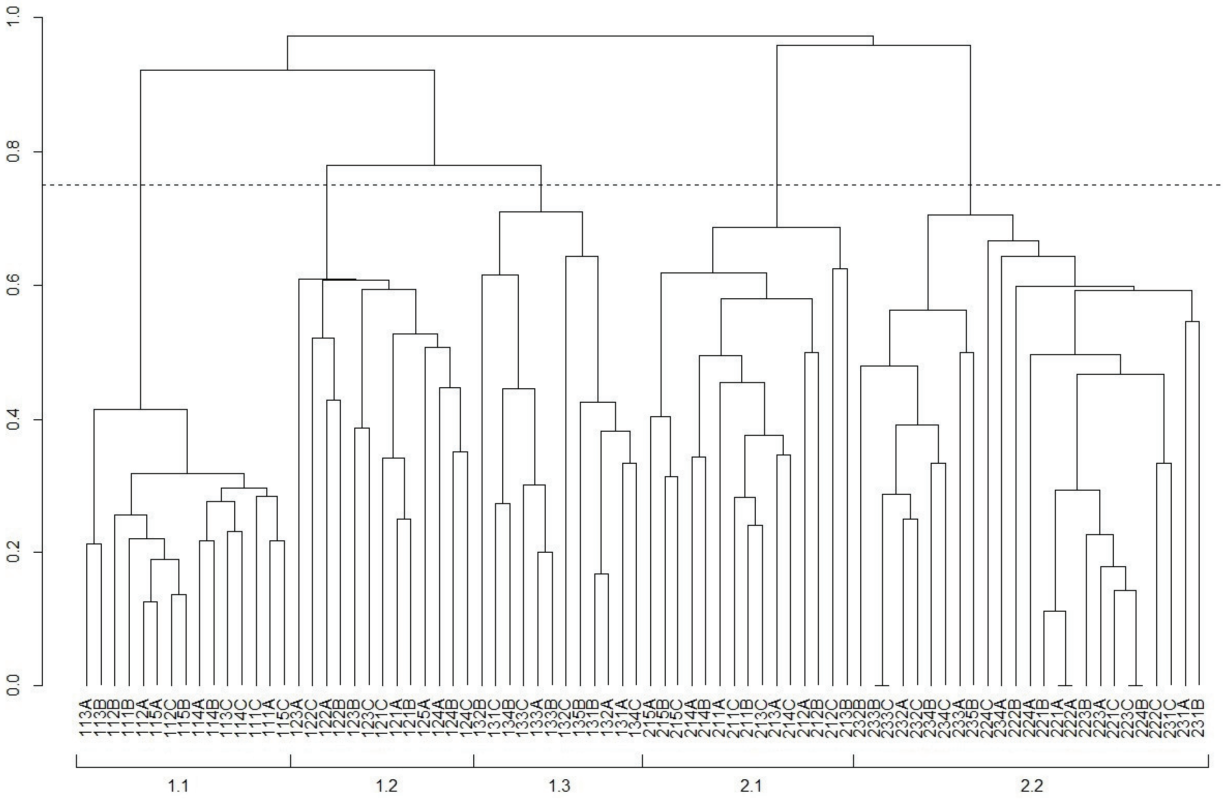

Fig. 3 - Dendrogram resulting from the cluster analysis of relevés. The dotted line indicates the dissimilarity value of 0,75.

and scree slope. Data are reported in the analytic table (tab. 1) and the synoptic table (tab. 2).

Cluster 1.1: stable slope on silicate substrate

The stable slope of Val d'Ultimo (fig. 4) is a seamless patchwork of humps and hollows covered by a continuous alpine grassland. *Carex curvula* and A*nthoxanthum alpinum* dominate the community, with a scarce shrubby layer of *Loiseleuria procumbens*, *Vaccinium gaultherioides* and *Rhododendron ferrugineum*. Locally, canopy overlapping may be quite high and species like *Potentilla aurea*, *Leontodon helveticus*, *Ligusticum mutellina*, *Homogyne alpina* and *Soldanella alpicola* can reach remarkable cover values. The micro-topographic pattern at centimeter scale allows the coexistence of hummock species (e.g. *Loiseleuria procumbens* and *Vaccinium gaultherioides*) and snowbed elements (e.g. *Primula glutinosa* and *Gnaphalium supinum*). Such situation made difficult a phytosociological outline at the association level, but the community could be ascribed to the alliance *Caricion curvulae* Br.-Bl. in Br.-Bl. et Jenny 1926.

Fig. 4 - *Caricion curvulae* on the stable slope of Val d'Ultimo (cluster 1.1).

Cluster 1.2: scree slope on silicate substrate

The scree slope of Val d'Ultimo (fig. 5) includes a wide range of particle size and hosts a scattered glareicolous vegetation rather rich in species. Among the preferential elements, *Geum reptans*, *Oxyria digyna*, *Saxifraga seguieri*, *Saxifraga oppositifolia*, *Silene acaulis* and *Pritzelago brevicaulis* are the most frequent. *Luzula alpino-pilosa*, *Poa laxa*, *Saxifraga bryoides* and *Cerastium uniflorum* are likewise widespread and abundant, but all shared with the cluster 1.3. Species assemblage is ascribable to the association *Sieversio-Oxyrietum digynae* Friedel 1956 em. Englisch *et al.* 1993 for the dominance and constancy of *Geum reptans* and *Oxyria dygina*. Some element of

Fig. 5 - *Sieversio-Oxyrietum digynae* with *Geum reptans* and *Oxyria digyna* on the scree slope of Val d'Ultimo (cluster 1.2).

Salicetea herbaceae Br.-Bl. in Br.-Bl. et Jenny 1926 like *Soldanella alpicola*, *Sedum alpestre* and *Veronica alpina* are also present where fine-grained material is available.

Cluster 1.3: rock glacier on silicate substrate

On the rock glacier of Val d'Ultimo (fig. 6) vegetation changes notably depending on geomorphological situation, with few species occurring with high frequency: *Luzula alpino-pilosa*, *Poa laxa*, *Saxifraga bryoides*, *Cerastium uniflorum* and *Doronicum clusii*. Plant cover on the surface is mainly represented by sporadic individuals growing among coarse boulders, or patches of herbaceous vegetation on pockets of fine-grained substrate (relevés 131A, 131B, 131C, 132A, 132C, 134B, 134C, 135B). On the slopes and the edges, the vegetation is more rich and dense, probably in response to higher stability and presence of fine-grained material. In these zones, the above mentioned assemblage includes some typical element of the stable environments, as *Carex curvula*, *Agrostis rupestris*, *Festuca halleri*, *Campanula scheuchzeri*, *Senecio carniolicus* and *Erigeron uniflorus*, locally accompanied by *Rhododendron ferrugineum* and *Salix serpyllifolia* (relevés 132B, 133A, 133B, 133C). The community is roughly attributable to the alliance *Androsacion alpinae* Br.-Bl. in Br.-Bl. et Jenny 1926, with low frequency of species belonging to *Caricetea curvulae* Br.-Bl. 1948 and *Salicetea herbaceae* Br.-Bl. in Br.-Bl. et Jenny 1926, while the characteristic elements of *Sieversio-Oxyrietum digynae* are totally absent.

Fig. 6 - Community with *Luzula-alpino pilosa* and *Doronicum clusii* on the rock glacier of Val d'Ultimo (cluster 1.3).

Cluster 2.1: stable slope on carbonate substrate

The stable slope of Valle del Braulio (fig. 7) is colonized by a fragmented alpine grassland alternated with outcrops and debris, locally interrupted by ample hollows. The community is dominated by *Carex firma*, *Sesleria caerulea* and *Dryas octopetala*, with a conspicuous group of low-covering exclusive species: *Saxifraga caesia*, *Agrostis alpina*, *Carex ornithopoda*, *Minuartia verna*, *Helianthemum alpestre*, *Anthyllis vulneraria*, *Draba aizoides*, *Sedum atratum*, *Polygonum viviparum*, *Aster bellidiastrum*, *Bartsia alpina*, ecc. Such plant assemblage is ascribable to the alliance *Caricion firmae* Gams 1936 (relevés 211A, 211B, 212A, 212B, 212C, 213A, 213B, 213C). In the depressions, the above mentioned species sharply decrease and are replaced by high cover of *Silene acaulis*, *Ranunculus alpestris* and *Soldanella alpina*, with *Gnaphalium hoppeanum* and other sporadic species of *Arabidion caeruleae* Br.-Bl. in Br.-Bl. et Jenny 1926 (relevés 214A, 214B, 215A, 215B, 215C and to a lesser extent 211C, 214C).

Fig. 7 - *Caricion firmae* on the stable slope of Valle del Braulio (cluster 2.1).

Cluster 2.2: scree slope and rock glacier on carbonate substrate

On the unstable substrates of Valle del Braulio, plant cover is scarce or absent, with isolated individuals even where fine-grained material is available. Even though two clusters are recognizable, their dissimilarity index is < 0,75 and the lack of a clear distinction between scree slope and rock glacier brings us to attribute the whole community to the same association: *Papaveretum rhaetici* Wikus 1959. The two landform are joined by the constant presence of *Poa minor*, *Arabis alpina* and *Arabis pumila*, but the relative frequency of other species shows some difference. The scree slope (fig. 8) is colonized by a well-expressed *Papaveretum rhaetici*, where *Papaver aurantiacum*, *Saxifraga aphylla*, *Pritzelago alpina* and *Moehringia ciliata* are widespread (relevés 221A, 221B, 221C, 222A, 222B, 222C, 223A, 223B, 223C, 224A, 224B, 224C). The rock glacier (fig. 9) shows a lower frequency and abundance of these elements and is better characterized by the exclusive coexistence of *Arabis caerulea* and *Saxifraga oppositifolia*, both rare on stable slope and scree slope respectively (relevés 232A, 232B, 232C, 233A, 233B, 233C, 234B, 234C, 235B). Species richness reaches the highest values on the peripheral zones of the rock glacier, where the elements of both aspects equally coexist (relevés 231A, 231B, 231C and to a lesser extent 234A).

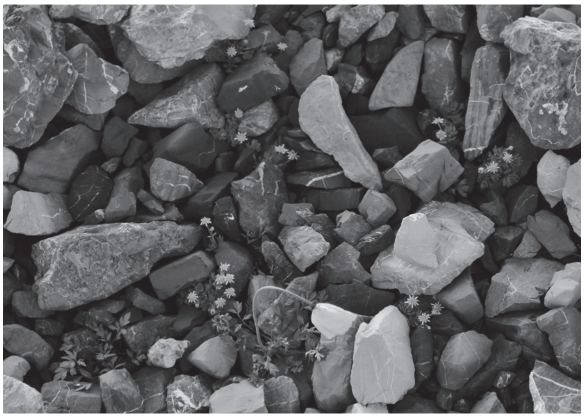

Fig. 8 - *Papaveretum rhaetici* with *Papaver aurantiacum* and *Saxifraga aphylla* on the scree slope of Valle del Braulio (cluster 2.2).

Fig. 9 - *Papaveretum rhaetici* with *Arabis caerulea* and *Saxifraga oppositifolia* on the rock glacier of Valle del Braulio (cluster 2.2).

Discussion

The nature of the bedrock appears to be the main factor influencing floristic composition of the studied landforms. Cluster analysis clearly grouped relevés as a function of the study site rather than of the different landforms. Being our study sites very close to each other, without geographical barrier between them and located at similar elevation, aspect and slope, the different floristic composition can be attributed to the different substrate. The landforms could be discriminated only within each site, with stable slopes always clearly different from scree slopes and rock glaciers.

Particularly interesting is the comparison between scree slopes and rock glaciers, environments similar to each other but except for the occurrence of ice. In Val d'Ultimo the difference between these two landforms emerges at the community level, with *Sieversio-Oxyrietum digynae* on the scree slope and an *Androsacion alpinae* community on the rock glacier. The latter looks like a transition toward the association *Luzuletum spadiceae* Rübel 1911 (class *Salicetea herbaceae*) for the dominance of *Luzula alpino-pilosa* and the elective presence of *Doronicum clusii*, even though the scarcity of characteristic species of the class make this collocation uncertain. *Luzuletum spadiceae* is strictly linked to silicate coarse substrates at high elevation, and is considered as an indicator of low temperatures during the whole year and snow permanence up to 8-9 months (Giacomini & Pignatti, 1955; Grabherr & Mucina, 1993; Oberdorfer, 1977). In summary, the community detected on the rock glacier could be interpreted either as an *Androsacion alpinae* conditioned by cold-moist microclimate and long-lasting snow cover or as a species-poor aspect of *Luzuletum spadiceae* where the elements of *Salicetea herbaceae* are limited by the unavailability of fine-grained substrate. However, both cases implicate the crucial role of microclimate in determining this plant assemblage. This result contrasts with the previous studies on silicate rock glaciers (Burga *et al*., 2004; Cannone & Gerdol, 2003; Gobbi *et al*., 2014; Rieg *et al*., 2012), where the high frequencies of *Oxyria digyna* and *Geum reptans* and the lack of *Luzula alpino-pilosa* and *Doronicum clusii* allow the attribution of the vegetation cover to *Oxyrietum digynae*. A better knowledge of the whole vegetation contest of these rock glaciers, including the surrounding landforms, is necessary for an ecological interpretation of such difference.

Concerning Valle del Braulio, the communities of scree slope and rock glacier are very similar and both attributable to *Papaveretum rhaetici*, but some floristic difference emerges analyzing the distribution of single species. Particularly interesting is the exclusive coexistence of *Arabis caerulea* and *Saxifraga oppositifolia* on the rock glacier, a plant assemblage to our

Tab. 2 - Synoptic table of mean relevés values and species frequency classes for each landform (I = 1-20%, II = 21-40%, III = 41-60%, IV = 61-80%, V = 81-100%).

Val d'Ultimo	Stable slope	Scree slope	Rock glacier	Valle del Braulio	Stable slope	Scree slope	Rock glacier
Shrubs cover (%)	11	0	3	**Shrubs cover (%)**	1	0	0
Herbaceous cover (%)	70	15	15	**Herbaceous cover (%)**	65	5	2
Bryophytes and lichens cover (%)	12	4	4	**Bryophytes and lichens cover (%)**	6	0	0
Outcrop cover (%)	16	4	0	**Outcrop cover (%)**	7	4	0
Debris cover (%)	0	77	76	**Debris cover (%)**	18	91	98
Soil cover (%)	0	0	2	**Soil cover (%)**	7	0	0
Species richness	23	17	10	**Species richness**	23	7	8
Loiseleuria procumbens	V			*Agrostis alpina*	V		
Potentilla aurea	V			*Carex firma*	V		
Primula glutinosa	V			*Dryas octopetala*	V		
Vaccinium gaultherioides	V			*Polygonum viviparum*	V		
Helictotrichon versicolor	IV			*Sedum atratum*	V		
Geum montanum	II			*Bartsia alpina*	IV		
Hieracium glanduliferum	II			*Minuartia verna*	IV		
Huperzia selago	II			*Sesleria caerulea*	IV		
Nardus stricta	II			*Anthyllis vulneraria*	III		
Alchemilla vulgaris aggr.	I			*Carex ornithopoda*	III		
Bartsia alpina	I			*Draba aizoides*	III		
Calluna vulgaris	I			*Helianthemum alpestre*	III		
Cirsium spinosissimum	I			*Carex parviflora*	II		
Diphasiastrum alpinum	I			*Gentiana verna*	II		
Juniperus nana	I			*Leontodon helveticus*	II		
Larix decidua	I			*Myosotis alpestris*	II		
Luzula lutea	I			*Pinguicula alpina*	II		
Pinguicula leptoceras	I			*Salix herbacea*	II		
Selaginella selaginoides	I			*Salix reticulata*	II		
Sibbaldia procumbens	I			*Selaginella selaginoides*	II		
Pedicularis kerneri	I	II		*Silene acaulis*	II		
Gnaphalium supinum	IV	II		*Valeriana saxatilis*	II		
Poa alpina	V	II		*Arenaria biflora*	I		
Polygonum viviparum	V	II		*Crepis kerneri*	I		
Ligusticum mutellina	V	I		*Cystopteris fragilis*	I		
Oreochloa disticha	I	I		*Daphne striata*	I		
Silene exscapa	I	V		*Euphrasia minima*	I		
Geum reptans		V		*Gentiana bavarica*	I		
Oxyria digyna		V		*Gentiana engadinensis*	I		
Saxifraga oppositifolia		IV		*Globularia cordifolia*	I		
Saxifraga seguieri		IV		*Hieracium bifidum*	I		
Pritzelago brevicaulis		III		*Hieracium villosum*	I		
Arabis alpina		II		*Juniperus nana*	I		
Artemisia genipi		II		*Larix decidua*	I		
Ranunculus glacialis		II		*Ligusticum mutellina*	I		
Taraxacum alpinum s. l.		II		*Poa alpina*	I		
Androsace alpina		I		*Potentilla brauneana*	I		
Cryptogramma crispa		I		*Saxifraga hostii*	I		
Linaria alpina		I		*Vaccinium gaultherioides*	I		
Saxifraga androsacea		I		*Veronica aphylla*	I		
Saxifraga paniculata		I		*Asplenium viride*	III	I	
Saxifraga bryoides		V	V	*Homogyne alpina*	III	I	
Cerastium uniflorum		V	IV	*Aster bellidiastrum*	IV	I	
Poa laxa		IV	V	*Cerastium latifolium*		I	
Doronicum clusii		II	V	*Festuca quadriflora*		I	
Saxifraga exarata		II	II	*Salix retusa*		I	
Myosotis alpestris		II	I	*Saxifraga aizoides*		I	
Cystopteris fragilis		II	I	*Cerastium uniflorum*		III	II
Lloydia serotina		I	I	*Saxifraga aphylla*		V	I
Sempervivum montanum		I	I	*Papaver aurantiacum*		V	II
Senecio carniolicus		I	III	*Arabis alpina*		V	V
Erigeron uniflorus			II	*Saxifraga oppositifolia*		II	V
Gentiana verna			I	*Leucanthemopsis alpina*			I
Anthoxanthum alpinum	V		I	*Linaria alpina*			I
Carex curvula	V		I	*Carex rupestris*	I		I
Leontodon helveticus	V		I	*Pinus mugo*	I		I
Euphrasia minima	V		I	*Veronica alpina*	I		I
Phyteuma hemisphaericum	IV		I	*Arabis caerulea*	II		IV
Campanula scheuchzeri	I		II	*Gnaphalium hoppeanum*	II		I
Agrostis rupestris	V	III	III	*Erigeron uniflorus*	III		I
Cardamine resedifolia	I	III	III	*Soldanella alpina*	III		I
Festuca halleri	I	I	III	*Ranunculus alpestris*	V		I
Homogyne alpina	V	I	I	*Salix serpillifolia*	V		II
Leucanthemopsis alpina	IV	I	III	*Achillea atrata*	IV	I	I
Luzula alpinopilosa	II	V	V	*Arabis pumila*	II	V	IV
Rhododendron ferrugineum	V	I	I	*Campanula cochleariifolia*	III	I	I
Salix herbacea	V	II	I	*Moehringia ciliata*	I	III	II
Salix serpillifolia	I	I	I	*Poa minor*	I	V	V
Sedum alpestre	I	IV	II	*Pritzelago alpina*	I	V	II
Soldanella alpicola	V	IV	I	*Saxifraga caesia*	V	I	II
Veronica alpina	I	IV	I	*Taraxacum alpinum s. l.*	II	I	II
Total species richness	45	43	30	**Total species richness**	60	20	24

knowledge never evaluated before within *Thlaspietalia rotundifolii*. *Arabis caerulea* is the characteristic species of *Arabidetum caeruleae* Br.-Bl. 1918, typical of snowbeds on carbonate substrates (Giacomini & Pignatti, 1955; Grabherr & Mucina, 1993; Oberdorfer, 1977). *Saxifraga oppositifolia* is a glareicolous plant widespread on many different substrates, provided the suitable elevation (Aeschimann *et al*., 2004; Landolt *et al*., 2010; Pignatti, 1982; Webb & Gornall, 1989). Although the syntaxonomical interpretation of these species could be unclear, their ecological information appears evident, since both find their optimum in cold and moist habitats typical of the nival belt. In our case the presence of *Arabis caerulea* and *Saxifraga oppositifolia* was not sufficient to discriminate a well-defined community, but collecting data from further carbonate sites, it would be probably possible to formalize a new variant of the association *Papaveretum rhaetici* Wikus 1959 differentiated by these species as plausible indicators of cold and moist microclimates.

Therefore, in spite of the remarkable floristic differences due to the substrate, the vegetation of both rock glaciers suggest a general adjustment to cold-moist microclimate and long-lasting snow cover, differentiating more or less evidently from the adjacent scree slopes and enhancing the survival of nival entities at the elevation of alpine grasslands. The role of microclimatic heterogeneity in matter of refugia is more and more acknowledged (Ashcroft *et al*., 2012; Birks & Willis, 2008; Dobrowski 2011; Rull, 2009; Stewart *et al*., 2010). Active rock glaciers seem to increase the environmental variability between alpine and nival belts at the landscape level, providing potential warm-stage refugia for cold-adapted species. Our observations may thus establish a basis for further researches about rock glaciers plant communities, focused on the ecological and biogeographical significance of these landforms in the global change context.

Syntaxonomic scheme

THLASPIETEA ROTUNDIFOLII Br.-Bl. 1948
THLASPIETALIA ROTUNDIFOLII Br.-Bl. in Br.-Bl. et Jenny 1926
Thlaspion rotundifolii Jenny-Lips 1930
Papaveretum rhaetici Wikus 1959
ARABIDETALIA CAERULEAE Rübel ex Br.-Bl. 1948
Arabidion caeruleae Br.-Bl. in Br.-Bl. et Jenny 1926
ANDROSACETALIA ALPINAE Br.-Bl. in Br.-Bl. et Jenny 1926
Androsacion alpinae Br.-Bl. in Br.-Bl. et Jenny 1926
Sieversio-Oxyrietum digynae Friedel 1956 em. Englisch *et al*. 1993

CARICETEA CURVULAE Br.-Bl. 1948
CARICETALIA CURVULAE Br.-Bl. in Br.-Bl. et Jenny 1926
Caricion curvulae Br.-Bl. in Br.-Bl. et Jenny 1926

SALICETEA HERBACEAE Br.-Bl. 1948
SALICETALIA HERBACEAE Br.-Bl. in Br.-Bl. et Jenny 1926
Salicion herbaceae Br.-Bl. in Br.-Bl. et Jenny 1926
Salicetum herbaceae Rübel 1911
Luzuletum spadiceae Rübel 1911

SESLERIETEA ALBICANTIS Oberd. 1978 corr. Oberd. 1990
SESLERIETALIA COERULEAE Br.-Bl. in Br.-Bl. et Jenny 1926
Caricion firmae Gams 1936

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Tab. 1 - Analytic table of relevés.

Cluster	1.1														
Code	113A	113B	112B	111B	112A	115A	112C	115B	114A	114B	113C	114C	111C	111A	115C
Date	07.08.2014	07.08.2014	07.08.2014	06.08.2014	07.08.2014	21.08.2014	07.08.2014	21.08.2014	21.08.2014	21.08.2014	07.08.2014	21.08.2014	06.08.2014	06.08.2014	21.08.2014
Coordinates	N46 27.567 E10 48.805	N46 27.572 E10 48.808	N46 27.541 E10 48.821	N46 27.522 E10 48.848	N46 27.545 E10 48.827	N46 27.582 E10 48.863	N46 27.533 E10 48.823	N46 27.587 E10 48.870	N46 27.625 E10 48.830	N46 27.628 E10 48.842	N46 27.578 E10 48.813	N46 27.632 E10 48.851	N46 27.521 E10 48.841	N46 27.517 E10 48.846	N46 27.595 E10 48.875
Area	Ultimo	Ultimo	Ultimo	Ultimo	Ultimo	Ultimo	Ultimo	Ultimo	Ultimo	Ultimo	Ultimo	Ultimo	Ultimo	Ultimo	Ultimo
Landform	Stable slope	Stable slope	Stable slope	Stable slope	Stable slope	Stable slope	Stable slope	Stable slope	Stable slope	Stable slope	Stable slope	Stable slope	Stable slope	Stable slope	Stable slope
Elevation (m a.s.l.)	2380	2380	2390	2415	2390	2380	2395	2380	2365	2365	2380	2360	2415	2415	2375
Aspect (°)	280	290	305	330	305	315	310	330	320	320	315	340	315	340	340
Slope (°)	20	25	15	20	15	10	20	10	20	20	25	20	20	15	20
Shrubs cover (%)	10	5	<5	5	5	10	5	10	5	15	35	25	15	10	5
Herbaceous cover (%)	70	70	85	75	75	70	75	65	85	65	50	55	70	70	70
Bryophytes and lichens cover (%)	10	10	15	5	10	10	10	10	20	20	30	10	5	5	10
Outcrop cover (%)	15	25	15	15	20	20	20	20	10	20	5	10	10	15	20
Debris cover (%)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Soil cover (%)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Species richness	27	33	19	23	22	23	20	21	21	21	24	22	20	22	20
Differential of stable slope on silicate substrate															
Anthoxanthum alpinum	1	1	2	1	2	1	2	1	1	1	1	1	2	2	1
Geum montanum	+	+	.	+	.	.	+	+	.	.	.	.	.	.	.
Nardus stricta	.	.	1	+	1	+	+	.	.	.	.	.	.	.	.
Poa alpina	1	1	+	1	+	1	+	+	1	+	1	.	+	+	+
Rhododendron ferrugineum	1	+	+	+	+	+	+	+	.	+	+	+	+	+	+
Caricion curvulae															
Carex curvula	1	2	1	2	2	1	3	1	2	2	2	2	2	2	2
Festuca halleri	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.
Gnaphalium supinum	+	+	+	+	1	+	+	+	.	.	+	.	+	+	.
Hieracium glanduliferum	.	.	.	.	+	.	.	.	+	+	+	+	.	.	.
Ligusticum mutellina	1	1	1	1	1	1	1	+	+	1	+	+	1	1	1
Loiseleuria procumbens	1	+	+	+	1	1	+	+	1	1	2	1	1	+	.
Oreochloa disticha	.	.	.	.	.	.	.	.	.	.	+	+	.	.	.
Pedicularis kerneri	+	+	.	.	.	.	.	.	.	.	+	.	.	.	.
Primula glutinosa	+	+	+	+	1	+	+	+	+	+	+	1	+	+	+
Senecio carniolicus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Silene exscapa	1	+	.	.	.	.	.	.	.	.	.	.	.	.	+
Vaccinium gaultherioides	+	+	.	+	+	1	1	1	+	1	1	1	1	1	1
Caricetea curvulae e Caricetalia curvulae															
Agrostis rupestris	1	1	+	+	+	1	+	1	1	+	1	1	+	+	1
Euphrasia minima	+	+	+	+	+	+	+	+	+	+	+	+	.	+	+
Helictotrichon versicolor	1	1	+	.	.	+	.	+	1	1	1	+	.	+	+
Huperzia selago	.	+	.	.	.	.	.	.	.	.	+	+	+	+	+
Leontodon helveticus	1	1	+	+	1	+	1	+	+	+	1	+	1	1	+
Leucanthemopsis alpina	+	+	+	+	+	+	+	+	+	.	.	+	.	+	+
Luzula lutea	.	.	.	.	.	+	.	.	.	.	1	.	.	.	.
Phyteuma hemisphaericum	+	+	.	.	+	+	+	+	+	+	+	+	+	.	+
Potentilla aurea	1	1	1	+	+	+	+	+	1	+	+	+	+	+	+
Sieversio-Oxyrietum digynae															
Geum reptans	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Oxyria digyna	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Androsacetalia alpinae and Androsacion alpinae															
Androsace alpina	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Artemisia genipi	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cardamine resedifolia	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.
Poa laxa	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Pritzelago brevicaulis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Ranunculus glacialis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Saxifraga bryoides	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Saxifraga exarata	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Saxifraga seguieri	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Luzuletum spadiceae															
Doronicum clusii	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Luzula alpinopilosa	.	+	.	+	+	+	.	.	+	.	.	.	.	.	.
Salicetea herbaceae, Salicetalia herbaceae and Salicion herbaceae															
Salix herbacea	.	+	+	1	1	+	+	+	+	+	+	+	+	1	+
Sedum alpestre	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.
Soldanella alpicola	1	1	1	1	1	1	1	1	1	1	+	1	+	1	1
Veronica alpina	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.
Differential of stable slope on carbonate substrate															
Asplenium viride	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Erigeron uniflorus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Salix reticulata	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Salix serpyllifolia	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.
Valeriana saxatilis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Caricion firmae															
Carex firma	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Crepis kerneri	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Dryas octopetala	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Helianthemum alpestre	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Saxifraga caesia	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Seslerietea albicantis and Seslerietalia coeruleae															
Agrostis alpina	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Anthyllis vulneraria	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Aster bellidiastrum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Bartsia alpina	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Carex ornithopoda	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Carex rupestris	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Draba aizoides	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Gentiana verna	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Minuartia verna	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Myosotis alpestris	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Selaginella selaginoides	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.
Sesleria caerulea	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Silene acaulis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Veronica aphylla	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Differential of rock glacier on carbonate substrate															
Arabis caerulea	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Saxifraga oppositifolia	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Papaveretum rhaetici															
Arabis pumila	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Moehringia ciliata	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Papaver aurantiacum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Saxifraga aphylla	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Thlaspietalia rotundifolii and Thlaspion rotundifolii															
Achillea atrata	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Campanula cochleariifolia	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Poa minor	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Pritzelago alpina	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Arabidetalia caeruleae and Arabidion caeruleae															
Carex parviflora	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Gentiana bavarica	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Gnaphalium hoppeanum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Ranunculus alpestris	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Soldanella alpina	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Sedum atratum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Thlaspietea rotundifolii															
Arabis alpina	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cerastium uniflorum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Linaria alpina	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Companion species															
Alchemilla vulgaris aggr.	1	+	.	.	.	.	.	.	.	.	.	.	.	.	.
Calluna vulgaris	.	.	.	.	.	.	.	.	+	.	.	.	+	.	.
Campanula scheuchzeri	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.
Cystopteris fragilis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Homogyne alpina	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1
Juniperus nana	.	+	.	+	.	.	.	.	.	.	.	+	.	.	.
Larix decidua	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.
Lloydia serotina	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Pinguicula alpina	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Pinus mugo	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Polygonum viviparum	+	+	.	+	+	+	.	+	+	+	+	+	+	+	+
Sempervivum montanum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Taraxacum alpinum s. l.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Sporadic species															
Arenaria biflora	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cerastium latifolium	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cirsium spinosissimum	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.
Cryptogramma crispa	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Daphne striata	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Diphasiastrum alpinum	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.
Festuca quadriflora	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Gentiana engadinensis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Globularia cordifolia	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hieracium bifidum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hieracium villosum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Pinguicula leptoceras	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.
Potentilla brauneana	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Salix retusa	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Saxifraga aizoides	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Saxifraga androsacea	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Saxifraga hostii	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Saxifraga paniculata	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Sibbaldia procumbens	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.

Cluster	1.2												
Code	123A	122C	122A	122B	123B	123C	121C	121A	121B	125A	124A	124B	124C
Date	07.08.2014	06.08.2014	06.08.2014	06.08.2014	07.08.2014	07.08.2014	06.08.2014	06.08.2014	06.08.2014	07.08.2014	07.08.2014	07.08.2014	07.08.2014
Coordinates	N46 27.334 E10 48.749	N46 27.329 E10 48.696	N46 27.321 E10 48.679	N46 27.325 E10 48.687	N46 27.329 E10 48.747	N46 27.325 E10 48.754	N46 27.336 E10 48.642	N46 27.326 E10 48.657	N46 27.330 E10 48.651	N46 27.369 E10 48.827	N46 27.328 E10 48.789	N46 27.330 E10 48.797	N46 27.334 E10 48.808
Area	Ultimo	Ultimo	Ultimo	Ultimo	Ultimo	Ultimo	Ultimo	Ultimo	Ultimo	Ultimo	Ultimo	Ultimo	Ultimo
Landform	Scree slope	Scree slope	Scree slope	Scree slope	Scree slope	Scree slope	Scree slope	Scree slope	Scree slope	Scree slope	Scree slope	Scree slope	Scree slope
Elevation (m a.s.l.)	2520	2490	2490	2490	2525	2530	2470	2475	2470	2485	2530	2525	2530
Aspect (°)	325	315	315	315	340	340	310	310	310	355	350	345	330
Slope (°)	35	35	35	35	40	40	15	30	20	35	40	40	30
Shrubs cover (%)	0	0	0	0	0	5	<5	0	0	0	0	0	0
Herbaceous cover (%)	10	20	15	10	20	20	15	15	15	10	10	20	20
Bryophytes and lichens cover (%)	0	5	0	5	5	5	5	5	5	0	5	5	5
Outcrop cover (%)	0	0	0	0	0	25	0	0	0	0	0	10	15
Debris cover (%)	90	75	85	85	75	50	80	80	80	90	85	65	60
Soil cover (%)	0	0	0	0	0	0	0	0	0	0	0	0	0
Species richness	8	18	20	13	22	22	19	16	20	13	13	17	16
Differential of stable slope on silicate substrate													
Anthoxanthum alpinum	.	.	.	.	.	.	.	.	.	.	.	.	.
Geum montanum	.	.	.	.	.	.	.	.	.	.	.	.	.
Nardus stricta	.	.	.	.	.	.	.	.	.	.	.	.	.
Poa alpina	.	.	.	.	+	+	.	.	+	.	.	.	.
Rhododendron ferrugineum	.	.	.	.	.	.	+	.	.	.	.	.	.
Caricion curvulae													
Carex curvula	.	.	.	.	.	.	.	.	.	.	.	.	.
Festuca halleri	.	+	.	.	.	+	.	.	.	.	.	.	.
Gnaphalium supinum	.	.	.	.	.	.	+	+	+	+	.	.	.
Hieracium glanduliferum	.	.	.	.	.	.	.	.	.	.	.	.	.
Ligusticum mutellina	.	.	1	.	.	.	.	.	.	.	.	.	.
Loiseleuria procumbens	.	.	.	.	.	.	.	.	.	.	.	.	.
Oreochloa disticha	.	.	.	.	.	.	.	.	.	.	+	.	.
Pedicularis kerneri	.	+	.	.	.	+	.	.	+	.	.	.	.
Primula glutinosa	.	.	.	.	.	.	.	.	.	.	.	.	.
Senecio carniolicus	.	.	.	.	.	.	.	.	.	+	.	.	+
Silene exscapa	+	+	+	.	+	1	+	+	+	+	+	+	1
Vaccinium gaultherioides	.	.	.	.	.	.	.	.	.	.	.	.	.
Caricetea curvulae e Caricetalia curvulae													
Agrostis rupestris	.	.	.	.	+	+	+	+	+	.	.	+	+
Euphrasia minima	.	.	.	.	.	.	.	.	.	.	.	.	.
Helictotrichon versicolor	.	.	.	.	.	.	.	.	.	.	.	.	.
Huperzia selago	.	.	.	.	.	.	.	.	.	.	.	.	.
Leontodon helveticus	.	.	.	.	.	.	.	.	.	.	.	.	.
Leucanthemopsis alpina	.	.	.	.	.	.	.	.	.	.	+	.	.
Luzula lutea	.	.	.	.	.	.	.	.	.	.	.	.	.
Phyteuma hemisphaericum	.	.	.	.	.	.	.	.	.	.	.	.	.
Potentilla aurea	.	.	.	.	.	.	.	.	.	.	.	.	.
Sieversio-Oxyrietum digynae													
Geum reptans	1	+	+	+	1	+	+	1	+	.	.	1	1
Oxyria digyna	+	+	+	+	1	1	1	1	1	+	1	1	1
Androsacetalia alpinae and Androsacion alpinae													
Androsace alpina	.	.	.	.	.	+	+	.	.	.	.	.	.
Artemisia genipi	.	.	+	.	+	+	.	.	.	.	.	.	.
Cardamine resedifolia	.	+	+	+	+	.	.	+	+	.	.	+	.
Poa laxa	+	+	+	+	+	+	.	.	.	+	+	+	+
Pritzelago brevicaulis	.	+	.	.	+	+	.	+	+	.	.	+	.
Ranunculus glacialis	.	+	.	.	+	+	.	.	.	+	.	+	.
Saxifraga bryoides	+	1	+	1	+	.	+	+	+	.	+	+	+
Saxifraga exarata	.	+	.	+	+	+	.	.	.	.	.	.	+
Saxifraga seguieri	.	.	+	.	+	+	+	+	1	+	+	+	+
Luzuletum spadiceae													
Doronicum clusii	.	+	+	+	.	.	.	.	.	.	.	.	.
Luzula alpinopilosa	+	1	1	1	1	1	+	+	1	1	+	1	+
Salicetea herbaceae, Salicetalia herbaceae and Salicion herbaceae													
Salix herbacea	.	.	.	.	+	.	+	+	+	.	.	.	.
Sedum alpestre	.	+	+	+	.	.	+	.	+	+	+	+	.
Soldanella alpicola	.	.	1	.	.	.	1	+	+	+	+	+	+
Veronica alpina	.	.	+	+	+	.	+	+	+	+	+	+	+
Differential of stable slope on carbonate substrate													
Asplenium viride	.	.	.	.	.	.	.	.	.	.	.	.	.
Erigeron uniflorus	.	.	.	.	.	.	.	.	.	.	.	.	.
Salix reticulata	.	.	.	.	.	.	.	.	.	.	.	.	.
Salix serpyllifolia	.	.	.	.	.	1	.	.	.	.	.	.	.
Valeriana saxatilis	.	.	.	.	.	.	.	.	.	.	.	.	.
Caricion firmae													
Carex firma	.	.	.	.	.	.	.	.	.	.	.	.	.
Crepis kerneri	.	.	.	.	.	.	.	.	.	.	.	.	.
Dryas octopetala	.	.	.	.	.	.	.	.	.	.	.	.	.
Helianthemum alpestre	.	.	.	.	.	.	.	.	.	.	.	.	.
Saxifraga caesia	.	.	.	.	.	.	.	.	.	.	.	.	.
Seslerietea albicantis and Seslerietalia coeruleae													
Agrostis alpina	.	.	.	.	.	.	.	.	.	.	.	.	.
Anthyllis vulneraria	.	.	.	.	.	.	.	.	.	.	.	.	.
Aster bellidiastrum	.	.	.	.	.	.	.	.	.	.	.	.	.
Bartsia alpina	.	.	.	.	.	.	.	.	.	.	.	.	.
Carex ornithopoda	.	.	.	.	.	.	.	.	.	.	.	.	.
Carex rupestris	.	.	.	.	.	.	.	.	.	.	.	.	.
Draba aizoides	.	.	.	.	.	.	.	.	.	.	.	.	.
Gentiana verna	.	.	.	.	.	.	.	.	.	.	.	.	.
Minuartia verna	.	.	.	.	.	.	.	.	.	.	.	.	.
Myosotis alpestris	.	1	+	+	.	.	.	.	.	.	.	.	.
Selaginella selaginoides	.	.	.	.	.	.	.	.	.	.	.	.	.
Sesleria caerulea	.	.	.	.	.	.	.	.	.	.	.	.	.
Silene acaulis	.	.	.	.	.	.	.	.	.	.	.	.	.
Veronica aphylla	.	.	.	.	.	.	.	.	.	.	.	.	.
Differential of rock glacier on carbonate substrate													
Arabis caerulea	.	.	.	.	.	.	.	.	.	.	.	.	.
Saxifraga oppositifolia	+	.	+	.	+	1	+	.	+	.	+	+	+
Papaveretum rhaetici													
Arabis pumila	.	.	.	.	.	.	.	.	.	.	.	.	.
Moehringia ciliata	.	.	.	.	.	.	.	.	.	.	.	.	.
Papaver aurantiacum	.	.	.	.	.	.	.	.	.	.	.	.	.
Saxifraga aphylla	.	.	.	.	.	.	.	.	.	.	.	.	.
Thlaspietalia rotundifolii and Thlaspion rotundifolii													
Achillea atrata	.	.	.	.	.	.	.	.	.	.	.	.	.
Campanula cochleariifolia	.	.	.	.	.	.	.	.	.	.	.	.	.
Poa minor	.	.	.	.	.	.	.	.	.	.	.	.	.
Pritzelago alpina	.	.	.	.	.	.	.	.	.	.	.	.	.
Arabidetalia caeruleae and Arabidion caeruleae													
Carex parviflora	.	.	.	.	.	.	.	.	.	.	.	.	.
Gentiana bavarica	.	.	.	.	.	.	.	.	.	.	.	.	.
Gnaphalium hoppeanum	.	.	.	.	.	.	.	.	.	.	.	.	.
Ranunculus alpestris	.	.	.	.	.	.	.	.	.	.	.	.	.
Soldanella alpina	.	.	.	.	.	.	.	.	.	.	.	.	.
Sedum atratum	.	.	.	.	.	.	.	.	.	.	.	.	.
Thlaspietea rotundifolii													
Arabis alpina	.	+	.	.	+	+	.	.	.	.	.	+	+
Cerastium uniflorum	+	+	1	+	1	+	+	+	+	+	+	+	1
Linaria alpina	.	+	.	.	+	.	.	.	.	.	.	.	.
Companion species													
Alchemilla vulgaris aggr.	.	.	.	.	.	.	.	.	.	.	.	.	.
Calluna vulgaris	.	.	.	.	.	.	.	.	.	.	.	.	.
Campanula scheuchzeri	.	.	.	.	.	.	.	.	.	.	.	.	.
Cystopteris fragilis	.	.	+	+	.	.	+	+	.	+	.	.	.
Homogyne alpina	.	.	+	.	.	.	.	.	.	.	.	.	.
Juniperus nana	.	.	.	.	.	.	.	.	.	.	.	.	.
Larix decidua	.	.	.	.	.	.	.	.	.	.	.	.	.
Lloydia serotina	.	.	.	.	+	.	.	.	.	.	.	.	.
Pinguicula alpina	.	.	.	.	.	.	.	.	.	.	.	.	.
Pinus mugo	.	.	.	.	.	.	.	.	.	.	.	.	.
Polygonum viviparum	.	.	.	.	+	+	.	.	.	.	.	.	+
Sempervivum montanum	.	.	.	.	.	.	+	.	.	.	.	.	.
Taraxacum alpinum s. l.	.	.	+	.	.	.	+	+	+	.	.	.	.
Sporadic species													
Arenaria biflora	.	.	.	.	.	.	.	.	.	.	.	.	.
Cerastium latifolium	.	.	.	.	.	.	.	.	.	.	.	.	.
Cirsium spinosissimum	.	.	.	.	.	.	.	.	.	.	.	.	.
Cryptogramma crispa	.	.	.	.	.	.	.	.	+	.	.	.	.
Daphne striata	.	.	.	.	.	.	.	.	.	.	.	.	.
Diphasiastrum alpinum	.	.	.	.	.	.	.	.	.	.	.	.	.
Festuca quadriflora	.	.	.	.	.	.	.	.	.	.	.	.	.
Gentiana engadinensis	.	.	.	.	.	.	.	.	.	.	.	.	.
Globularia cordifolia	.	.	.	.	.	.	.	.	.	.	.	.	.
Hieracium bifidum	.	.	.	.	.	.	.	.	.	.	.	.	.
Hieracium villosum	.	.	.	.	.	.	.	.	.	.	.	.	.
Pinguicula leptoceras	.	.	.	.	.	.	.	.	.	.	.	.	.
Potentilla brauneana	.	.	.	.	.	.	.	.	.	.	.	.	.
Salix retusa	.	.	.	.	.	.	.	.	.	.	.	.	.
Saxifraga aizoides	.	.	.	.	.	.	.	.	.	.	.	.	.
Saxifraga androsacea	.	.	.	.	.	+	.	.	.	.	.	.	.
Saxifraga hostii	.	.	.	.	.	.	.	.	.	.	.	.	.
Saxifraga paniculata	.	.	.	.	.	+	.	.	.	.	.	.	.
Sibbaldia procumbens	.	.	.	.	.	.	.	.	.	.	.	.	.

Cluster	1.3											
Code	132B	131C	134B	133C	133A	133B	132C	135B	131B	132A	131A	134C
Date	06.08.2014	06.08.2014	06.08.2014	06.08.2014	06.08.2014	06.08.2014	06.08.2014	06.08.2014	06.08.2014	06.08.2014	06.08.2014	06.08.2014
Coordinates	N46 27.555 E10 48.879	N46 27.469 E10 48.890	N46 27.513 E10 48.963	N46 27.507 E10 48.950	N46 27.528 E10 48.935	N46 27.522 E10 48.935	N46 27.551 E10 48.887	N46 27.490 E10 48.994	N46 27.481 E10 48.893	N46 27.553 E10 48.868	N46 27.485 E10 48.882	N46 27.520 E10 48.985
Area	Ultimo	Ultimo	Ultimo	Ultimo	Ultimo	Ultimo	Ultimo	Ultimo	Ultimo	Ultimo	Ultimo	Ultimo
Landform	Rock glacier	Rock glacier	Rock glacier	Rock glacier	Rock glacier	Rock glacier	Rock glacier	Rock glacier	Rock glacier	Rock glacier	Rock glacier	Rock glacier
Elevation (m a.s.l.)	2420	2470	2480	2470	2445	2450	2420	2500	2465	2415	2460	2480
Aspect (°)	350	340	310	235	265	250	20	320	335	330	330	315
Slope (°)	25	25	30	45	45	40	20	35	35	5	30	35
Shrubs cover (%)	15	0	0	0	15	5	0	0	0	0	0	0
Herbaceous cover (%)	30	10	5	45	35	50	<5	<5	<5	5	5	<5
Bryophytes and lichens cover (%)	15	5	0	5	5	10	0	0	0	5	0	0
Outcrop cover (%)	0	0	0	0	0	0	0	0	0	0	0	0
Debris cover (%)	40	85	95	40	35	35	100	100	100	90	95	100
Soil cover (%)	0	0	0	10	10	0	0	0	0	0	0	0
Species richness	19	9	10	16	20	16	3	3	5	6	5	5
Differential of stable slope on silicate substrate												
Anthoxanthum alpinum	.	.	.	+	.	.	.	.	.	.	.	.
Geum montanum	.	.	.	.	.	.	.	.	.	.	.	.
Nardus stricta	.	.	.	.	.	.	.	.	.	.	.	.
Poa alpina	.	.	.	.	.	.	.	.	.	.	.	.
Rhododendron ferrugineum	1	.	.	.	.	.	.	.	.	.	.	.
Caricion curvulae												
Carex curvula	1	.	.	.	.	.	.	.	.	.	.	.
Festuca halleri	+	.	+	+	1	1	.	.	.	.	.	.
Gnaphalium supinum	.	.	.	.	.	.	.	.	.	.	.	.
Hieracium glanduliferum	.	.	.	.	.	.	.	.	.	.	.	.
Ligusticum mutellina	.	.	.	.	.	.	.	.	.	.	.	.
Loiseleuria procumbens	.	.	.	.	.	.	.	.	.	.	.	.
Oreochloa disticha	.	.	.	.	.	.	.	.	.	.	.	.
Pedicularis kerneri	.	.	.	.	.	.	.	.	.	.	.	.
Primula glutinosa	.	.	.	.	.	.	.	.	.	.	.	.
Senecio carniolicus	+	+	+	+	+	+	.	.	.	.	.	.
Silene exscapa	.	.	.	.	.	.	.	.	.	.	.	.
Vaccinium gaultherioides	.	.	.	.	.	.	.	.	.	.	.	.
Caricetea curvulae e Caricetalia curvulae												
Agrostis rupestris	+	+	.	+	1	+	.	.	.	.	.	.
Euphrasia minima	+	.	.	.	+	.	.	.	.	.	.	.
Helictotrichon versicolor	.	.	.	.	.	.	.	.	.	.	.	.
Huperzia selago	.	.	.	.	.	.	.	.	.	.	.	.
Leontodon helveticus	+	.	.	.	.	.	.	.	.	.	.	.
Leucanthemopsis alpina	+	+	+	+	+	+	.	.	.	.	.	+
Luzula lutea	.	.	.	.	.	.	.	.	.	.	.	.
Phyteuma hemisphaericum	+	.	.	.	.	.	.	.	.	.	.	.
Potentilla aurea	.	.	.	.	.	.	.	.	.	.	.	.
Sieversio-Oxyrietum digynae												
Geum reptans	.	.	.	.	.	.	.	.	.	.	.	.
Oxyria digyna	.	.	.	.	.	.	.	.	.	.	.	.
Androsacetalia alpinae and Androsacion alpinae												
Androsace alpina	.	.	.	.	.	.	.	.	.	.	.	.
Artemisia genipi	.	.	.	.	.	.	.	.	.	.	.	.
Cardamine resedifolia	.	+	+	+	+	+	.	.	.	.	.	.
Poa laxa	1	+	+	+	1	1	+	+	+	+	+	+
Pritzelago brevicaulis	.	.	.	.	.	.	.	.	.	.	.	.
Ranunculus glacialis	.	.	.	.	.	.	.	.	.	.	.	.
Saxifraga bryoides	1	+	+	1	1	+	+	+	+	+	+	+
Saxifraga exarata	.	.	+	+	+	+	.	.	.	.	.	.
Saxifraga seguieri	.	.	.	.	.	.	.	.	.	.	.	.
Luzuletum spadiceae												
Doronicum clusii	1	1	+	1	1	1	.	.	+	+	1	+
Luzula alpinopilosa	1	1	+	2	1	1	.	+	+	+	+	+
Salicetea herbaceae, Salicetalia herbaceae and Salicion herbaceae												
Salix herbacea	+	.	.	.	.	.	.	.	.	.	.	.
Sedum alpestre	.	.	.	+	+	+	.	.	.	.	.	.
Soldanella alpicola	+	.	.	.	.	.	.	.	.	.	+	.
Veronica alpina	.	.	.	.	+	+	.	.	.	.	.	.
Differential of stable slope on carbonate substrate												
Asplenium viride	.	.	.	.	.	.	.	.	.	.	.	.
Erigeron uniflorus	+	.	.	+	+	.	.	.	.	+	.	.
Salix reticulata	.	.	.	.	.	.	.	.	.	.	.	.
Salix serpyllifolia	.	.	.	.	1	1	.	.	.	.	.	.
Valeriana saxatilis	.	.	.	.	.	.	.	.	.	.	.	.
Caricion firmae												
Carex firma	.	.	.	.	.	.	.	.	.	.	.	.
Crepis kerneri	.	.	.	.	.	.	.	.	.	.	.	.
Dryas octopetala	.	.	.	.	.	.	.	.	.	.	.	.
Helianthemum alpestre	.	.	.	.	.	.	.	.	.	.	.	.
Saxifraga caesia	.	.	.	.	.	.	.	.	.	.	.	.
Seslerietea albicantis and Seslerietalia coeruleae												
Agrostis alpina	.	.	.	.	.	.	.	.	.	.	.	.
Anthyllis vulneraria	.	.	.	.	.	.	.	.	.	.	.	.
Aster bellidiastrum	.	.	.	.	.	.	.	.	.	.	.	.
Bartsia alpina	.	.	.	.	.	.	.	.	.	.	.	.
Carex ornithopoda	.	.	.	.	.	.	.	.	.	.	.	.
Carex rupestris	.	.	.	.	.	.	.	.	.	.	.	.
Draba aizoides	.	.	.	.	.	.	.	.	.	.	.	.
Gentiana verna	.	.	.	+	+	.	.	.	.	.	.	.
Minuartia verna	.	.	.	.	.	.	.	.	.	.	.	.
Myosotis alpestris	.	.	.	.	+	1	.	.	.	.	.	.
Selaginella selaginoides	.	.	.	.	.	.	.	.	.	.	.	.
Sesleria caerulea	.	.	.	.	.	.	.	.	.	.	.	.
Silene acaulis	.	.	.	.	.	.	.	.	.	.	.	.
Veronica aphylla	.	.	.	.	.	.	.	.	.	.	.	.
Differential of rock glacier on carbonate substrate												
Arabis caerulea	.	.	.	.	.	.	.	.	.	.	.	.
Saxifraga oppositifolia	.	.	.	.	.	.	.	.	.	.	.	.
Papaveretum rhaetici												
Arabis pumila	.	.	.	.	.	.	.	.	.	.	.	.
Moehringia ciliata	.	.	.	.	.	.	.	.	.	.	.	.
Papaver aurantiacum	.	.	.	.	.	.	.	.	.	.	.	.
Saxifraga aphylla	.	.	.	.	.	.	.	.	.	.	.	.
Thlaspietalia rotundifolii and Thlaspion rotundifolii												
Achillea atrata	.	.	.	.	.	.	.	.	.	.	.	.
Campanula cochleariifolia	.	.	.	.	.	.	.	.	.	.	.	.
Poa minor	.	.	.	.	.	.	.	.	.	.	.	.
Pritzelago alpina	.	.	.	.	.	.	.	.	.	.	.	.
Arabidetalia caeruleae and Arabidion caeruleae												
Carex parviflora	.	.	.	.	.	.	.	.	.	.	.	.
Gentiana bavarica	.	.	.	.	.	.	.	.	.	.	.	.
Gnaphalium hoppeanum	.	.	.	.	.	.	.	.	.	.	.	.
Ranunculus alpestris	.	.	.	.	.	.	.	.	.	.	.	.
Soldanella alpina	.	.	.	.	.	.	.	.	.	.	.	.
Sedum atratum	.	.	.	.	.	.	.	.	.	.	.	.
Thlaspietea rotundifolii												
Arabis alpina	.	.	.	.	.	.	.	.	.	.	.	.
Cerastium uniflorum	+	+	+	1	+	1	.	.	+	+	.	.
Linaria alpina	.	.	.	.	.	.	.	.	.	.	.	.
Companion species												
Alchemilla vulgaris aggr.	.	.	.	.	.	.	.	.	.	.	.	.
Calluna vulgaris	.	.	.	.	.	.	.	.	.	.	.	.
Campanula scheuchzeri	.	.	.	+	+	+	.	.	.	.	.	.
Cystopteris fragilis	.	.	.	.	.	.	+	.	.	.	.	.
Homogyne alpina	+	.	.	.	.	.	.	.	.	.	.	.
Juniperus nana	.	.	.	.	.	.	.	.	.	.	.	.
Larix decidua	.	.	.	.	.	.	.	.	.	.	.	.
Lloydia serotina	.	.	.	.	+	.	.	.	.	.	.	.
Pinguicula alpina	.	.	.	.	.	.	.	.	.	.	.	.
Pinus mugo	.	.	.	.	.	.	.	.	.	.	.	.
Polygonum viviparum	.	.	.	.	.	.	.	.	.	.	.	.
Sempervivum montanum	+	.	.	.	.	.	.	.	.	.	.	.
Taraxacum alpinum s. l.	.	.	.	.	.	.	.	.	.	.	.	.
Sporadic species												
Arenaria biflora	.	.	.	.	.	.	.	.	.	.	.	.
Cerastium latifolium	.	.	.	.	.	.	.	.	.	.	.	.
Cirsium spinosissimum	.	.	.	.	.	.	.	.	.	.	.	.
Cryptogramma crispa	.	.	.	.	.	.	.	.	.	.	.	.
Daphne striata	.	.	.	.	.	.	.	.	.	.	.	.
Diphasiastrum alpinum	.	.	.	.	.	.	.	.	.	.	.	.
Festuca quadriflora	.	.	.	.	.	.	.	.	.	.	.	.
Gentiana engadinensis	.	.	.	.	.	.	.	.	.	.	.	.
Globularia cordifolia	.	.	.	.	.	.	.	.	.	.	.	.
Hieracium bifidum	.	.	.	.	.	.	.	.	.	.	.	.
Hieracium villosum	.	.	.	.	.	.	.	.	.	.	.	.
Pinguicula leptoceras	.	.	.	.	.	.	.	.	.	.	.	.
Potentilla brauneana	.	.	.	.	.	.	.	.	.	.	.	.
Salix retusa	.	.	.	.	.	.	.	.	.	.	.	.
Saxifraga aizoides	.	.	.	.	.	.	.	.	.	.	.	.
Saxifraga androsacea	.	.	.	.	.	.	.	.	.	.	.	.
Saxifraga hostii	.	.	.	.	.	.	.	.	.	.	.	.
Saxifraga paniculata	.	.	.	.	.	.	.	.	.	.	.	.
Sibbaldia procumbens	.	.	.	.	.	.	.	.	.	.	.	.

Cluster	2.1														
Code	215A	215B	215C	214A	214B	211A	211C	211B	213C	213A	214C	212A	212B	212C	213B
Date	05.08.2014	05.08.2014	05.08.2014	05.08.2014	05.08.2014	04.08.2014	04.08.2014	04.08.2014	04.08.2014	04.08.2014	05.08.2014	04.08.2014	04.08.2014	04.08.2014	04.08.2014
Coordinates	N46 30.215 E10 23.994	N46 30.219 E10 23.989	N46 30.227 E10 23.988	N46 30.186 E10 24.053	N46 30.190 E10 24.051	N46 30.173 E10 24.013	N46 30.157 E10 24.021	N46 30.179 E10 24.013	N46 30.253 E10 24.001	N46 30.247 E10 24.001	N46 30.202 E10 24.054	N46 30.202 E10 24.038	N46 30.209 E10 24.039	N46 30.210 E10 24.030	N46 30.247 E10 24.007
Area	Braulio	Braulio	Braulio	Braulio	Braulio	Braulio	Braulio	Braulio	Braulio	Braulio	Braulio	Braulio	Braulio	Braulio	Braulio
Landform	Stable slope	Stable slope	Stable slope	Stable slope	Stable slope	Stable slope	Stable slope	Stable slope	Stable slope	Stable slope	Stable slope	Stable slope	Stable slope	Stable slope	Stable slope
Elevation (m a.s.l.)	2470	2470	2465	2450	2450	2485	2485	2485	2440	2440	2445	2470	2465	2460	2440
Aspect (°)	15	30	45	330	320	270	155	70	85	310	275	290	300	290	15
Slope (°)	10	10	15	15	10	20	10	20	15	15	20	20	15	25	15
Shrubs cover (%)	5	<5	<5	<5	5	0	5	<5	<5	<5	<5	<5	<5	<5	0
Herbaceous cover (%)	35	45	25	85	75	70	70	65	80	85	70	75	55	80	60
Bryophytes and lichens cover (%)	15	5	10	5	5	5	10	5	5	5	5	5	5	0	5
Outcrop cover (%)	0	10	5	0	0	20	0	25	10	5	0	5	15	5	5
Debris cover (%)	5	15	40	10	10	10	25	10	10	10	20	25	30	15	35
Soil cover (%)	40	25	20	10	5	0	0	0	0	0	5	0	0	0	0
Species richness	20	25	30	36	34	20	27	25	22	23	27	21	15	13	9
Differential of stable slope on silicate substrate															
Anthoxanthum alpinum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Geum montanum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Nardus stricta	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Poa alpina	.	.	.	1	+	.	.	.	.	.	.	.	.	.	.
Rhododendron ferrugineum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Caricion curvulae															
Carex curvula	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Festuca halleri	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Gnaphalium supinum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hieracium glanduliferum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Ligusticum mutellina	.	.	.	1	+	.	.	.	.	.	.	.	.	.	.
Loiseleuria procumbens	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Oreochloa disticha	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Pedicularis kerneri	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Primula glutinosa	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Senecio carniolicus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Silene exscapa	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Vaccinium gaultherioides	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.
Caricetea curvulae e Caricetalia curvulae															
Agrostis rupestris	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Euphrasia minima	1	.	.	+	.	.	.	.	.	.	.	.	.	.	.
Helictotrichon versicolor	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Huperzia selago	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Leontodon helveticus	.	+	.	+	+	.	.	.	.	.	+	.	.	.	.
Leucanthemopsis alpina	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Luzula lutea	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Phyteuma hemisphaericum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Potentilla aurea	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Sieversio-Oxyrietum digynae															
Geum reptans	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Oxyria digyna	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Androsacetalia alpinae and Androsacion alpinae															
Androsace alpina	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Artemisia genipi	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cardamine resedifolia	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Poa laxa	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Pritzelago brevicaulis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Ranunculus glacialis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Saxifraga bryoides	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Saxifraga exarata	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Saxifraga seguieri	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Luzuletum spadiceae															
Doronicum clusii	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Luzula alpinopilosa	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Salicetea herbaceae, Salicetalia herbaceae and Salicion herbaceae															
Salix herbacea	1	1	1	1	.	.	.	.	.	.	.	.	.	+	.
Sedum alpestre	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Soldanella alpicola	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Veronica alpina	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.
Differential of stable slope on carbonate substrate															
Asplenium viride	.	+	+	.	+	.	.	+	+	.	+	+	+	.	.
Erigeron uniflorus	.	.	+	+	+	+	+	+	+	+	+	.	.	.	.
Salix reticulata	+	+	+	+	1	.	.	.	.	.	.	.	.	+	.
Salix serpyllifolia	1	+	+	+	+	.	1	+	+	+	+	+	+	+	.
Valeriana saxatilis	.	.	.	.	+	+	+	.	+	.	.	+	.	.	.
Caricion firmae															
Carex firma	1	+	+	1	1	2	2	2	2	3	2	2	1	1	2
Crepis kerneri	.	.	.	.	.	+	.	.	.	.	.	.	+	.	.
Dryas octopetala	.	+	.	+	1	2	+	2	2	2	1	1	2	3	1
Helianthemum alpestre	.	+	+	.	.	+	+	+	1	+	+	.	.	.	.
Saxifraga caesia	+	+	+	+	+	+	+	+	+	+	+	+	+	+	1
Seslerietea albicantis and Seslerietalia coeruleae															
Agrostis alpina	+	+	+	+	+	1	1	1	+	+	1	1	+	+	+
Anthyllis vulneraria	.	.	+	+	+	.	.	.	.	+	+	+	+	.	.
Aster bellidiastrum	.	.	+	+	1	+	1	+	.	+	1	+	.	+	.
Bartsia alpina	+	.	+	+	+	+	+	+	+	+	+	.	.	+	.
Carex ornithopoda	.	.	+	.	+	.	+	+	+	1	+	+	.	.	+
Carex rupestris	.	.	.	.	.	+	+	.	.	.	.	.	.	.	.
Draba aizoides	.	.	.	+	+	+	+	+	+	+	+	.	.	.	.
Gentiana verna	.	.	.	+	+	+	+	+	.	+	.	.	.	.	.
Minuartia verna	.	+	+	+	+	+	+	+	+	.	+	+	.	.	.
Myosotis alpestris	.	.	.	+	+	.	+	+	+	.	.	.	.	.	.
Selaginella selaginoides	.	.	.	+	+	.	.	+	.	+	+	.	.	.	.
Sesleria caerulea	.	.	.	+	1	1	1	1	1	1	1	1	1	1	1
Silene acaulis	1	1	+	1	+	+	.	.	.	.	.	.	.	.	.
Veronica aphylla	.	.	.	.	.	.	+	+	.	.	.	.	.	.	.
Differential of rock glacier on carbonate substrate															
Arabis caerulea	+	+	+	.	+	.	.	.	.	.	.	.	.	.	.
Saxifraga oppositifolia	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Papaveretum rhaetici															
Arabis pumila	+	+	+	.	.	.	.	.	.	.	+	+	.	.	.
Moehringia ciliata	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.
Papaver aurantiacum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Saxifraga aphylla	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Thlaspietalia rotundifolii and Thlaspion rotundifolii															
Achillea atrata	+	+	+	+	+	.	+	+	+	.	+	+	+	.	.
Campanula cochleariifolia	.	+	+	+	.	+	+	+	+	+	.	+	.	.	.
Poa minor	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.
Pritzelago alpina	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.
Arabidetalia caeruleae and Arabidion caeruleae															
Carex parviflora	+	+	+	+	.	.	.	.	.	.	.	+	.	.	.
Gentiana bavarica	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.
Gnaphalium hoppeanum	+	+	+	+	.	.	+	.	.	.	+	.	.	.	.
Ranunculus alpestris	1	1	1	1	1	.	+	+	+	+	+	+	+	+	.
Soldanella alpina	1	1	1	1	1	.	1	.	.	+	1	+	.	.	.
Sedum atratum	+	+	+	+	+	+	+	+	+	+	+	+	+	.	.
Thlaspietea rotundifolii															
Arabis alpina	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cerastium uniflorum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Linaria alpina	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Companion species															
Alchemilla vulgaris aggr.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Calluna vulgaris	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Campanula scheuchzeri	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cystopteris fragilis	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.
Homogyne alpina	.	.	.	1	1	+	1	+	+	+	1	.	.	.	+
Juniperus nana	.	.	.	.	.	.	+	.	.	.	.	.	.	+	.
Larix decidua	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.
Lloydia serotina	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Pinguicula alpina	+	.	.	.	.	.	.	.	.	.	+	.	+	.	+
Pinus mugo	.	.	.	.	+	.	.	.	.	.	.	+	.	.	.
Polygonum viviparum	+	+	+	+	+	+	+	+	.	+	+	+	+	+	+
Sempervivum montanum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Taraxacum alpinum s. l.	+	+	+	+	.	.	.	.	.	.	.	.	+	.	.
Sporadic species															
Arenaria biflora	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.
Cerastium latifolium	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cirsium spinosissimum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cryptogramma crispa	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Daphne striata	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.
Diphasiastrum alpinum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Festuca quadriflora	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Gentiana engadinensis	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.
Globularia cordifolia	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.
Hieracium bifidum	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.
Hieracium villosum	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.
Pinguicula leptoceras	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Potentilla brauneana	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.
Salix retusa	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Saxifraga aizoides	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Saxifraga androsacea	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Saxifraga hostii	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.
Saxifraga paniculata	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Sibbaldia procumbens	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

Cluster	2.2																								
Code	232B	233B	233C	232A	232C	234B	234C	233A	235B	224C	234A	222B	224A	221B	221A	222A	223B	223A	221C	223C	224B	222C	231C	231A	231B
Date	04.08.2014	04.08.2014	04.08.2014	04.08.2014	04.08.2014	22.08.2014	22.08.2014	04.08.2014	04.08.2014	04.08.2014	22.08.2014	05.08.2014	04.08.2014	05.08.2014	05.08.2014	05.08.2014	05.08.2014	05.08.2014	05.08.2014	05.08.2014	04.08.2014	05.08.2014	04.08.2014	04.08.2014	04.08.2014
Coordinates	N46 30.019 E10 24.072	N46 30.004 E10 24.189	N46 30.004 E10 24.177	N46 30.023 E10 24.077	N46 30.015 E10 24.068	N46 29.951 E10 24.205	N46 29.968 E10 24.195	N46 30.005 E10 24.195	N46 29.965 E10 24.234	N46 30.058 E10 24.291	N46 29.934 E10 24.210	N46 30.204 E10 24.292	N46 30.066 E10 24.294	N46 30.279 E10 24.174	N46 30.274 E10 24.172	N46 30.200 E10 24.287	N46 30.130 E10 24.290	N46 30.136 E10 24.298	N46 30.272 E10 24.178	N46 30.128 E10 24.283	N46 30.066 E10 24.300	N46 30.210 E10 24.294	N46 30.079 E10 24.016	N46 30.075 E10 24.035	N46 30.076 E10 24.031
Area	Braulio	Braulio	Braulio	Braulio	Braulio	Braulio	Braulio	Braulio	Braulio	Braulio	Braulio	Braulio	Braulio	Braulio	Braulio	Braulio	Braulio	Braulio	Braulio	Braulio	Braulio	Braulio	Braulio	Braulio	Braulio
Landform	Rock glacier	Rock glacier	Rock glacier	Rock glacier	Rock glacier	Rock glacier	Rock glacier	Rock glacier	Rock glacier	Scree slope	Rock glacier	Scree slope	Scree slope	Scree slope	Scree slope	Scree slope	Scree slope	Scree slope	Scree slope	Scree slope	Scree slope	Scree slope	Rock glacier	Rock glacier	Rock glacier
Elevation (m a.s.l.)	2545	2575	2575	2540	2545	2610	2605	2575	2590	2610	2620	2555	2620	2445	2445	2555	2595	2595	2450	2590	2610	2555	2520	2525	2525
Aspect (°)	345	330	315	355	350	345	355	0	325	295	350	300	285	310	310	300	285	285	310	285	295	290	340	75	340
Slope (°)	0	10	25	5	0	15	10	0	15	35	25	35	35	30	30	35	35	35	30	35	35	35	10	5	15
Shrubs cover (%)	<5	0	0	0	<5	0	0	0	0	0	0	0	0	0	0	0	0	0	<5	0	0	0	0	0	<5
Herbaceous cover (%)	<5	5	<5	5	<5	<5	<5	<5	<5	<5	<5	10	5	10	5	5	5	<5	5	5	<5	5	5	5	5
Bryophytes and lichens cover (%)	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0
Outcrop cover (%)	0	0	0	0	0	0	0	0	0	0	0	15	10	0	0	0	0	0	0	0	0	25	0	0	0
Debris cover (%)	100	95	100	95	100	100	100	100	100	100	100	70	85	90	95	95	95	100	95	95	100	70	95	95	95
Soil cover (%)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Species richness	9	5	5	7	7	5	5	3	3	3	5	8	10	11	8	8	5	7	8	6	6	9	11	16	17
Differential of stable slope on silicate substrate																									
Anthoxanthum alpinum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Geum montanum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Nardus stricta	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Poa alpina	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Rhododendron ferrugineum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Caricion curvulae																									
Carex curvula	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Festuca halleri	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Gnaphalium supinum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hieracium glanduliferum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Ligusticum mutellina	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Loiseleuria procumbens	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Oreochloa disticha	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Pedicularis kerneri	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Primula glutinosa	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Senecio carniolicus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Silene exscapa	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Vaccinium gaultherioides	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Caricetea curvulae e Caricetalia curvulae																									
Agrostis rupestris	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Euphrasia minima	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Helictotrichon versicolor	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Huperzia selago	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Leontodon helveticus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Leucanthemopsis alpina	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.
Luzula lutea	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Phyteuma hemisphaericum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Potentilla aurea	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Sieversio-Oxyrietum digynae																									
Geum reptans	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Oxyria digyna	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Androsacetalia alpinae and Androsacion alpinae																									
Androsace alpina	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Artemisia genipi	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cardamine resedifolia	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Poa laxa	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Pritzelago brevicaulis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Ranunculus glacialis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Saxifraga bryoides	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Saxifraga exarata	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Saxifraga seguieri	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Luzuletum spadiceae																									
Doronicum clusii	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Luzula alpinopilosa	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Salicetea herbaceae, Salicetalia herbaceae and Salicion herbaceae																									
Salix herbacea	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Sedum alpestre	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Soldanella alpicola	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Veronica alpina	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+
Differential of stable slope on carbonate substrate																									
Asplenium viride	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.
Erigeron uniflorus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.
Salix reticulata	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Salix serpyllifolia	+	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+
Valeriana saxatilis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Caricion firmae																									
Carex firma	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Crepis kerneri	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Dryas octopetala	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Helianthemum alpestre	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Saxifraga caesia	.	.	.	+	.	.	+	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	+
Seslerietea albicantis and Seslerietalia coeruleae																									
Agrostis alpina	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Anthyllis vulneraria	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Aster bellidiastrum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.
Bartsia alpina	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Carex ornithopoda	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Carex rupestris	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.
Draba aizoides	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Gentiana verna	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Minuartia verna	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Myosotis alpestris	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Selaginella selaginoides	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Sesleria caerulea	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Silene acaulis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Veronica aphylla	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Differential of rock glacier on carbonate substrate																									
Arabis caerulea	+	+	+	+	+	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	+
Saxifraga oppositifolia	+	1	+	+	+	+	+	+	+	.	+	+	+	.	.	.	.	.	.	.	.	+	+	+	+
Papaveretum rhaetici																									
Arabis pumila	+	+	+	+	+	+	+	.	.	.	.	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Moehringia ciliata	.	.	.	.	.	.	.	.	.	.	.	1	.	+	+	+	.	.	.	.	.	+	+	+	+
Papaver aurantiacum	.	.	.	+	+	.	.	.	.	+	.	.	+	+	+	+	+	+	+	+	+	+	+	+	+
Saxifraga aphylla	.	.	.	.	.	.	.	.	.	.	+	.	+	+	1	+	+	+	1	+	+	+	.	+	.
Thlaspietalia rotundifolii and Thlaspion rotundifolii																									
Achillea atrata	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	+	.
Campanula cochleariifolia	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	+
Poa minor	+	+	+	+	+	+	+	.	+	.	.	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Pritzelago alpina	.	.	.	.	.	.	.	.	.	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Arabidetalia caeruleae and Arabidion caeruleae																									
Carex parviflora	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Gentiana bavarica	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Gnaphalium hoppeanum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.
Ranunculus alpestris	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+
Soldanella alpina	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+
Sedum atratum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Thlaspietea rotundifolii																									
Arabis alpina	+	+	+	+	+	+	+	+	.	+	+	+	.	+	+	+	.	+	+	+	+	+	+	+	+
Cerastium uniflorum	+	.	.	.	.	+	.	.	.	.	+	.	+	+	+	+	.	.	+	.	.	.	.	+	+
Linaria alpina	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.
Companion species																									
Alchemilla vulgaris aggr.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Calluna vulgaris	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Campanula scheuchzeri	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cystopteris fragilis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Homogyne alpina	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.
Juniperus nana	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Larix decidua	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Lloydia serotina	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Pinguicula alpina	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Pinus mugo	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Polygonum viviparum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Sempervivum montanum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Taraxacum alpinum s. l.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	+	+	+
Sporadic species																									
Arenaria biflora	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cerastium latifolium	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.
Cirsium spinosissimum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cryptogramma crispa	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Daphne striata	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Diphasiastrum alpinum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Festuca quadriflora	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.
Gentiana engadinensis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Globularia cordifolia	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hieracium bifidum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hieracium villosum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Pinguicula leptoceras	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Potentilla brauneana	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Salix retusa	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.
Saxifraga aizoides	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.
Saxifraga androsacea	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Saxifraga hostii	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Saxifraga paniculata	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Sibbaldia procumbens	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

Ecology of active rock glaciers and surrounding landforms: climate, soil, plants and arthropods

Running title: ecology of rock glaciers

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Abstract

Active rock glaciers are periglacial landforms consisting of coarse debris with interstitial ice or ice core. Recent papers showed that such landforms are able to support plant and arthropod life and could act as warm-stage refugia for cold-adapted species due to their microclimate features and thermal inertia. However, integrated research comparing rock glaciers with surrounding landforms to outline their ecological peculiarities are still scarce. We analyzed the abiotic (ground surface temperature and humidity, soil physical and chemical parameters) and biotic features (plant and arthropod communities) of two Alpine active rock glaciers with contrasting lithology (silicate and carbonate), comparing them with the surrounding iceless landforms as reference sites (control slopes and scree slopes). Our data show remarkable differences between control slopes and debris-featured landforms as a whole, while few differences occurs between scree slopes and rock glaciers: such landforms show similar soil features but different ground surface temperatures (lower on rock glaciers) and different occurrence of cold-adapted species (more frequent/abundant on rock glaciers). Both plant and arthropod species distribution depend on the geographic context as a function of soil pH and on the landform (control slope versus debris-featured landforms) as a function of coarse debris fraction and organic matter content; the differences between scree slopes and rock glaciers can be likely attribute to microclimate. The role of rock glaciers as warm stage refugia is supported by their topoclimatic peculiarities but, at least on European Alps, it could be less remarkable than that of debris-covered glaciers, which are able to descend below the climatic treeline.

Key-words: climate change, flora, carabid beetles, permafrost, spiders, refugia, vegetation

Introduction

Geomorphological heterogeneity at landscape level is known to enhance biodiversity of mountain regions, providing a wide range of environmental conditions for plant and animal taxa (Körner, 2003; Brandmayr et al., 2003; Thaler, 2003; Gentili et al., 2015). Such ecological variability may have in turn biogeographical implications within the frame of the ongoing climate variations, since specific landforms can preserve suitable microclimate conditions for cold-adapted species even when the macroclimate became adverse (e.g. warmer and drier) (Ashcroft et al., 2012; Birks and Willis, 2008; Dobrowski, 2011; Keppel et al., 2015; Scherrer & Körner, 2010; Stewart et al., 2010). Glacial and periglacial landforms were proposed as source of ecological variability and potential warm-stage refugia for cold-adapted species, because of their microclimate features and thermal inertia (Millar et al., 2010, 2013; Gobbi et al., 2011, 2014; Caccianiga et al., 2011; Gentili et al., 2015).

Active rock glaciers are periglacial landforms consisting of coarse debris with interstitial ice or ice core, characterized by creeping movement due to ice deformation (Barsch, 1996; Haeberli et al., 2006; Janke et al., 2013). These landforms are the main expression of permafrost in mountain regions, particularly where climate is cold and dry (Barsch, 1977; Haeberli, 1985) and the relative contribution of debris and snow at topoclimatic scale is adequate (Humlum, 1998; Janke, 2007). The occurrence of subsurface ice in debris deposits is promoted by the prevalence of coarse blocks over fine matrix, a grain size distribution that achieves a cold thermal regime partially decoupled from that of the surrounding free-atmosphere (Harris & Pedersen, 1998; Hanson & Hoelzle, 2004; Juliussen & Humlum, 2008). Ice deformation gives rock glaciers a creep movement similar to that of glaciers, but generally slower (less than 1 m/y) (Haeberli, 1985; Barsch, 1996; Janke et al., 2013).

In spite of the harsh environmental conditions, active rock glaciers are able to support plant and animal life (Cannone & Gerdol, 2003; Burga et al., 2004; Rieg et al., 2012; Millar et al., 2010, 2013; Gobbi et al., 2014). Vegetation cover and plant assemblage on active rock glaciers depend on creeping intensity and substrate grain-size: surfaces with coarse-grained debris and high creeping activity are scarcely or not colonized at all by plants, while surfaces with fine-grained debris and low creeping intensity can be colonized by pioneer plant species adapted to mechanical disturbance and low temperatures (Cannone & Gerdol, 2003; Burga et al., 2004). Rieg et al. (2012) found a threshold of 1.5 m/y for surface creeping velocity: below such value, plants cover depends on fine-grained debris availability, while above that it is heavily affected by ground instability.

The microclimate features can also play an important role in species occurrence. The low temperatures recorded in coarse-grained zones can represent a limiting factor for plants establishment, but also an opportunity for cold-adapted arthropods (especially ground beetles) to find suitable thermal conditions in an unfavorable environmental context outside the rock glacier (Gobbi et al., 2014). In dry mountain ranges like Sierra Nevada (USA), the microclimate features of rock glaciers allow cold-adapted plant species to live below their normal altitudinal distribution. Furthermore, the wetlands fed by springs originating from seasonal melting of permafrost act as water reserve for hydrophilic plant and arthropod species when other kinds of springs desiccate (Millar et al., 2013).

Even if rock glaciers as habitat are increasingly known, we are still far from an overall view on the ecological features of such landforms. In particular: no studies compared rock glaciers with the surrounding landforms as reference sites; no studies compared such landforms on different lithology; no studies clearly contextualize rock glaciers with respect to the altitudinal zonation of mountain ecosystems (e.g. with respect to the climatic treeline) to infer their potentiality as warm-stage refugia for cold-adapted species.

In the present paper we analyzed the abiotic (ground surface temperature and humidity, soil physical and chemical parameters) and biotic features (plant and arthropod communities) of two active rock glaciers of the central Italian Alps with contrasting lithology (silicate and carbonate), comparing them with the surrounding landforms as reference sites (control slopes and scree slopes).

Our hypotheses are: 1) rock glaciers differ from the surrounding landforms for (a) ground surface temperature/humidity and (b) soil physical/chemical parameters; 2) rock glaciers differ from the surrounding landforms for (a) plant/arthropod species richness/abundance, (b) cold-adapted plant/arthropod species; 3) the soil variables drive the distribution of plant/arthropod species through the investigated landforms.

Furthermore, we infer the arrangement of active rock glaciers with respect to the climatic treeline as lower limit of the alpine belt (Körner, 2003), to improve the discussion about such landforms as potential warm-stage refugia for cold-adapted species.

Data collection

Study area

The analyzed rock glaciers (Fig. 1) are located in two valleys of the Ortles-Cevedale Massif (central Italian Alps), within the area of the Stelvio National Park. The first one ("Lago Lungo", 46°27' N 10°49' E) is located in Val d'Ultimo, lies on a NW-facing slope between 2350 and 2550 m a.s.l and is fed by silicate debris (micaschist and ortogneiss) (Seppi et al., 2005; Martin et al., 2009); the second one ("Vedrettino", 46°30' N 10°24' E) is located in Valle del Braulio, lies in a NW-facing glacial cirque between 2500 and 2650 m a.s.l and is fed by carbonate debris (dolomite limestone) (Bonardi et al., 2012; Montrasio et al., 2012).

The study areas are c. 32 km apart and are both characterized by the typical continental climate of the inner Alps (Tampucci et al., 2015a); both the investigated active rock glaciers are the lowest of the respective area (Seppi et al., 2005; Scotti et al., 2013). The climatic treeline at regional scale resulted to be located at c. 2210 m a.s.l.., thus c. 150 and 300 m below the lowest active rock glaciers of the two study areas, respectively. It was estimated as follows: eight years (2004-2011) of mean daily temperature at 1900, 2255 and 3124 m a.s.l. were used to calculate the monthly mean altitudinal temperature lapse rate at regional scale; thirty years (1983-2012) of mean daily temperature at 1900 m a.s.l. were used to get the altitude of the climatic treeline at regional scale following Paulsen and Körner (2014) (data provided by Meteo Service of the Province of Bolzano).

Sampling design

We selected three adjacent landforms for each study area, corresponding to three different ecological conditions: 1) control slope (stable slope without permafrost evidences, supposed to have the potentiality for the full development of soil and plant and arthropod communities), 2) scree slope (unstable debris-featured landform without permafrost evidences), 3) active rock glacier (unstable debris-featured landform with permafrost evidences).

A data-logger (Tinytag TGP-4500) was placed at each landform in order to analyze the patterns of mean daily ground surface temperature (GST) and mean daily ground surface humidity (GSH) during the year 2014. The devices were placed between stones at a depth ranging from 10 to 15 cm, in order to shield them from direct solar radiation. The recording was set at one-hour interval; the temperature data have an accuracy of ± 0.20°C from 0 to 50°C and a resolution of 0.25°C at 0°C; the humidity data have an accuracy of ± 3% at 25°C and a resolution better than 0.5%.

We selected 5 plots for each landform (Fig. 1) and 3 sampling points for each plot, randomly placed at least c. 10 m apart from each other. Substrate samples were taken at the surface for physical and chemical analysis: at each plot a sample of c. 1 kg was taken for particle size distribution analysis; at each sampling point a sample of c. 200 g was taken to measure soil pH (in 1:2.5 soil:water), calcium carbonate content (Dietrich-Fruhling calcimeter) and organic matter content (Walkley-Black method). At each sampling point, plant and arthropod community data were collected as follows: plant species surveys of 25m^2 were performed, estimating the percentage of bare soil surface and the cover of each plant species with a resolution of 5% (we conventionally assigned 1% cover to rare species); arthropod species sampling was performed placing a pitfall trap (a plastic cup buried up to the edge and filled with approximately 20 ml of wine-vinegar and salt solution) (Brandmayr et al., 2005). Pitfall traps were collected and re-set every 20 days during the snow-free season (July-September 2013–14). The analysis concerned ground beetles (Coleoptera: Carabidae) and spiders (Arachnida: Araneae), since they are two taxa well known by the ecological viewpoint (Brandmayr et al., 2003; Thaler, 2003) and extensively used as bioindicators of climate change in high latitude-altitude ecosystems (e.g. Bråten et al., 2012; Gobbi et al., 2006, 2007).

Environmental and community variables

Data were recorded in a matrix of 90 rows (one for each sampling point) and 169 columns, including: the landform, five soil variables, four community variables and abundance for 118 plant species and 41 arthropod species.

The landform was considered as a categorical variable in three classes (control slope, scree slope, rock glacier). The following soil variables were considered: bare soil surface ("Bar.so", expressed in percentage), coarse debris fraction ("Coa.fr", sum of gravel and sand fractions expressed in percentage), soil pH ("pH"), calcium carbonate content ("Cal.ca", expressed in percentage), organic matter content ("Org.ma", expressed in g/kg). The following community variables were considered: plant species richness ("Pla.ri", number of plant species), cumulative ground cover ("Pla.ab", sum of every plant species cover expressed in percentage), arthropod species richness ("Art.ri", number of ground beetle species plus number of spider species), total arthropod activity density ("Art.ab", sum of ground beetle and spider activity density: ratio among number of captured specimens and number of days of trap activity). Each plant species abundance was expressed as cover percentage with a resolution of 5%; each arthropod species abundance was expressed as activity density.

Species nomenclature refers to Landolt et al. (2010) for plants, Vigna Taglianti (2004) for ground beetles and World Spider Catalog (2016) for spiders.

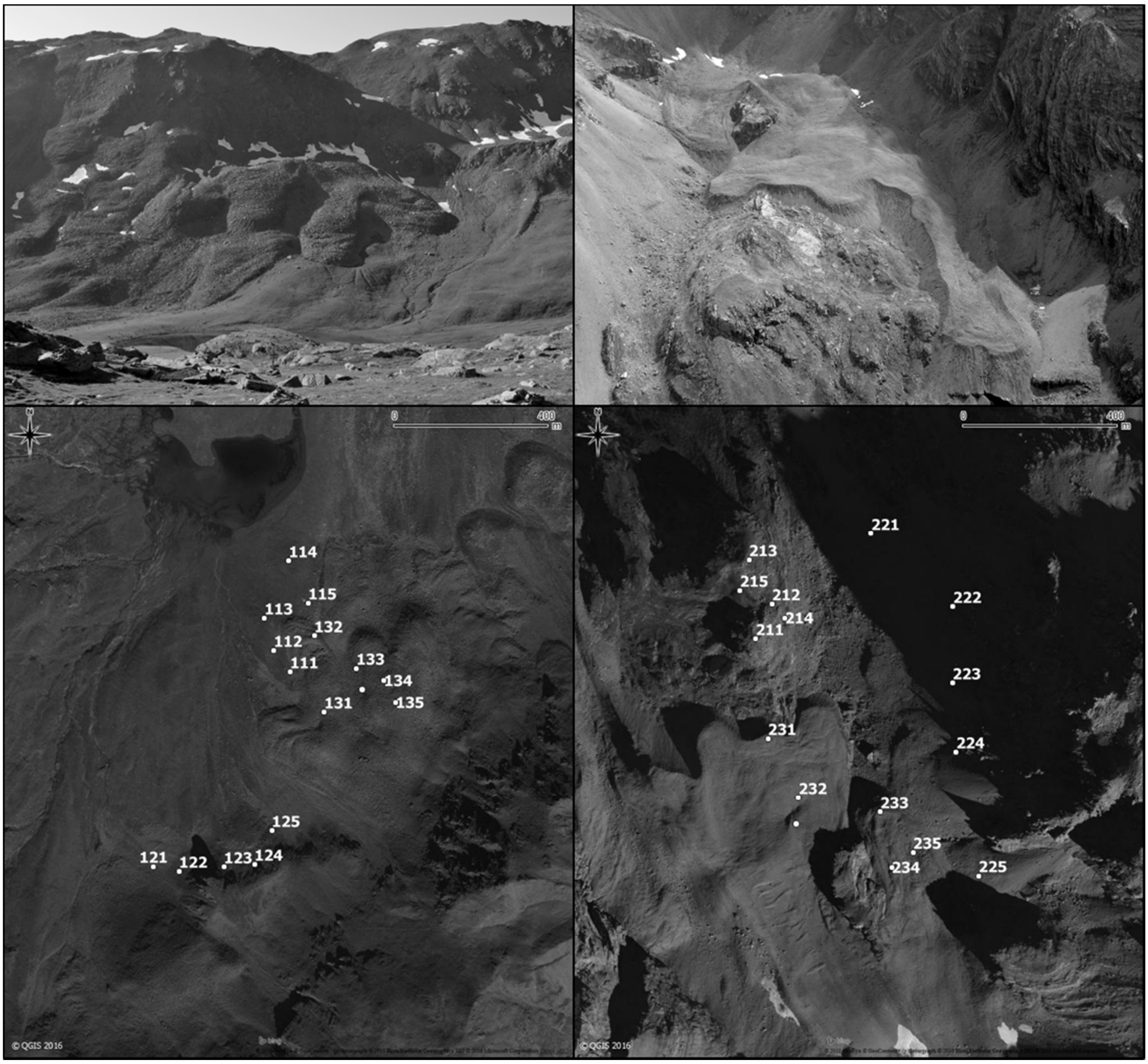


Fig. 1. Investigated landforms in Val d'Ultimo (left) and Valle del Braulio (right) with respective plots position (bottom). Sites code are organized as follows: first digit represent the study area (1= Val d'Ultimo, 2 = Valle del Braulio), second digit represent the landform (1 = control slope, 2 = scree slope, 3 = rock glacier), third digit represent the plot number.

Data analysis

Comparison among landforms

To compare the landforms in terms of microclimate features, descriptive statistics (mean value and standard deviation) of GST and GSH were calculated for the year 2014. Following Schmid et al. (2012), two distinct periods of the year were discerned: the snow-cover period (period with daily GST standard deviation < 0.2°C on the basis of 1 hour sampling rate) and the snow-free period (period with daily GST standard deviation > 0.2°C on the basis of 1 hour sampling rate). The snow cover period includes the zero-curtain one, which is the period affected by the latent heat effect in maintaining GST of freezing or thawing soils near 0°C (Outcalt et al., 1990) (period with GST ranging from -0.25 to 0.25°C in Gubler et al., 2011). To analyze the difference of GST and GSH among the landforms during the snow-cover period, two months during which all the landforms of both the areas were snow-covered but outside the zero-curtain period were analyzed: February and March 2014. To analyze the difference of GST and GSH among the landforms during the snow-free period, two months during which all the landforms of both the areas were snow-free were analyzed: August and September 2014.

To compare the landforms in terms of soil and community variables, regression methods were used: each variable was included in a regression model as response variable, except the landform which was included as explicative one. For all soil variables and cumulative ground cover, Quantile Regression Models (QRM) (Cade and Noon, 2003) were used, thus the median values of each variable were compared among landforms. To account for the correlation among sampling points within each plot, a random effect with Laplace distribution was included in each model (Geraci & Bottai, 2014).

For the remaining community variables (plant species richness, arthropod species richness and activity density), Generalized Linear Models (GLM) with Poisson error were used. To account for the correlation among sampling points within each plot, the models were estimated with Generalized Estimating Equation methods (Zeger et al., 1988), using an exchangeable working covariance matrix.

Results from all the models were reported in terms of estimated differences among medians (QRM) and mean ratios (GLM) among different landforms, with respective 95% Confidence Intervals. The Confidence Intervals were adjusted for multiple comparisons with the Bonferroni rule.

To identify characteristic plant and arthropod species of each landform, Indicator Species Analysis (ISA) (Dufrêne & Legendre, 1997) were used; the IndVal index for abundance data was used to quantify the association between species and the three landforms. Once identified the species with the highest association for each landform, such associations were assessed through permutation tests (number of permutations: 9999). In order to control for the "block effect" of sampling points within each plot, a restricted permutation scheme was adopted, in which sampling points within each plot permute, but cannot be exchanged with sampling points outside the plot.

All the analyses were performed with the R software (R Core Team 2015), with the packages FactoMineR (Husson et al., 2016), vegan (Oksanen et al., 2015), lqmm (Geraci, 2014), geepack (Højsgaard et al., 2006) and indicspecies (De Caceres & Legendre, 2009).

Relationships among variables and species ordination

To analyze the relationships among variables and species ordination, data were summarized at the level of plots (n=30) by using the median value for each soil and community variable, the mean cover for each plant species (22 plant species out of 118 were omitted since occurring in only one plot) and the sum of activity density for each arthropod species.

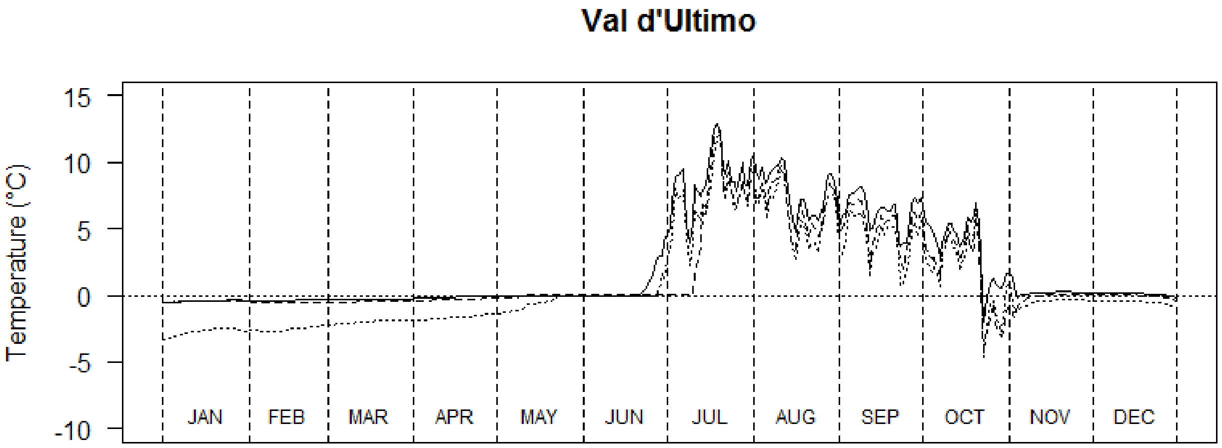
To evaluate the association among soil and community variables, Principal Component Analysis (PCA) methods were used. The assumption of linear correlation was checked by examining monotone correlation coefficients (Spearman's rho) and scatterplots for each couple of variables; due to the presence of some non-linear relationship, a PCA on the ranks of the variables was carried out. Soil parameters were used as active variables, community parameters were included as passive variables to evaluate their association with soil patterns.

To describe the patterns of species distribution and their relationships with environmental variables, Canonical Correspondence Analysis (CCA) (Ter Braak, 1986) was used. On the basis of the PCA results, coarse debris fraction, organic matter content and soil pH were selected as explanatory variables of the CCA, both for plant and arthropod species.

Results

Comparison among landforms

The investigated landforms showed the same GST pattern in both the study areas: control slopes and scree slopes were characterized by a similar thermal regime, while rock glaciers always showed lower temperature (Fig. 2, table 1). Mean daily GST in the snow-cover period of February-March were characterized by constant values, slightly below zero on the control slopes (-0.33 and -0.72°C for Val d'Ultimo and Valle del Braulio, respectively) and the scree slopes (-0.48 and -0.82°C) and much lower on the rock glaciers (-2.25 and -2.27°C). Mean daily GST during the snow-free period of August-September was characterized by less remarkable differences, but rock glaciers were again colder (5.25 and 3.95°C for Val d'Ultimo and Valle del Braulio, respectively) than surrounding control slopes (7.13 and 5.30°C) and scree slopes (6.12 and 5.09°C). Concerning GSH, all the landforms reached the constant value of 100% during the snow-cover period of period February-March, while the percentage varies during the snow-free period of August-September with the highest values generally reached on debris-featured landforms (table 1).



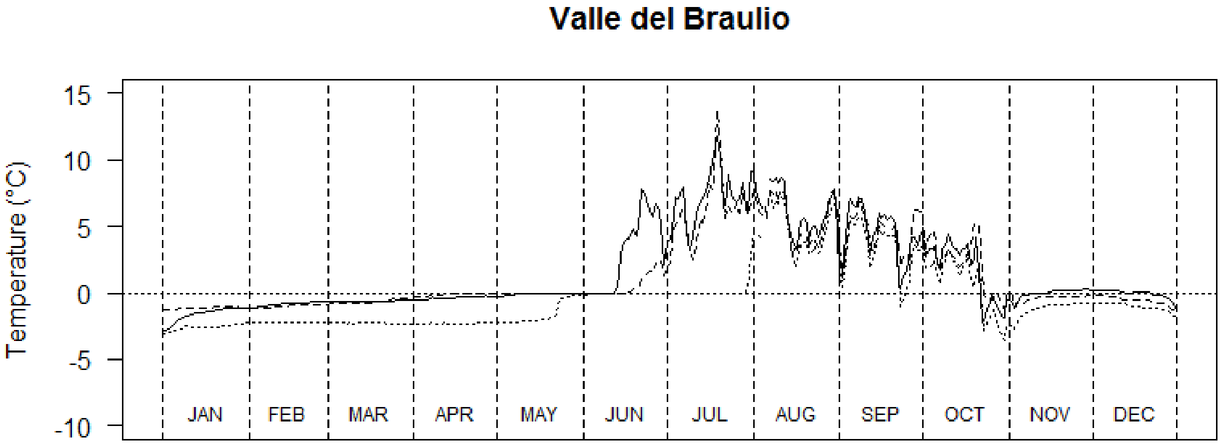


Fig. 2. Patterns of mean daily temperature of the investigated landforms over 2014: stables slopes (continuous line), scree slopes (dashed lines) and rock glaciers (dotted lines).

1. Val d'Ultimo

Landform	Altitude (m a.s.l.)	Aspect (°)	Slope (°)	Period	Length (days)	Ground surface temperature (°C)	Ground surface humidity (%)
1. Control slope	2415	330	20	Snow-cover	232	-0.11 (0.23)	100.00 (0.00)
				Snow-free	133	6.25 (2.91)	91.42 (8.44)
				February-March	59	-0.33 (0.05)	100.00 (0.00)
				Augus-September	61	7.13 (1.68)	92.27 (7.86)
				Year	365	2.21 (3.54)	96.85 (6.57)
2. Scree slope	2470	310	20	Snow-cover	249	-0.21 (0.24)	100.00 (0.00)
				Snow-free	116	5.10 (3.40)	95.43 (7.08)
				February-March	59	-0.48 (0.05)	100.00 (0.00)
				Augus-September	61	6.12 (1.85)	95.03 (6.85)
				Year	365	1.47 (3.13)	98.54 (4.53)
3. Rock glacier	2500	320	20	Snow-cover	236	-1.33 (0.99)	100.00 (0.00)
				Snow-free	129	4.63 (3.06)	92.72 (10.83)
				February-March	59	-2.25 (0.30)	100.00 (0.00)
				Augus-September	61	5.25 (2.00)	95.51 (6.94)
				Year	365	0.77 (3.48)	97.41 (7.33)

2. Valle del Braulio

Landform	Altitude (m a.s.l.)	Aspect (°)	Slope (°)	Period	Length (days)	Ground surface temperature (°C)	Ground surface humidity (%)
1. Control slope	2485	270	20	Snow-cover	221	-0.49 (0.59)	100.00 (0.00)
				Snow-free	144	4.72 (2.86)	96.88 (5.22)
				February-March	59	-0.72 (0.15)	100.00 (0.00)
				Augus-September	61	5.30 (2.09)	96.89 (4.89)
				Year	365	1.55 (3.14)	98.78 (3.60)
2. Scree slope	2610	295	35	Snow-cover	234	-0.46 (0.50)	100.00 (0.00)
				Snow-free	131	4.40 (2.50)	96.37 (7.02)
				February-March	59	-0.82 (0.23)	100.00 (0.00)
				Augus-September	61	5.09 (1.65)	96.48 (6.51)
				Year	365	1.28 (2.80)	98.69 (4.56)
3. Rock glacier	2595	330	15	Snow-cover	268	-1.49 (0.96)	100.00 (0.00)
				Snow-free	97	2.60 (2.66)	99.65 (1.58)
				February-March	59	-2.27 (0.04)	100.00 (0.00)
				Augus-September	61	3.95 (1.86)	99.42 (2.00)
				Year	365	-0.42 (2.40)	99.91 (0.82)

Table 1. Ground surface temperature and humidity recorded during 2014 on each landform. Results were reported as mean values (with standard deviation in brackets) for five periods of different length.

Debris-featured landforms differ from the control slope for higher values of bare soil surface, coarse debris fraction, soil pH and calcium carbonate content (where present) and lower values of organic matter content (except for Val d'Ultimo, where the organic matter content of the rock glacier is substantially equal to that of the control slope) (Fig. 3, table 2, table S1).

Similarly, debris-featured landforms differ from the control slope for lower plant species richness and cumulative ground cover (Fig. 3, table 2, table S1). The median values of arthropod community variables at the level of plot showed no differences among the landforms (Fig. 3, table 2, table S1), but the total values at the level of landform showed remarkable differences at least between control slopes and debris-featured landforms, the first being characterized by higher species richness and total activity density (table S1).

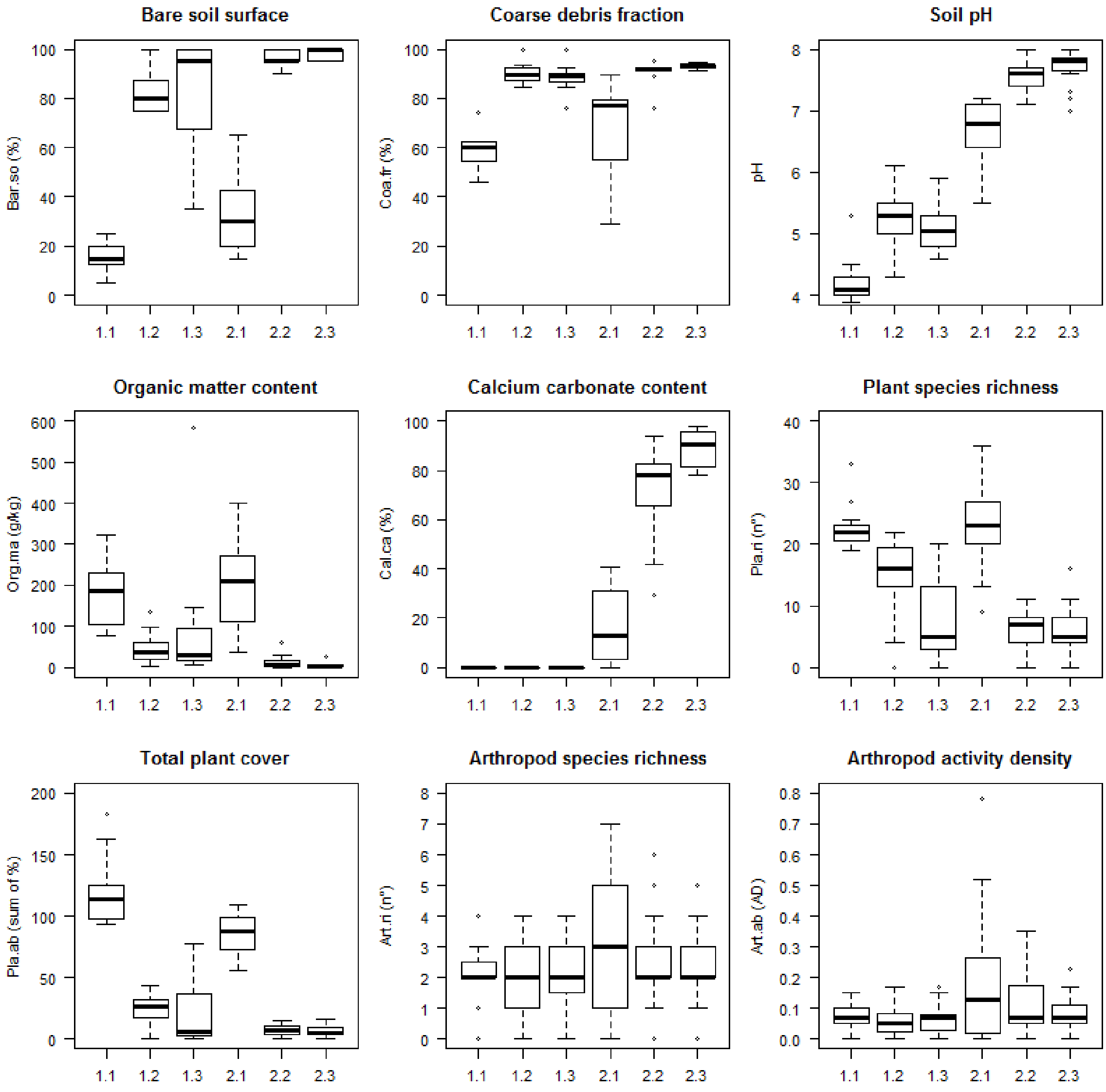


Fig. 3. Boxplot of each variable for the investigated landforms. Val d'Ultimo: control slope (1.1), scree slope (1.2), rock glacier (1.3); Valle del Braulio: control slope (2.1), scree slope (2.2), rock glacier (2.3).

1. Val d'Ultimo	**3 vs 2**	**3 vs 1**	**2 vs 1**
Bare soil surface (%)	15.1 (-15.0, 20.0)	80.2 (52.6, 85.0)	65.1 (60.0, 75.0)
Coarse debris fraction (%)	-2.6 (-6.2, 3.2)	25.4 (21.7, 36.9)	28.0 (22.0, 36.8)
Soil pH	0.0 (-0.6, 0.4)	0.9 (0.5, 1.4)	1.0 (0.5, 1.4)
Organic matter content (g/kg)	-1.4 (-46.9, 141.9)	-152.0 (-209.0, 14.0)	-150.6 (-212.0, -39.5)
Calcium carbonate content (%)	0.0 (-0.3, 0.3)	0.0 (-0.2, 0.5)	0.0 (-0.3, 0.3)
Plant species richness *	0.54 (0.22, 1.31)	0.65 (0.44, 0.97)	0.35 (0.16, 0.80)
Cumulative ground cover (%)	-23.7 (-28.4, 23.7)	-83.7 (-130.5, -65.0)	-107.4 (-111.4, -65.1)
Arthropod species richness *	1.10 (0.77, 1.56)	0.94 (0.64, 1.36)	1.03 (0.74, 1.43)
Arthropod total activity density *	1.09 (0.63, 1.90)	0.83 (0.49, 1.39)	0.90 (0.53, 1.54)
2. Valle del Braulio	**3 vs 2**	**3 vs 1**	**2 vs 1**
Bare soil surface (%)	5.0 (-2.8, 7.5)	70.0 (54.4, 80.0)	65.0 (51.9, 76.2)
Coarse debris fraction (%)	-2.6 (-1.0, 4.0)	15.6 (10.9, 38.3)	14.1 (9.6, 36.9)
Soil pH	0.2 (-0.1, 0.4)	1.0 (0.5, 1.5)	0.9 (0.5, 1.4)
Organic matter content (g/kg)	-1.0 (-17.7, 3.6)	-205.6 (-301.3, -111.0)	-204.5 (-298.8, -110.9)
Calcium carbonate content (%)	12.5 (-0.1, 32.4)	77.7 (46.6, 92.1)	65.2 (33.7, 80.6)
Plant species richness *	1.07 (0.39, 2.88)	0.26 (0.14, 0.50)	0.28 (0.12, 0.66)
Cumulative ground cover (%)	-1.0 (-6.1, 3.6)	-85.0 (-96.2, -62.7)	-83.9 (-96.7, -59.8)
Arthropod species richness *	0.95 (0.57, 1.58)	0.85 (0.41, 1.77)	0.81 (0.39, 1.66)
Arthropod total activity density *	0.70 (0.24, 2.04)	0.63 (0.15, 2.68)	0.44 (0.14, 1.36)

Table 2. Results of the multiple comparisons of variables among landforms: control slopes (1), scree slopes (2), rock glaciers (3). All the comparisons were carried out with QRM, except plant species richness, arthropod species richness and arthropod total activity density, which were carried out with GLM (Poisson distribution) (*). Results were reported as Est (95% C.I.).

The ISA (table S1) selected forty-eight plant species significantly linked to the control slopes (twenty-one on silicate substrate and twenty-seven on carbonate ones), among which the most significant (IndVal ≥ 0.90, $p \leq 0.0006$) were: *Anthoxanthum alpinum*, *Potentilla aurea*, *Primula glutinosa*, *Carex curvula*, *Leontodon helveticus*, *Loiseleuria procumbens*, *Vaccinium gaultherioides*, *Ligusticum mutellina* and *Soldanella alpicola* for silicate substrates; *Agrostis alpina*, *Carex firma*, *Dryas octopetala*, *Sedum atratum*, *Ranunculus alpestris* and *Saxifraga caesia* for carbonate substrates. Fourteen plant species were significantly linked to the scree slopes: nine on silicate substrates (*Oxyria digyna*, *Saxifraga seguieri*, *Geum reptans*, *Pritzelago brevicaulis*, *Ranunculus glacialis*, *Veronica alpina*, *Sedum alpestre*, *Cystopteris fragilis* and *Cerastium uniflorum*) and five on carbonate ones (*Saxifraga aphylla*, *Pritzelago alpina*, *Papaver aurantiacum*, *Arabis pumila* and *Poa minor*). Six plant species were significantly linked to the rock glaciers: four on silicate substrates (*Poa laxa*, *Doronicum clusii*, *Senecio carniolicus* and *Saxifraga bryoides*) and two on carbonate ones (*Arabis caerulea* and *Arabis alpina*).

The ISA (table S1) selected four arthropod species significantly linked to the control slopes: the carabid beetles *Cymindis vaporariorum* (found both on silicate and carbonate control slopes) and *Carabus sylvestris* (found only on carbonate control slope) and the spiders *Pardosa giebeli* and *Xysticus desidiosus* (both found only on carbonate control slope). One spider was significantly linked to the scree slopes: *Anguliphantes monticola* (found both on silicate and carbonate substrates). Two spiders were significantly linked to the rock glaciers: *Pardosa nigra* (found both on silicate and carbonate substrates) and *Sitticus longipes* (found only on carbonate substrate).

Relationships among variables and species ordination

Soil parameters were all correlated with each other (Fig. 4, table 3). High positive correlations occurred between soil pH and calcium carbonate content and between bare soil surface and coarse debris fraction, while all of them were negatively correlated with organic matter content. Plant species richness and cumulative ground cover were both positively correlated with organic matter content and thus negatively correlated to the other soil variables; arthropod species richness and activity density were positively correlated with each other but lowly correlated with the other variables (Fig. 4, table 3).

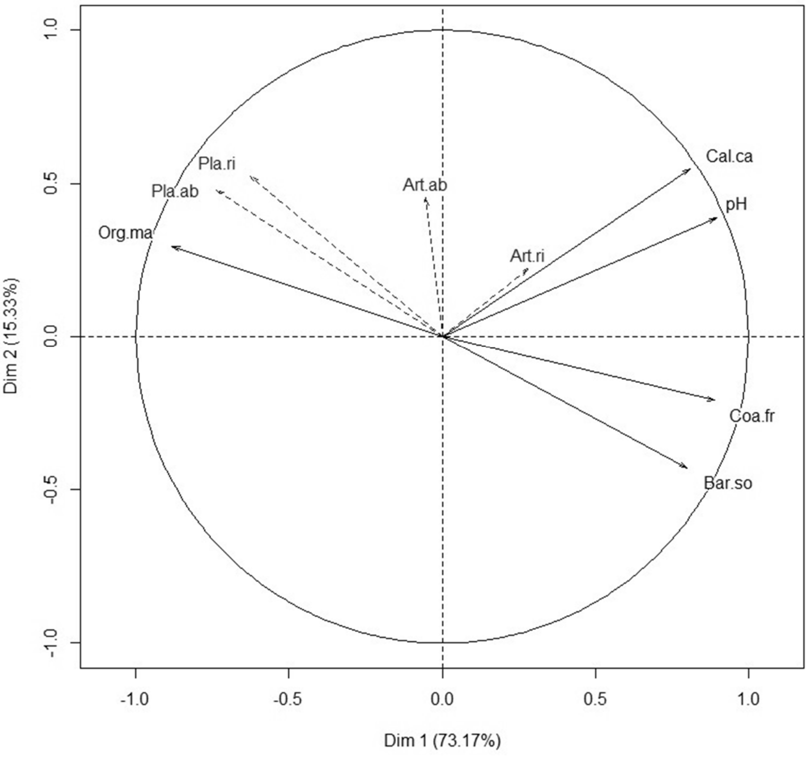


Fig. 4. PCA diagram showing the mutual relations among variables.

	Bar.so	Coa.fr	pH	Org.ma	Cal.ca	Pla.ri	Pla.ab	Art.ri	Art.ab
Bar.so	1	0,69	0,55	-0,73	0,46	-0,88	-0,96	0,15	-0,29
Coa.fr	0,69	1	0,70	-0,81	0,57	-0,57	-0,63	0,24	-0,07
pH	0,55	0,70	1	-0,67	0,90	-0,35	-0,48	0,34	0,10
Org.ma	-0,73	-0,81	-0,67	1	-0,54	0,62	0,72	-0,13	0,18
Cal.ca	0,46	0,57	0,90	-0,54	1	-0,27	-0,37	0,34	0,22
Pla.ri	-0,88	-0,57	-0,35	0,62	-0,27	1	0,93	0,11	0,40
Pla.ab	-0,96	-0,63	-0,48	0,72	-0,37	0,93	1	-0,09	0,35
Art.ri	0,15	0,24	0,34	-0,13	0,34	0,11	-0,09	1	0,66
Art.ab	-0,29	-0,07	0,10	0,18	0,22	0,40	0,35	0,66	1

Table 3. Correlation table among variables: bare soil surface (Bar.so), coarse debris fraction (Coa.fr), soil pH (pH), organic matter content (Org.ma), calcium carbonate content (Cal.ca), plant species richness (Pla.ri), cumulative ground cover (Pla.ab), arthropod species richness (Art.ri), total arthropod activity density (Art.ab). Results were reported as Spearman's index of monotone correlation (rho).

The first two axis of CCA of plant species (Fig. 5) explained 32.31% of the total explained inertia (18.45 and 13.86 % for the first and second axis, respectively). The first axes was highly correlated with soil pH (r index = 0.97) and separated the control slope on silicate substrate from the other landforms, while the second axes was correlated with organic matter content and coarse debris fraction (r index = 0.82 and -0.59, respectively) and separated control slopes from debris-featured landforms. The CCA plot showed a clear partition in four main groups of sites corresponding to control slope and debris-featured landforms on silicate and carbonate substrates, respectively. No distinction resulted between scree slopes and rock glaciers.

The first two axis of CCA of arthropod species (Fig. 5) explained 17.78% of the total explained inertia (10.19 and 7.59 % for the first and second axis, respectively). The first axes was correlated with organic matter content (r index = -0.71) and separated the control slope on carbonate substrates from the other landforms, while the second was highly correlated with soil pH (r index = 0.92) and separated the control slope and debris-featured landforms on silicate substrate from debris-featured landforms on carbonate one. Coarse debris fraction was quite equally correlated with the first and the second axis (r index = 0.58 and 0.64, respectively). The CCA plot did not show a clear partition, but a cloud of sites and species in which two main gradients are recognizable: the main one occurring from control slopes to debris-featured landforms and a slighter one tending to separate the two study areas. No distinction resulted between scree slopes and rock glaciers.

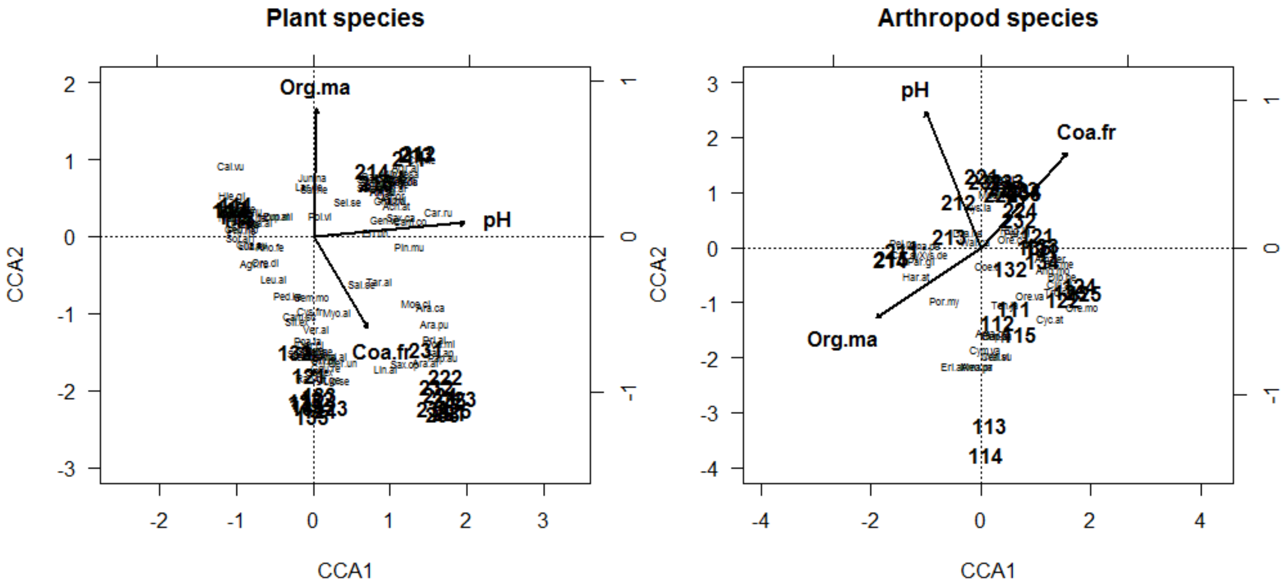


Fig. 5. CCA ordination plots of plant and arthropod species with soil variables: coarse debris fraction (Coa.fr), soil pH (pH), organic matter content (Org.ma). Sites code are organized as follows: first digit represent the study area (1= Val d'Ultimo, 2 = Valle del Braulio), second digit represent the landform (1 = control slope, 2 = scree slope, 3 = rock glacier), third digit represent the plot number. Species codes are reported in table 5.

Discussion

Ecology of active rock glaciers and surrounding landforms

The comparison among landforms in terms of abiotic and biotic features shows overall remarkable differences between control slopes and debris-featured landforms, while few differences occur between scree slopes and rock glaciers.

The GST of control slopes are characterized by a pattern typically expected at the considered altitude where permafrost is absent: a long-lasting snow-cover period with values constantly around 0°C due to the snow-cover insulation from air temperature; a zero-curtain period maintaining approximately 0°C due to the latent heat effect of freezing or thawing soil; a relatively brief snow-free period with values affected by air temperature, generally ranging above 0°C (Outcalt et al., 1990; Hoelzle et al., 1999; Schmid et al. 2012). While scree slopes show a GST pattern substantially analogue to that of control slope, rock glaciers are characterized by overall lower values (despite not necessarily higher GSH and longer-lasting snow cover), likely as a consequence of the thermal effect of underlying ice (Hoelzle et al., 1999). The hypothesis 1a (rock glaciers differ from the surrounding landforms for ground surface temperature/humidity) is thus supported by our data concerning temperature.

The soils of control slope can be likely considered as more developed than those of debris-featured landforms, since organic matter content is higher and coarse debris fraction, calcium carbonate content (where present) and soil pH are lower (Matthews, 1992; Tampucci et al., 2015b). Scree slopes and rock glaciers show opposite soil features, substantially analogue to each other. The hypothesis 1b (rock glaciers differ from the surrounding landforms for soil physical/chemical parameters) is thus overall supported by our data only concerning the comparison with control slopes.

The control slopes show high plant species richness and cumulative ground cover, including species generally expected in alpine grasslands like *Carex curvula*, *Primula glutinosa* and *Loiseleuria procumbens* on silicate substrates and *Carex firma*, *Dryas octopetala* and *Saxifraga caesia* on carbonate ones (Grabherr & Mucina, 1993; Oberdorfer, 1998). Coherently, arthropod community are characterized by relatively high species richness and activity density, with typical species of alpine grasslands like the ground beetles *Carabus sylvestris* and *Cymindis vaporariorum* (Casale et al., 1982; Gobbi et al., 2007) or the spider *Xysticus desidiosus* (Nentwig et al., 2016; Pantini & Isaia, 2016). Even if plant and arthropod communities of scree slopes and rock glaciers show few differences in terms of species richness and abundance, some characteristic species of the two debris-featured landforms can be identified. Scree slopes are characterized by plant species typically adapted to mechanical disturbance (e.g. *Geum reptans* and *Oxyria digyna* on silicate substrates or *Saxifraga aphylla* and *Papaver aurantiacum* on carbonate ones) (Grabherr & Mucina, 1993; Oberdorfer, 1998) and by a spider widespread on a wide altitudinal range (*Anguliphantes monticola*) (Nentwig et al., 2016); rock glaciers host plant species known as indicators of cold-wet microclimates and long-lasting snow cover (e.g. *Doronicum clusii* on silicate substrates and *Arabis caerulea* on carbonate ones) (Grabherr & Mucina, 1993; Oberdorfer, 1998) and strictly cold-adapted spiders (e.g. *Pardosa nigra* and *Sitticus longipes*) (Thaler, 2003; Negro et al., 2010). Therefore, the hypothesis 2a (rock glaciers differ from the surrounding landforms for plant/arthropod species richness/abundance) is overall supported by our data only concerning the comparison with control slopes, while the hypothesis 2b (rock glaciers differ from the surrounding landforms for cold-adapted plant/arthropod species) is overall supported by our data.

Our results show that plant and arthropod species distributions throughout the investigated areas and landforms are driven by the same soil variables: soil pH is linked to the different substrates occurring in the two areas; coarse debris fraction and organic matter content indicate the distinction between control slopes and debris-featured landforms as whole. If the plant species mutually exclusive of the two areas can be certainly attributed to the substrate and its related soil pH (e.g. Aeschimann et al., 2004; Landolt et al., 2010), the possible influence of such factor on arthropod fauna is unclear: species found only on one of the two substrates in our study (e.g. the carabid beetle *Carabus sylvestris* and the spiders *Xysticus desidiosus* and *Pardosa giebeli* on carbonate substrate) were found on the other substrate as well in previous studies (e.g. Gobbi et al., 2006a, 2006b, 2010, 2014). The differences of arthropod fauna between the two study areas are thus likely not imputable to the substrate itself, but probably to the presence of niche defined by scenopoetic variables (Soberón, 2010).

Soil features explain the plant and arthropod community differences between control slopes and debris-featured landforms as a whole, but are not enough to discern those of scree slopes and rock glaciers. Our third hypothesis (the soil variables drive the distribution of plant/arthropod species through the investigated landforms) is thus supported by our data only concerning the difference between control slopes and debris-featured landforms as a whole, both on silicate and carbonate substrates.

Summarizing, scree slopes and rock glaciers show substantially analogue soil features, but different GST (lower on rock glaciers) and different occurrence of cold-adapted species (more frequent/abundant on rock glaciers). The peculiarity of active rock glaciers as habitat for plant and arthropod species seems thus to be linked to microclimate rather than soil features.

The results obtained by our study can be compared only with the data collected by Gobbi et al. (2014) in the near (c. 30 and 40 km far from our study areas, respectively) Amola rock glacier (Val d'Amola, Adamello-Presanella Massif), to our knowledge the only previous study with a similar approach. The rock glacier of Val d'Amola, in contrast with those of Val d'Ultimo and Valle del Braulio, is characterized by the presence of exclusive and large populations of cold-adapted ground beetle species. This difference could be linked to some peculiarities of the physical environment of such landform, in particular: 1) the occurrence of boulders up to some meters in diameter able to prevent a continuous snow-cover insulation from air in winter; 2) mean annual GST much lower with respect to the surrounding scree slope (5.40°C lower, against 0.70°C lower in Val d'Ultimo and 1.70°C lower in Valle del Braulio). These features probably also act as limiting factor for plant survival. On the herein investigated rock glaciers the occurrence of smaller boulders and annual GST more similar between rock glaciers and scree slopes may sustain cold-adapted plants, but are likely not enough to affect ground beetles distribution (Gobbi et al. 2014).

The variability of grain size and microclimate features of active rock glaciers may provide suitable habitat for different taxa depending on their own thermal requirement, making the ecological role of these landforms in mountain landscape more complex than previously believed. Even if the sample size is low (two rock glaciers plus that described by Gobbi et al., 2014), the observed sites cover a broad array of substrate conditions: carbonate substrate with relatively small debris size (Valle del Braulio), metamorphic rocks with coarse substrate (Val d'Ultimo) and igneous rocks with metric boulders (Val d'Amola, Gobbi et al., 2014). Such variability explains the observed heterogeneity in many soils parameters but does not affect the coherent overall picture of a marked influence of rock glaciers on local topoclimate.

Active rock glaciers as warm-stage refugia?

Cold-adapted species are the first to be threatened by current climate change, as consequence of the progressive reduction of their habitat due to the temperature increase and to the upshift of altitudinal belts (Theurillat & Guisan, 2001; Pauli et al., 2003; Thuiller et al., 2005; Dullinger et al., 2012; Pizzolotto et al., 2014; Moret et al., 2016). Active rock glaciers were previously proposed as potential warm-stage refugia for cold-adapted species because of their microclimate features (Millar et al., 2010, 2013; Gobbi et al., 2014; Gentili et al., 2015), a role similar to that proposed for debris-covered glaciers (Caccianiga et al., 2011; Gobbi et al., 2011).

The thermal profile observed on our rock glaciers supports this view, indicating a decoupling of the local topoclimate from the regional climate, a key factor for a site to serve as refugium (Dobrowski, 2011; Keppel et al., 2012). A critical point lies in the capability of rock glaciers to persist under adverse conditions: many studies showed that active rock glaciers, despite their thermal inertia (Frauenfelder & Kääb, 2000), tend to become climatically inactive and then relict (without ice) once climate becomes no more suitable (Barsch, 1996; Sorg et al. 2015). Furthermore, enhanced activity may occur at decadal scale in correspondence with warm periods (Sorg et al., 2015), making rock glaciers difficult to colonize during such already critical climatic stages.

Even though the investigated active rock glaciers are the lowest of the respective study areas, they still stand well above the climatic treeline: control slopes host primary alpine grasslands where cold-adapted species already occur (e.g. Landolt et al., 2010; Nentwig et al., 2016; Homburg et al., 2014). On drier, continental mountain ranges the altitude of active rock glaciers tends to decrease (Scotti et al., 2013), whereas that of the climatic treeline increases (Caccianiga et al., 2008). As a consequence, on extremely dry-continental mountain ranges such as the American Sierra Nevada (Millar et al., 2013) and Tien Shan Mountains in Central Asia (Sorg et al.., 2015) active rock glaciers occur below the climatic treeline, allowing cold-adapted species to occur well below their normal altitudinal distribution. For this reason, the role of rock glaciers as warm-stage refugia seems more important on such mountain range than on European Alps, where ecological heterogeneity and topoclimate decoupling induced by rock glaciers with respect of the surrounding landscape appear less consistent. On European Alps a more marked refigium role could be played by debris-covered glaciers, whose peculiar mass balance allows them to descend below the treeline (Caccianiga et al., 2011; Gobbi et al., 2011).

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Table S1. Synoptic table at landform level: soil and community variables were expressed as median values (with minimum and maximum values in brackets), followed by total values at landform level (for community variables ony); plant species cover (Ab) were expressed as mean value of cover in percentage; arthropod species abundances (Ab) were expressed as sum of activity density (ara = spider; car = carabid beetles); for each species were indicated: IndVal for each landform (IndVal), best-fitting landform (BFL), significance of the association with the best-fitting landform (p-value, with * for significantly association).

ID	**Area**	**1. Val d'Ultimo**						**2. Valle del Braulio**								
	Landform	**1. Control slope**		**2. Scree slope**		**3. Rock glacier**		**1. Control slope**		**2. Scree slope**		**3. Rock glacier**				
Bar.so	**Bare soil surface (%)**	15 (5, 25)		80 (75, 100)		95 (35, 100)		30 (15, 65)		95 (90, 100)		100 (95, 100)				
Coa.fr	**Coarse debris fraction (%)**	60 (46, 74)		90 (84, 100)		89 (76, 100)		77 (29, 89)		92 (76, 95)		93 (91, 95)				
pH	**Soil pH**	4.1 (3.9, 5.3)		5.3 (4.3, 6.1)		5.1 (4.6, 5.9)		6.8 (5.5, 7.2)		7.6 (7.1, 8.0)		7.8 (7.0, 8.0)				
Org.ma	**Organic matter content (g/kg)**	184.71 (77.24, 320.80)		36.67 (2.63, 134.30)		29.47 (6.31, 582.80)		208.80 (36.94, 398.80)		4.61 (0.33, 61.15)		3.94 (1.00, 25.45)				
Cal.ca	**Calcium carbonate content (%)**	0.00 (0.00, 0.00)		0.00 (0.00, 0.00)		0.00 (0.00, 0.00)		12.86 (0.00, 40.82)		78.01 (29.46, 93.63)		90.56 (77.84, 98.07)				
Pla.ri	**Plant species richness**	22 (19, 33), 45		16 (0, 22), 43		5 (0, 20), 30		23 (9, 36), 60		7 (0, 11), 20		5 (0, 16), 24				
Pla.ab	**Cumulative ground cover (%)**	114 (93, 183), 118		27 (0, 43), 24		6 (0, 78), 22		88 (56, 109), 86		7 (0, 15), 7		5 (0, 16), 7				
Art.ri	**Arthropod species richness**	2 (0, 4), 21		2 (0, 4), 10		2 (0, 4), 8		3 (0, 7), 15		2 (0, 6), 14		2 (0, 5), 9				
Art.ab	**Arthropod total activity density**	0.07 (0.00, 0.15), 1.12		0.05 (0.00, 0.17), 0.97		0.07 (0.00, 0.17), 1.01		0.13 (0.00, 0.78), 3.14		0.07 (0.00, 0.35), 1.86		0.07 (0.00, 0.23), 1.31				
Plant species		**Ab**	**IndVal**	**Ab**	**IndVal**	**Ab**	**IndVal**	**Ab**	**IndVal**	**Ab**	**IndVal**	**Ab**	**IndVal**	**BFL**	**p-value**	**Sig.**
Ant.al	***Anthoxanthum alpinum***	18,00	1,00	0,00	0,00	0,07	0,02	0,00	0,00	0,00	0,00	0,00	0,00	1.1	0,0006	*
Pot.au	***Potentilla aurea***	3,40	1,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	1.1	0,0006	*
Pri.gl	***Primula glutinosa***	1,53	1,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	1.1	0,0006	*
Car.cu	***Carex curvula***	26,67	0,99	0,00	0,00	0,33	0,03	0,00	0,00	0,00	0,00	0,00	0,00	1.1	0,0006	*
Leo.he	***Leontodon helveticus***	4,53	0,97	0,00	0,00	0,07	0,03	0,27	0,12	0,00	0,00	0,00	0,00	1.1	0,0006	*
Loi.pr	***Loiseleuria procumbens***	6,07	0,97	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	1.1	0,0006	*
Vac.ga	***Vaccinium gaultherioides***	4,33	0,96	0,00	0,00	0,00	0,00	0,07	0,03	0,00	0,00	0,00	0,00	1.1	0,0006	*
Lig.mu	***Ligusticum mutellina***	4,27	0,95	0,07	0,03	0,00	0,00	0,40	0,11	0,00	0,00	0,00	0,00	1.1	0,0006	*
Sol.al1	***Soldanella alpicola***	11,80	0,95	1,07	0,21	0,13	0,04	0,00	0,00	0,00	0,00	0,00	0,00	1.1	0,0006	*
Hel.ve	***Helictotrichon versicolor***	3,40	0,86	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	1.1	0,0006	*
Phy.he	***Phyteuma hemisphaericum***	0,80	0,86	0,00	0,00	0,07	0,07	0,00	0,00	0,00	0,00	0,00	0,00	1.1	0,0006	*
Poa.al	***Poa alpina***	3,20	0,89	0,20	0,10	0,00	0,00	0,40	0,12	0,00	0,00	0,00	0,00	1.1	0,0012	*
Hom.al	***Homogyne alpina***	12,33	0,86	0,07	0,02	0,07	0,02	4,00	0,38	0,07	0,02	0,00	0,00	1.1	0,0012	*
Agr.ru	***Agrostis rupestris***	4,47	0,90	0,47	0,20	0,60	0,19	0,00	0,00	0,00	0,00	0,00	0,00	1.1	0,0018	*
Geu.mo	***Geum montanum***	0,33	0,58	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	1.1	0,0018	*
Hup.se	***Huperzia selago***	0,40	0,63	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	1.1	0,0030	*
Gna.su	***Gnaphalium supinum***	1,00	0,76	0,27	0,24	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	1.1	0,0036	*
Leu.al	***Leucanthemopsis alpina***	0,80	0,68	0,07	0,06	0,47	0,39	0,00	0,00	0,00	0,00	0,07	0,06	1.1	0,0054	*

Eup.mi	***Euphrasia minima***	0,93	0,77	0,00	0,00	0,13	0,11	0,40	0,19	0,00	0,00	0,00	0,00	1.1	0,0072	*
Nar.st	***Nardus stricta***	1,87	0,58	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	1.1	0,0167	*
Hie.gl	***Hieracium glanduliferum***	0,33	0,58	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	1.1	0,0196	*
Jun.na	***Juniperus nana***	0,20	0,35	0,00	0,00	0,00	0,00	0,13	0,23	0,00	0,00	0,00	0,00	1.1	0,1022	
Cal.vu	***Calluna vulgaris***	0,13	0,37	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	1.1	0,1223	
Luz.lu	***Luzula lutea***	0,40	0,37	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	1.1	0,1372	
Ore.di	***Oreochloa disticha***	0,13	0,30	0,07	0,15	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	1.1	0,3224	
Rho.fe	***Rhododendron ferrugineum***	1,20	0,70	0,07	0,04	1,00	0,17	0,00	0,00	0,00	0,00	0,00	0,00	1.1	0,3980	
Pin.le	***Pinguicula leptoceras***	0,07	0,26	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	1.1	0,6403	
Sib.pr	***Sibbaldia procumbens***	0,07	0,26	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	1.1	0,6403	
Alc.vu	***Alchemilla* gr. *vulgaris***	0,40	0,37	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	1.1	0,6574	
Cir.sp	***Cirsium spinosissimum***	0,07	0,26	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	1.1	0,6574	
Dip.al	***Diphasiastrum alpinum***	0,07	0,26	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	1.1	0,6591	
Ped.ke	***Pedicularis kerneri***	0,20	0,32	0,20	0,32	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	1.1	0,6637	
Lar.de	***Larix decidua***	0,07	0,18	0,00	0,00	0,00	0,00	0,07	0,18	0,00	0,00	0,00	0,00	1.1	0,8806	
Oxy.di	***Oxyria digyna***	0,00	0,00	3,00	0,93	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	1.2	0,0006	*
Sax.se	***Saxifraga seguieri***	0,00	0,00	0,93	0,82	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	1.2	0,0006	*
Geu.re	***Geum reptans***	0,00	0,00	2,07	0,86	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	1.2	0,0018	*
Pri.br	***Pritzelago brevicaulis***	0,00	0,00	0,40	0,63	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	1.2	0,0018	*
Ran.gl	***Ranunculus glacialis***	0,00	0,00	0,33	0,58	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	1.2	0,0024	*
Ver.al	***Veronica alpina***	0,13	0,13	0,67	0,65	0,13	0,13	0,07	0,06	0,00	0,00	0,07	0,06	1.2	0,0042	*
Sed.al	***Sedum alpestre***	0,07	0,07	0,60	0,64	0,20	0,21	0,00	0,00	0,00	0,00	0,00	0,00	1.2	0,0084	*
Cys.fr	***Cystopteris fragilis***	0,00	0,00	0,33	0,49	0,07	0,10	0,07	0,10	0,00	0,00	0,00	0,00	1.2	0,0471	*
Cer.un	***Cerastium uniflorum***	0,00	0,00	1,67	0,65	1,07	0,41	0,00	0,00	0,33	0,18	0,33	0,18	1.2	0,0476	*
Sil.ex	***Silene exscapa***	0,80	0,27	1,33	0,71	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	1.2	0,0693	
Car.re	***Cardamine resedifolia***	0,07	0,07	0,47	0,50	0,33	0,36	0,00	0,00	0,00	0,00	0,00	0,00	1.2	0,0872	
Art.ge	***Artemisia genipi***	0,00	0,00	0,20	0,45	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	1.2	0,1308	
And.al	***Androsace alpina***	0,00	0,00	0,13	0,37	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	1.2	0,1319	
Sax.ex	***Saxifraga exarata***	0,00	0,00	0,33	0,43	0,27	0,34	0,00	0,00	0,00	0,00	0,00	0,00	1.2	0,2630	
Lin.al	***Linaria alpina***	0,00	0,00	0,13	0,26	0,00	0,00	0,00	0,00	0,00	0,00	0,13	0,26	1.2	0,5260	
Cry.cr	***Cryptogramma crispa***	0,00	0,00	0,07	0,26	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	1.2	0,6512	
Sax.an	***Saxifraga androsacea***	0,00	0,00	0,07	0,26	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	1.2	0,6709	
Sax.pa	***Saxifraga paniculata***	0,00	0,00	0,07	0,26	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	1.2	0,6709	
Myo.al	***Myosotis alpestris***	0,00	0,00	0,47	0,28	0,40	0,21	0,33	0,30	0,00	0,00	0,00	0,00	1.2	0,7729	
Sem.mo	***Sempervivum montanum***	0,00	0,00	0,07	0,18	0,07	0,18	0,00	0,00	0,00	0,00	0,00	0,00	1.2	0,8875	
Llo.se	***Lloydia serotina***	0,00	0,00	0,07	0,18	0,07	0,18	0,00	0,00	0,00	0,00	0,00	0,00	1.2	0,8918	
Poa.la	***Poa laxa***	0,00	0,00	0,73	0,44	2,00	0,80	0,00	0,00	0,00	0,00	0,00	0,00	1.3	0,0036	*
Dor.cl	***Doronicum clusii***	0,00	0,00	0,20	0,11	2,93	0,79	0,00	0,00	0,00	0,00	0,00	0,00	1.3	0,0036	*
Sen.ca	***Senecio carniolicus***	0,00	0,00	0,13	0,18	0,40	0,55	0,00	0,00	0,00	0,00	0,00	0,00	1.3	0,0125	*
Sax.br	***Saxifraga bryoides***	0,00	0,00	1,33	0,57	2,00	0,72	0,00	0,00	0,00	0,00	0,00	0,00	1.3	0,0413	*
Luz.al	***Luzula alpinopilosa***	0,33	0,10	3,73	0,58	6,40	0,67	0,00	0,00	0,00	0,00	0,00	0,00	1.3	0,0766	
Fes.ha	***Festuca halleri***	0,07	0,06	0,13	0,11	1,20	0,53	0,00	0,00	0,00	0,00	0,00	0,00	1.3	0,1372	
Cam.sc	***Campanula scheuchzeri***	0,13	0,23	0,00	0,00	0,20	0,35	0,00	0,00	0,00	0,00	0,00	0,00	1.3	0,6709	

Agr.al	***Agrostis alpina***	0,00	0,00	0,00	0,00	0,00	0,00	2,67	1,00	0,00	0,00	0,00	0,00	2.1	0,0006	*
Car.fi	***Carex firma***	0,00	0,00	0,00	0,00	0,00	0,00	22,80	1,00	0,00	0,00	0,00	0,00	2.1	0,0006	*
Dry.oc	***Dryas octopetala***	0,00	0,00	0,00	0,00	0,00	0,00	17,53	0,93	0,00	0,00	0,00	0,00	2.1	0,0006	*
Sed.at	***Sedum atratum***	0,00	0,00	0,00	0,00	0,00	0,00	0,87	0,93	0,00	0,00	0,00	0,00	2.1	0,0006	*
Ran.al	***Ranunculus alpestris***	0,00	0,00	0,00	0,00	0,00	0,00	2,53	0,92	0,00	0,00	0,07	0,04	2.1	0,0006	*
Sax.ca	***Saxifraga caesia***	0,00	0,00	0,00	0,00	0,00	0,00	1,27	0,91	0,07	0,05	0,20	0,16	2.1	0,0006	*
Ses.ca	***Sesleria caerulea***	0,00	0,00	0,00	0,00	0,00	0,00	5,07	0,89	0,00	0,00	0,00	0,00	2.1	0,0006	*
Min.ve	***Minuartia verna***	0,00	0,00	0,00	0,00	0,00	0,00	0,67	0,82	0,00	0,00	0,00	0,00	2.1	0,0006	*
Ast.be	***Aster bellidiastrum***	0,00	0,00	0,00	0,00	0,00	0,00	1,47	0,80	0,07	0,05	0,00	0,00	2.1	0,0006	*
Ach.at	***Achillea atrata***	0,00	0,00	0,00	0,00	0,00	0,00	0,73	0,79	0,07	0,07	0,07	0,07	2.1	0,0006	*
Car.or	***Carex ornithopoda***	0,00	0,00	0,00	0,00	0,00	0,00	0,87	0,77	0,00	0,00	0,00	0,00	2.1	0,0006	*
Sol.al2	***Soldanella alpina***	0,00	0,00	0,00	0,00	0,00	0,00	5,13	0,77	0,00	0,00	0,07	0,03	2.1	0,0006	*
Asp.vi	***Asplenium viride***	0,00	0,00	0,00	0,00	0,00	0,00	0,53	0,69	0,07	0,09	0,00	0,00	2.1	0,0006	*
Cam.co	***Campanula cochleariifolia***	0,00	0,00	0,00	0,00	0,00	0,00	0,60	0,67	0,07	0,07	0,13	0,15	2.1	0,0006	*
Val.sa	***Valeriana saxatilis***	0,00	0,00	0,00	0,00	0,00	0,00	0,33	0,58	0,00	0,00	0,00	0,00	2.1	0,0006	*
Bar.al	***Bartsia alpina***	0,07	0,07	0,00	0,00	0,00	0,00	0,73	0,82	0,00	0,00	0,00	0,00	2.1	0,0012	*
Hel.al	***Helianthemum alpestre***	0,00	0,00	0,00	0,00	0,00	0,00	0,80	0,73	0,00	0,00	0,00	0,00	2.1	0,0018	*
Ant.vu	***Anthyllis vulneraria***	0,00	0,00	0,00	0,00	0,00	0,00	0,47	0,68	0,00	0,00	0,00	0,00	2.1	0,0024	*
Pin.al	***Pinguicula alpina***	0,00	0,00	0,00	0,00	0,00	0,00	0,27	0,52	0,00	0,00	0,00	0,00	2.1	0,0024	*
Pol.vi	***Polygonum viviparum***	0,87	0,61	0,20	0,14	0,00	0,00	0,93	0,66	0,00	0,00	0,00	0,00	2.1	0,0036	*
Eri.un	***Erigeron uniflorus***	0,00	0,00	0,00	0,00	0,27	0,28	0,60	0,62	0,00	0,00	0,07	0,07	2.1	0,0096	*
Sal.re1	***Salix reticulata***	0,00	0,00	0,00	0,00	0,00	0,00	0,67	0,63	0,00	0,00	0,00	0,00	2.1	0,0143	*
Car.pa	***Carex parviflora***	0,00	0,00	0,00	0,00	0,00	0,00	0,33	0,58	0,00	0,00	0,00	0,00	2.1	0,0143	*
Sil.ac	***Silene acaulis***	0,00	0,00	0,00	0,00	0,00	0,00	2,87	0,63	0,00	0,00	0,00	0,00	2.1	0,0149	*
Dra.ai	***Draba aizoides***	0,00	0,00	0,00	0,00	0,00	0,00	0,53	0,73	0,00	0,00	0,00	0,00	2.1	0,0155	*
Gna.ho	***Gnaphalium hoppeanum***	0,00	0,00	0,00	0,00	0,00	0,00	0,40	0,59	0,00	0,00	0,07	0,10	2.1	0,0279	*
Gen.ve	***Gentiana verna***	0,00	0,00	0,00	0,00	0,13	0,18	0,40	0,55	0,00	0,00	0,00	0,00	2.1	0,0407	*
Cre.ke	***Crepis kerneri***	0,00	0,00	0,00	0,00	0,00	0,00	0,13	0,37	0,00	0,00	0,00	0,00	2.1	0,1330	
Sel.se	***Selaginella selaginoides***	0,13	0,20	0,00	0,00	0,00	0,00	0,33	0,49	0,00	0,00	0,00	0,00	2.1	0,1582	
Sal.he	***Salix herbacea***	2,07	0,59	0,27	0,11	0,07	0,03	3,07	0,43	0,00	0,00	0,00	0,00	2.1	0,3008	
Pin.mu	***Pinus mugo***	0,00	0,00	0,00	0,00	0,00	0,00	0,13	0,30	0,00	0,00	0,07	0,15	2.1	0,3383	
Tar.al	***Taraxacum alpinum* s.l.**	0,00	0,00	0,27	0,29	0,00	0,00	0,33	0,36	0,07	0,07	0,20	0,21	2.1	0,4600	
Sal.se	***Salix serpillifolia***	0,13	0,07	0,33	0,08	1,33	0,23	1,40	0,60	0,00	0,00	0,20	0,11	2.1	0,5744	
Ver.ap	***Veronica aphylla***	0,00	0,00	0,00	0,00	0,00	0,00	0,13	0,37	0,00	0,00	0,00	0,00	2.1	0,6522	
Car.ru	***Carex rupestris***	0,00	0,00	0,00	0,00	0,00	0,00	0,13	0,30	0,00	0,00	0,07	0,15	2.1	0,6522	
Dap.st	***Daphne striata***	0,00	0,00	0,00	0,00	0,00	0,00	0,07	0,26	0,00	0,00	0,00	0,00	2.1	0,6522	
Glo.co	***Globularia cordifolia***	0,00	0,00	0,00	0,00	0,00	0,00	0,07	0,26	0,00	0,00	0,00	0,00	2.1	0,6564	
Hie.vi	***Hieracium villosum***	0,00	0,00	0,00	0,00	0,00	0,00	0,07	0,26	0,00	0,00	0,00	0,00	2.1	0,6564	
Sax.ho	***Saxifraga hostii***	0,00	0,00	0,00	0,00	0,00	0,00	0,07	0,26	0,00	0,00	0,00	0,00	2.1	0,6564	
Hie.bi	***Hieracium bifidum***	0,00	0,00	0,00	0,00	0,00	0,00	0,07	0,26	0,00	0,00	0,00	0,00	2.1	0,6576	
Gen.ba	***Gentiana bavarica***	0,00	0,00	0,00	0,00	0,00	0,00	0,13	0,37	0,00	0,00	0,00	0,00	2.1	0,6635	
Are.bi	***Arenaria biflora***	0,00	0,00	0,00	0,00	0,00	0,00	0,07	0,26	0,00	0,00	0,00	0,00	2.1	0,6635	
Gen.en	***Gentiana engadinensis***	0,00	0,00	0,00	0,00	0,00	0,00	0,07	0,26	0,00	0,00	0,00	0,00	2.1	0,6635	

Pot.br	***Potentilla brauneana***	0,00	0,00	0,00	0,00	0,00	0,00	0,07	0,26	0,00	0,00	0,00	0,00	2.1	0,6635	
Sax.ap	***Saxifraga aphylla***	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	1,20	0,77	0,13	0,12	2.2	0,0012	*
Pri.al	***Pritzelago alpina***	0,00	0,00	0,00	0,00	0,00	0,00	0,13	0,12	0,80	0,73	0,27	0,24	2.2	0,0042	*
Pap.au	***Papaver aurantiacum***	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,73	0,71	0,33	0,32	2.2	0,0072	*
Ara.pu	***Arabis pumila***	0,00	0,00	0,00	0,00	0,00	0,00	0,33	0,25	0,80	0,60	0,67	0,50	2.2	0,0214	*
Poa.mi	***Poa minor***	0,00	0,00	0,00	0,00	0,00	0,00	0,13	0,11	0,73	0,58	0,73	0,58	2.2	0,0372	*
Moe.ci	***Moehringia ciliata***	0,00	0,00	0,00	0,00	0,00	0,00	0,33	0,14	0,60	0,42	0,20	0,19	2.2	0,3254	
Cer.la	***Cerastium latifolium***	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,07	0,26	0,00	0,00	2.2	0,6695	
Fes.qu	***Festuca quadriflora***	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,33	0,26	0,00	0,00	2.2	0,6695	
Sal.re2	***Salix retusa***	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,07	0,26	0,00	0,00	2.2	0,6695	
Sax.ai	***Saxifraga aizoides***	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,07	0,26	0,00	0,00	2.2	0,6775	
Ara.ca	***Arabis caerulea***	0,00	0,00	0,00	0,00	0,00	0,00	0,27	0,28	0,00	0,00	0,67	0,69	2.3	0,0143	*
Ara.al	***Arabis alpina***	0,00	0,00	0,33	0,24	0,00	0,00	0,00	0,00	0,73	0,54	0,80	0,59	2.3	0,0366	*
Sax.op	***Saxifraga oppositifolia***	0,00	0,00	0,87	0,49	0,00	0,00	0,00	0,00	0,20	0,13	1,13	0,67	2.3	0,0648	
Arthropod species		**Ab**	**IndVal**	**Ab**	**IndVal**	**Ab**	**IndVal**	**Ab**	**IndVal**	**Ab**	**IndVal**	**Ab**	**IndVal**	**BFL**	**p-value**	**Sig.**
Cym.va	***Cymindis vaporariorum (car)***	0,34	0,66	0,00	0,00	0,00	0,00	0,02	0,06	0,00	0,00	0,00	0,00	1.1	0,0149	*
Eri.ar	***Erigone arctica (ara)***	0,05	0,26	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	1.1	0,6403	
Cen.pa	***Centromerus pabulator (ara)***	0,11	0,37	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	1.1	0,6574	
Car.pr	***Carabus problematicus (car)***	0,03	0,26	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	1.1	0,6574	
Hap.si	***Haplodrassus signifer (ara)***	0,02	0,26	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	1.1	0,6574	
Ama.pr	***Amara pratermissa (car)***	0,02	0,26	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	1.1	0,6591	
Mec.pa	***Mecynargus paetulus (ara)***	0,02	0,26	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	1.1	0,6591	
Cyc.at	***Cychrus attenuatus (car)***	0,07	0,22	0,03	0,14	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	1.1	0,6754	
Cen.su	***Centromerus subalpinus (ara)***	0,02	0,26	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	1.1	0,6822	
Wal.vi	***Walckenaeria vigilax (ara)***	0,02	0,26	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	1.1	0,6822	
Ten.ja	***Tenuiphantes jacksonoides (ara)***	0,02	0,18	0,02	0,18	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	1.1	0,8821	
Ama.qu	***Amara quenseli (car)***	0,02	0,18	0,00	0,00	0,02	0,18	0,00	0,00	0,00	0,00	0,00	0,00	1.1	0,8850	
Por.my	***Porrhomma myops (ara)***	0,03	0,18	0,00	0,00	0,00	0,00	0,03	0,18	0,00	0,00	0,00	0,00	1.1	0,8919	
Ang.mo	***Anguliphantes monticola (ara)***	0,02	0,05	0,36	0,60	0,14	0,32	0,00	0,00	0,02	0,05	0,00	0,00	1.2	0,0006	*
Ent.me	***Entelecara media (ara)***	0,00	0,00	0,04	0,37	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	1.2	0,1308	
Ore.va	***Oreonetides vaginatus (ara)***	0,02	0,14	0,05	0,31	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	1.2	0,2187	
Dip.he	***Diplocephalus helleri (ara)***	0,00	0,00	0,09	0,33	0,00	0,00	0,00	0,00	0,02	0,11	0,00	0,00	1.2	0,2308	
Rug.in	***Rugathodes instabilis (ara)***	0,00	0,00	0,06	0,35	0,00	0,00	0,00	0,00	0,04	0,23	0,00	0,00	1.2	0,6512	
Ore.mo	***Oreoneta montigena (ara)***	0,00	0,00	0,02	0,26	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	1.2	0,6598	
Par.ni	***Pardosa nigra (ara)***	0,02	0,05	0,02	0,05	0,28	0,51	0,02	0,05	0,08	0,13	0,23	0,41	1.3	0,0442	*
Tro.sc	***Troglohyphantes sciakyi (ara)***	0,00	0,00	0,00	0,00	0,02	0,26	0,00	0,00	0,00	0,00	0,00	0,00	1.3	0,6657	
Ama.er	***Amara erratica (car)***	0,00	0,00	0,00	0,00	0,02	0,26	0,00	0,00	0,00	0,00	0,00	0,00	1.3	0,6709	
Clu.al	***Clubiona alpicola (ara)***	0,00	0,00	0,00	0,00	0,02	0,26	0,00	0,00	0,00	0,00	0,00	0,00	1.3	0,6757	
Par.gi	***Pardosa giebeli (ara)***	0,00	0,00	0,00	0,00	0,00	0,00	0,18	0,63	0,00	0,00	0,00	0,00	2.1	0,0018	*
Xys.de	***Xysticus desidiosus (ara)***	0,00	0,00	0,00	0,00	0,00	0,00	0,15	0,52	0,00	0,00	0,00	0,00	2.1	0,0137	*
Car.sy	***Carabus sylvestris (car)***	0,00	0,00	0,00	0,00	0,00	0,00	1,71	0,68	0,00	0,00	0,00	0,00	2.1	0,0149	*
Gna.pe	***Gnaphosa petrobia (ara)***	0,00	0,00	0,00	0,00	0,00	0,00	0,10	0,45	0,00	0,00	0,00	0,00	2.1	0,1330	

Dra.he	***Drassodex heeri (ara)***	0,02	0,09	0,00	0,00	0,00	0,00	0,08	0,26	0,02	0,09	0,04	0,18	2.1	0,1899	
Coe.ti	***Coelotes pickardi tirolensis (ara)***	0,10	0,18	0,00	0,00	0,20	0,41	0,20	0,36	0,04	0,09	0,08	0,16	2.1	0,3450	
Pel.pa	***Pelecopsis parallela (ara)***	0,00	0,00	0,00	0,00	0,00	0,00	0,02	0,26	0,00	0,00	0,00	0,00	2.1	0,6522	
Har.at	***Harpalus atratus (car)***	0,00	0,00	0,00	0,00	0,00	0,00	0,02	0,26	0,00	0,00	0,00	0,00	2.1	0,6576	
Mug.va	***Mughiphantes variabilis (ara)***	0,02	0,07	0,00	0,00	0,00	0,00	0,02	0,07	0,14	0,39	0,13	0,37	2.2	0,2074	
Xys.la	***Xysticus lanio (ara)***	0,00	0,00	0,00	0,00	0,00	0,00	0,48	0,39	0,96	0,51	0,25	0,20	2.2	0,3695	
Wal.ca	***Walckenaeria capito (ara)***	0,03	0,11	0,00	0,00	0,00	0,00	0,06	0,27	0,07	0,30	0,00	0,00	2.2	0,4756	
Mer.tr	***Mermessus trilobatus (ara)***	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,02	0,26	0,00	0,00	2.2	0,6628	
Tro.lu	***Troglohyphantes lucifuga (ara)***	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,02	0,26	0,00	0,00	2.2	0,6628	
Cry.ni	***Cryphoeca nivalis (ara)***	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,02	0,26	0,00	0,00	2.2	0,6775	
Sit.lo	***Sitticus longipes (ara)***	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,07	0,25	0,16	0,53	2.3	0,0296	*
Ore.ca	***Oreonebria castanea (car)***	0,12	0,13	0,28	0,34	0,31	0,29	0,05	0,07	0,34	0,39	0,38	0,39	2.3	0,6191	
Mug.ar	***Mughiphantes armatus (ara)***	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,02	0,26	2.3	0,6645	
Ore.gl	***Oreonetides glacialis (ara)***	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,02	0,26	2.3	0,6645	

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Vegetation outlines of a debris-covered glacier descending below the treeline

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Abstract

Debris-covered glaciers are glaciers with the ablation zone covered by a debris layer, which are able to persist below the treeline and to support plant life. These landforms are increasing on many mountain regions of the world as consequence of climate change, providing new habitat for plant colonization, but their vegetation features are still little known. Our aim was to describe the vegetation of an alpine debris-covered glacier descending below the treeline (Belvedere: Western Italian Alps) and compare it with those of the adjacent iceless moraine and stable slope. Our hypothesis was that plant community of the supraglacial debris differs from those of the surrounding landforms for the presence of cold-adapted species. Data were collected by phytosociological method performing 45 relevés of 25 m^2. Plant communities were compared by a cluster analysis based on the presence/absence species matrix; species relative frequencies for each landform were calculated. The cluster analysis clearly separated three plant assemblages, each corresponding with one of the investigated landforms. Unlike the iceless moraine, debris-covered glacier stands out for the presence of cold-adapted species typically widespread in the alpine and nival belts (e.g. *Poa laxa* and *Cerastium pedunculatum*), allowing them to survive below their normal altitudinal distribution, where the stable slopes host subalpine woodlands and shrublands.

Key words: alpine flora, alpine vegetation, Belvedere glacier, climate change, moraine, refugia.

Introduction

Vegetation studies on glacial landforms date back to the beginning of 20th century (Lüdi, 1921; Braun-Blanquet & Jenny 1926; Negri, 1934, 1935, 1942; Valbusa, 1937; Friedel, 1938) and several reviews on the matter were performed by now (e.g. Lüdi, 1955, 1958; Matthews, 1992; Caccianiga & Andreis, 2004). However, most of the knowledge concerns plant colonization of glacier forelands and recent moraines within alpine and nival belts, while little is known about the vegetation of glacial landforms located below the treeline (Burga, 1999, Burga *et al*., 2010; Friedel, 1938; Richard, 1973, 1987). Among the latter, debris-covered glaciers can locally play an important role at landscape level because of their peculiar glaciological features. Debris-covered glaciers are glaciers with the ablation zone covered by a debris layer. They should not be confused with rock glaciers, periglacial landforms with different geomorphic and climatic significance (Humlum, 1998, 2000), in spite of some ecological affinities hailed from the coexistence of debris and ice (Tampucci *et al*., 2015). Debris-covered glaciers are relatively decoupled from atmosphere temperature, since a debris layer thicker than 1-2 cm acts as thermal insulator and protects the underlying ice from ablation (Mattson *et al*., 1993; Nakawo & Rana, 1999). Such glaciers thus differ from debris-free ones for less negative mass balance, smaller amplitude of frontal fluctuations and tongue descending to lower elevations (Kirkbride, 2000; Diolaiuti *et al*., 2003; Deline, 2005), sometimes overstepping the treeline and durably persisting in the forest context.

In spite of the harsh ecological conditions, debris-covered glaciers can provide suitable habitat for plant life, as showed by old observations (e.g. Negri, 1934, 1935, 1942; Valbusa, 1937; Birks, 1980) and more recent works focused on the matter (Fickert *et al*., 2007; Caccianiga *et al*., 2011; Pelfini *et al*., 2012). Supraglacial debris is colonized by pioneer herbaceous and woody species generally coherent with the altitudinal context, but can also allow cold-adapted plants to grow below their normal altitudinal distribution, probably as consequence of the thermal effect of underlying ice (Fickert *et al*. 2007; Caccianiga *et al*. 2011). Studies performed on Miage glacier (Western Italian Alps) showed that plant cover and species assemblages are affected by ground stability as a function of ice flow velocity (from 0.3 to 16.1 m/y) and by ground temperature as a function of debris thickness (from 10 to 56 cm) (Caccianga *et al*., 2011). The ecological features of debris-covered glaciers brought to different hypotheses about their contingent biogeographical role towards the glacial-interglacial periods. Fickert *et al*. (2007) proposed such landforms as refugia and dispersal pathways during the ice ages besides the unglaciated areas, complementing the hypotheses of *nunatakker* and *tabula-rasa* and calling into question the ice ages themselves as periods of biogeographical isolation. Other authors interpreted debris-covered glaciers

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as potential warm-stage refugia for cold-adapted plant (Caccianiga *et al*. 2011) and arthropod species (Gobbi *et al*., 2011), as consequence of the microclimate features due to the ice presence and the thermal inertia due to the debris cover.

The amount of supraglacial debris is currently increasing on many mountain systems of the world as response to climate change, because of the progressive exposure of endoglacial debris with ice melting and the increasing rock-falls from the slopes freed by glacier thinning (Kirkbride & Warren, 1999; Mattson, 2000; Diolaiuti *et al*., 2003; Stokes *et al*., 2007). Such landforms are thus taking on more and more relevance in mountain landscapes as expanding habitat for plant colonization. Further investigation are needed to clarify the syntaxonomical position of their plant communities, their spatial arrangement with respect to the vegetation belts and their ecological and biogeographical significance in the climate change context.

Aim of this paper is to describe the vegetation of an alpine debris-covered glacier descending below the treeline (Belvedere: Western Italian Alps) and to compare it with those of the neighboring iceless moraine and stable slope as reference sites. Our hypothesis is that plant community of the supraglacial debris differs from those of the surrounding landforms for the presence of cold-adapted species.

Study area

Belvedere glacier (Western Italian Alps; N45 57.685 E7 54.925) (fig. 1) is one of the most well-known debris-covered glaciers of the Alps (Monterin, 1923). Its fame is partially due to its interesting as hazardous dynamics, like the several outburst floods recorded from 1868 to 1979 and the surge-type movement performed between the summers of 2001 and 2002 (Haeberli *et al*., 2002; Mortara & Tamburini, 2009). The glacier takes origin from the confluence of four tongues descending from the ice cap of Monte Rosa (4633 m a.s.l.) and lies in the uppermost part of Valle Anzasca (I/B-9.III in Marazzi, 2005). It is c. 3400 m long and 700 m wide, covering a total surface of c. 7.5 km^2. The terminus splits into two divergent lobes which descend down to 1820 and 1785 m a.s.l. respectively, a minimum elevation second only to that of Miage glacier (1730 m a.s.l.) in the Italian Alps (Mortara & Tamburini, 2009). The glacier surface is almost completely covered by a debris layer thick from c. 5 cm in the upper tongue to 20-30 cm in the frontal lobes, with peaks level of c. 80 cm in the depressions (Diolaiuti *et al*. 2003). Two moraine systems delimit the glacier mass: an external one deposed in the Little Ice Age (at present consolidated and fully vegetated) and an internal more recent one (still unconsolidated and less vegetated). The substrate is composed by gneiss and schists (Mattirolo *et al*., 1951). Temperatures and precipitations of the area within the period 2000-2014 were analyzed using the records provided by ARPA Piemonte (station of Pecetto, 1360 m a.s.l.) (fig. 2). Calculating the Rivas-Martinez Index for thermal continentality (Rivas-Martínez & Rivas-Saenz, 1996-2009) and the Gams Index for hygric continentality (Ozenda, 1985), the area results to be characterized by a sub-oceanic climate regime (25,15 and 41,80° respectively).

Methods

Data were collected in July and August 2014. Forty-five vegetation relevés were performed by phytosociological method with the Braun-Blanquet scale as modified by Pignatti (1952) on three adjacent landforms corresponding to three different ecological conditions: stable slope (sites without ice, supposed to have the potentiality for climax vegetation), iceless moraine (unconsolidated debris substrate without underlying ice) and supraglacial debris (unconsolidated debris substrate with underlying ice) (fig. 3). All the relevés were performed on 25 m^2 surfaces, a value which allows a homogeneous and representative sampling of the main object of our research (glareicolous vegeta-

Fig. 1 - Belvedere glacier (photo by Lindsey Nicholson).

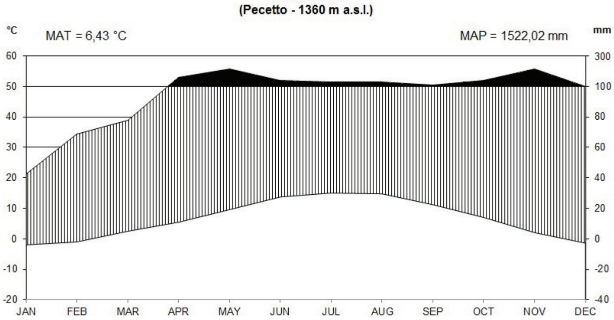

Fig. 2 - Climogram of Pecetto meteorological station.

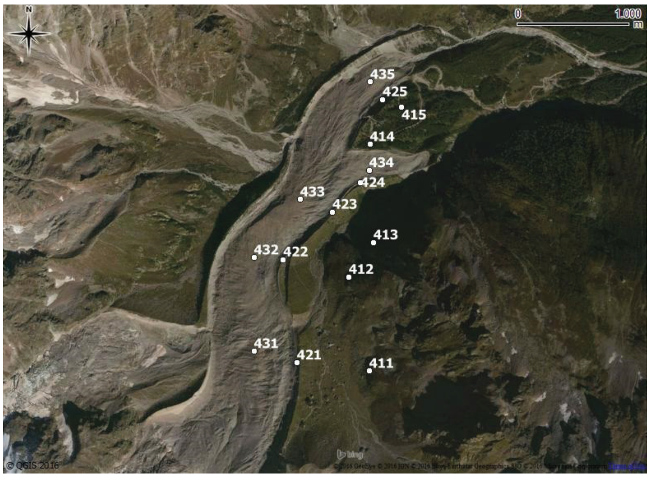

Fig. 3 - Sampling design with relevés position. Three relevés (A, B, C) c. 10 m far from each other were performed for each position.

tion of the iceless moraine and the supraglacial debris). Relevés were compared by a cluster analysis based on the presence/absence species matrix, using the UPGMA method with Jaccard dissimilarity index. Species relative frequencies for each landform were calculated and gathered in five frequency classes with resolution of 20%. The nomenclature follows Aeschimann *et al*. (2004) for species and Biondi *et al*. (2014) and Biondi & Blasi (2015) for syntaxa to the alliance level. The phytosociological interpretation generally agrees with Grabherr & Mucina (1993) and Oberdorfer (1977).

Results

We identified 117 vascular plant species. The cluster analysis (fig. 4) separated first of all the vegetation of the stable slope from those of the debris-featured landforms. Within the latter group, a further distinction between the iceless moraine and the supraglacial debris was clearly recognizable. It was thus possible to distinguish three main clusters that correspond to the analyzed landforms. Data were reported in the analytic table (tab. 1, in attachment on the inside back cover) and the synoptic table (tab. 2).

Cluster 1: stable slope

The stable slope embraced a wide range of vegetation structures: woodlands dominated by *Larix decidua* and *Salix appendiculata* (relevés 414, 415) (fig. 5), shrublands of *Alnus viridis* (relevés 413) or *Rhododendron ferrugineum* (relevés 411, 412) and all the seamless transitions between each other. However, a relatively homogeneous species assemblage was recognizable. The shrub layer was always dominated by *Rhododendron ferrugineum* and *Vaccinium myrtillus*, while the herbaceous one included *Calamagrostis villosa*, *Agrostis stolonifera*, *Avenella flexuosa* and *Dryopteris dilatata*. The presence of species like *Sorbus aucuparia*, *Melampyrum sylvaticum*, *Pyrola minor* and the sporadic but highly faithful *Corallorhiza trifida*, allowed a clear attribution of the woodlands to the class *Vaccinio myrtilli-Piceetea abietis* Br.-Bl. in

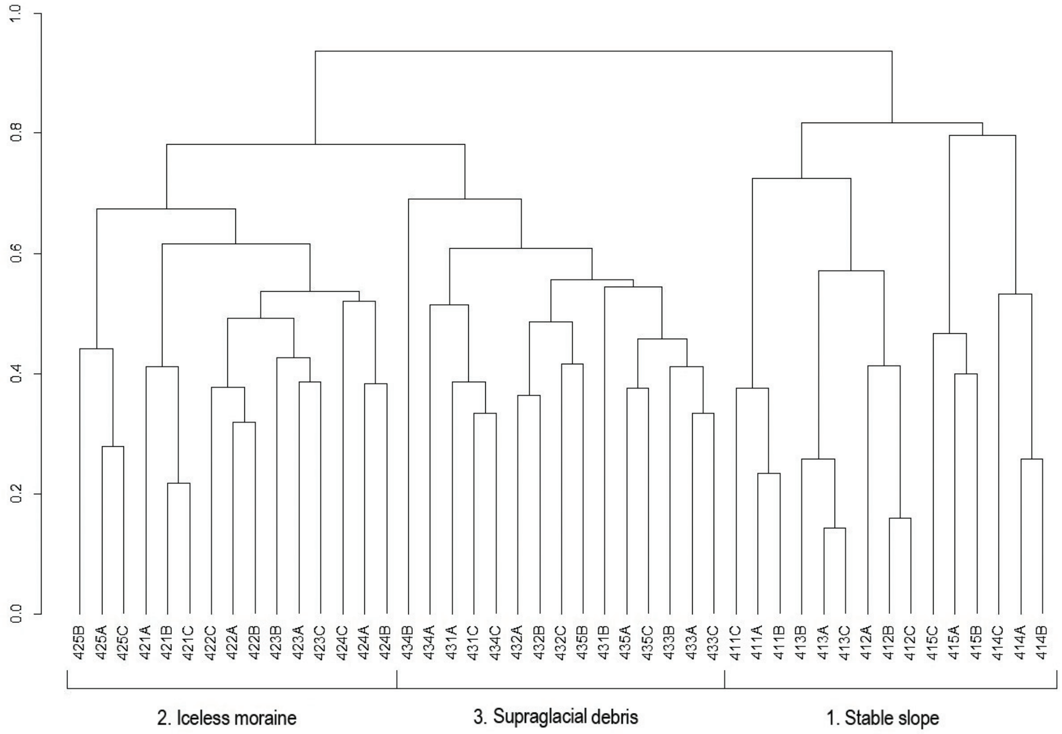

Fig. 4 - Dendrogram resulting from the cluster analysis of relevés.

Tab. 2 - Synoptic table of mean relevés values and species frequency classes for each landform (I = 1-20%, II = 21-40%, III = 41-60%, IV = 61-80%, V = 81-100%).

Species	1. Stable slope	2. Iceless moraine	3. Supraglacial debris
Arboreous cover (%)	20	0	0
High-shrubs cover (%)	25	0	0
Low-shrubs cover (%)	56	11	1
Herbaceous cover (%)	60	22	7
Bryophytes and lichens cover (%)	8	4	3
Outcrops cover (%)	0	0	0
Debris cover (%)	8	63	89
Soil cover (%)	7	0	0
Species richness	23	19	11
Avenella flexuosa	V		
Vaccinium myrtillus	V		
Dryopteris dilatata	IV		
Astrantia minor	III		
Gentiana purpurea	III		
Homogyne alpina	III		
Veratrum album subsp. lobelianum	III		
Arnica montana	II		
Campanula barbata	II		
Dryopteris filix-mas	II		
Helictotrichon versicolor	II		
Juniperus communis subsp. alpina	II		
Leontodon helveticus	II		
Ligusticum mutellina	II		
Luzula sieberi	II		
Melampyrum sylvaticum	II		
Nardus stricta	II		
Rumex alpestris	II		
Soldanella alpina	II		
Sorbus aucuparia	II		
Vaccinium gaultherioides	II		
Achillea macrophylla	I		
Adenostyles alliariae	I		
Alchemilla gr. alpina	I		
Alchemilla gr. vulgaris	I		
Carex curvula subsp. curvula	I		
Carex sempervirens	I		
Centaurea nervosa subsp. nervosa	I		
Chaerophyllum hirsutum	I		
Cicerbita alpina	I		
Corallorhiza trifida	I		
Dactylorhiza maculata	I		
Festuca arundinacea subsp. arundinacea	I		
Festuca nigrescens	I		
Geranium sylvaticum	I		
Geum montanum	I		
Hieracium pilosum	I		
Hieracium murorum	I		
Huperzia selago	I		
Maianthemum bifolium	I		
Milium effusum	I		
Oxalis acetosella	I		
Phyteuma hemisphaericum	I		
Poa nemoralis	I		
Polypodium vulgare	I		
Polystichum lonchitis	I		
Potentilla aurea	I		
Prenanthes purpurea	I		
Primula hirsuta	I		
Pseudorchis albida	I		
Pyrola minor	I		
Ranunculus gr. montanus	I		
Rubus idaeus	I		

Sedum alpestre	I		
Stellaria nemorum subsp. nemorum	I		
Streptopus amplexifolius	I		
Thesium alpinum	I		
Trifolium alpinum	I		
Viola biflora	I		
Myosotis alpestris	I	I	
Cerastium arvense subsp. strictum	I	II	
Alnus viridis	I	III	
Trifolium pratense subsp. nivale	I	III	
Sempervivum montanum subsp. montanum	II	III	
Anthoxanthum alpinum	III	III	
Silene vulgaris subsp. vulgaris	III	II	
Calamagrostis villosa	III	I	
Athyrium distentifolium	II	I	
Campanula scheuchzeri	II	I	
Cystopteris fragilis	II	I	
Peucedanum ostruthium	II	I	
Phleum alpinum	II	I	
Phyteuma betonicifolium	II	I	
Solidago virgaurea subsp. virgaurea	II	I	
Trifolium pallescens		V	
Achillea erba-rotta subsp. moschata		IV	
Epilobium fleischeri		III	
Festuca halleri		III	
Bartsia alpina		II	
Arabis alpina subsp. alpina		I	
Epilobium nutans		I	
Galium anisophyllon		I	
Hieracium staticifolium		I	
Pedicularis tuberosa		I	
Rhinanthus alpinus		I	
Saxifraga oppositifolia subsp. oppositifolia		I	
Silene rupestris		V	IV
Rumex scutatus		V	III
Cardamine resedifolia		IV	III
Luzula lutea		IV	II
Linaria alpina subsp. alpina		III	III
Saxifraga aspera		III	I
Sagina saginoides		II	II
Silene exscapa		II	I
Saxifraga bryoides		I	I
Cerastium pedunculatum		I	V
Poa laxa		I	V
Leucanthemopsis alpina		I	III
Luzula alpinopilosa subsp. alpinopilosa		I	III
Campanula excisa			II
Saxifraga stellaris			II
Betula pendula			I
Epilobium alsinifolium			I
Gnaphalium supinum			I
Oxyria digyna			I
Ranunculus glacialis			I
Agrostis rupestris	I	II	IV
Agrostis stolonifera	IV	V	V
Euphrasia minima	I	II	I
Festuca gr. varia	III	IV	I
Juncus trifidus	II	IV	I
Larix decidua	II	IV	II
Lotus alpinus	I	II	I
Poa alpina	I	III	I
Rhododendron ferrugineum	V	I	I
Salix appendiculata	I	V	V
Salix helvetica	II	III	I
Total species richness	85	51	31

Fig. 5 - *Larix decidua* subalpine woodlands on the stable slope (cluster 1).

Fig. 6 - Glareicolous vegetation of the iceless moraine, with *Trifolium pallescens*, *Achillea erba-rotta* subsp. *moschata* and *Agrostis stolonifera* (cluster 2).

Br.-Bl., Sissingh & Vlieger 1939. They likely belong to the association *Astrantio minoris-Laricetum deciduae* Andreis, Armiraglio, Caccianiga & Cerabolini 2009, which includes the sub-oceanic larch-dominated woodlands, as indicated by the presence of *Astrantia minor*, *Gentiana purpurea* and *Prenanthes purpurea*. By the other hand, differential species as *Rhododendron ferrugineum*, *Vaccinium myrtillus* and *Dryopteris dilatata* suggest that the shrublands may belong to the association *Rhododendro ferruginei-Alnetum viridis* Boscutti, Poldini & Buccheri 2014 (class *Betulo carpaticae-Alnetea viridis* Rejmánek in Huml, Lepš, Prach & Rejmánek 1979). Remarkable was also the massive occurrence of species belonging to the class *Mulgedio alpini-Aconitetea variegate* Hadac & Klika in Klika & Hadac 1944, like *Peucedanum ostruthium*, *Adenostyles alliariae*, *Achillea macrophylla*, *Cicerbita alpina* and *Geranium sylvaticum*.

Cluster 2: iceless moraine

The iceless moraine was colonized both by woody and herbaceous species (fig. 6). The shrub layer consisted of young individuals of *Salix appendiculata* and *S. helvetica*, locally accompanied by *Larix decidua* and *Alnus viridis*. Among the herbaceous elements, *Achillea erba-rotta* subsp. *moschata* and *Trifolium pallescens* were the most constant ones, followed by *Epilobium fleischeri*, *Euphrasia minima*, *Festuca halleri*, *Poa alpina*, *Trifolium pratense* subsp. *nivale* and *Saxifraga aspera*. As much frequent, but shared with the adjacent landforms, were *Agrostis stolonifera*, *Anthoxanthum alpinum*, *Cardamine resedifolia*, *Festuca varia*, *Juncus trifidus*, *Linaria alpina*, *Luzula lutea*, *Sempervivum montanum*, *Silene rupestris* and *Rumex scutatus*. The vegetation structure varied along the moraine ridge: the uppermost communities resemble those of the glacier surface (cluster 3), with *Poa laxa*, *Cerastium pedunculatum* and a scarce shrub layer (relevés 421); proceeding downstream, subalpine woody species as *Alnus viridis* and *Larix decidua* acquire more relevance (relevés 423, 424, 425). The community was clearly attributable to the alliance *Androsacion alpinae* Br.-Bl. in Br.-Bl. & Jenny 1926. It resembled the association *Agrostio rupestris-Trifolietum pallescentis* Caccianiga & Andreis 2004, except for the lacking of some *Caricetea curvulae* Br.-Bl. 1948 elements (e.g. *Agrostis rupestris* and *Minuartia recurva*) and the relatively high frequency of *Thlaspietea rotundifolii* Br.-Bl. 1948 ones (e.g. *Cardamine resedifolia*, *Linaria alpina* and *Rumex scutatus*).

Cluster 3: supraglacial debris

The community of supraglacial debris (fig. 7) stands out for the presence of high alpine species as *Poa laxa* and *Cerastium pedunculatum*, followed in frequency by *Luzula alpinopilosa*, *Leucanthemopsis alpina*, *Saxifraga stellaris* and *Agrostis rupestris*. Other abundant but not exclusive species were *Agrostis stolonifera*, *Silene rupestris*, *Rumex scutatus*, *Cardamine resedifolia* and *Linaria alpina*. Noteworthy was the presence of *Campanula excisa*, a Western Alps endemic species; even though in our study case it resulted exclusive of the supraglacial debris, it was frequently observed by the Authors in other not investigated environments (e.g. rocky pastures, eroded terrains and path edges). Unlike the moraine ridge, the supraglacial debris was homogeneously colonized, without evident discontinuities or gradients in terms of vegetation structure. The same plant assemblage can thus be found from the upper zones of the glacier to the minimum elevation of 1895 m a.s.l., even including sporadic individuals of the high-alpine *Ranunculus glacialis*. The shrub layer was absent, except for few young individuals of *Salix appendiculata* and to a lesser extent *Larix decidua*. As

Fig. 7 - Glareicolous vegetation of the supraglacial debris, with *Poa laxa* and *Cerastium pedunculatum* (cluster 3).

well as for the adjacent moraine, such plant assemblage was ascribable to the alliance *Androsacion alpinae* Br.-Bl. in Br.-Bl. & Jenny 1926, but its placement at the association level is uncertain.

Discussion

All the investigated landforms differ each other for distinct plant communities. Particularly interesting is the comparison between the iceless moraine and the supraglacial debris, environments similar to each other except for the occurrence of underlying ice. While the community of the iceless moraine is characterized by pioneer species generally widespread on a wide altitudinal range, that of supraglacial debris stands out for cold-adapted species typical of alpine and nival belts (Aeschimann *et al*., 2004; Landolt *et al*., 2010). Such phenomenon can be likely attributed to the thermal effect of underlying ice, according to Fickert *et al*. (2007) and Caccianiga *et al*. (2011). The supraglacial debris allows thus cold-adapted species to grow below their normal altitudinal distribution, where the stable slopes have the potentiality for subalpine woodlands (Andreis *et al*., 2009) and shrublands (Boscutti *et al*., 2014). Coherently with the geographical context and the results of our climate analyses, the woodlands belongs to the *Astrantio minoris-Laricetum deciduae*, a western-alpine association linked to the sub-oceanic climate regime, sometime able to include typical elements of montane broad-leaved forests (Andreis *et al*., 2009). This peculiar feature furtherly accentuates the contrast between supraglacial and potential vegetation, achieving the coexistence of nival species (e.g. *Ranunculus glacialis*) few meters aside from montane ones (e.g. *Prenanthes purpurea*).

Iceless moraine and supraglacial debris are also differently subjected to the colonization by subalpine woody species. On the moraine ridge, *Alnus viridis*, *Larix decidua* and *Salix* spp. built up a well-structured shrub layer up to one meter high, while the vegetation of supraglacial debris is mainly herbaceous and contingent individuals of *Salix appendiculata* and *Larix decidua* seems unable to grow above few decimeters. Summarizing, the community of the iceless moraine is interpretable as an ephemeral stage over the subalpine primary succession, where herbaceous early-successional species coherent with the altitudinal context are supposed to be rapidly replaced by woody late-successional ones. By contrast, the supraglacial debris appears more selective, promoting the persistence of pioneer cold-adapted species in an adverse altitudinal context and preventing the subalpine succession development. Unlike that of the iceless moraine, the vegetation of supraglacial debris should be thus considered as extrazonal at landscape level. Geomorphological and microclimatic heterogeneity enhances species turnover (Körner, 2003) and provides refugia opportunities for stenotherm species in spite of climate variations at large scale (Ashcroft *et al*., 2012; Birks & Willis, 2008; Dobrowski 2011; Gentili *et al*., 2015; Stewart *et al*., 2010). Our results suggest that Belvedere debris-covered glacier have the ecological requirements to act as refugia for plant species, especially for cold-adapted ones during warm-climatic stages, according to Caccianiga *et al*. (2011).

Concerning the phytosociological viewpoint, the iceless moraine and the supraglacial debris were colonized each one by a distinct aspect of the alliance *Androsacion alpinae*, but their placement at the association level is debatable. The association *Agrostio rupestris-Trifolietum pallescentis* was formerly referred to the terrain ice-free since the Little Ice Age on the glacier forelands located above the treeline (Caccianiga & Andreis, 2004). Our relevés on the iceless moraine of Belvedere glacier suggest that a subalpine variant of the same association may be proposed for the moraines younger than Little Ice Age located below the treeline, implying thus higher colonization speed at lower elevation. Less can be said about the vegetation of supraglacial debris because of species scarcity. More defined is the case of the not too far Miage glacier, mainly colonized by *Epilobium fleischeri*, *Saxifraga aizoides*, *Linaria alpina*, *Ranunculus glacialis*, *Geum reptans* and *Oxyria digyna* (Caccianiga *et al*., 2011). This plant assemblage can be attributed to the *Sieversio-Oxyrietum digynae* Friedel 1956 em. Englisch *et al*. 1993 (probably to the *Saxifraga aizoides* and *Epilobium fleischeri* subtype described in Caccianiga & Andreis, 2004), an association normally widespread on the scree slopes of alpine and nival belts (Grabherr & Mucina, 1993; Oberdorfer, 1977). Even if the plant assemblage found on Belvedere glacier cannot be certainly attributed to *Sieversio-Oxyrietum digynae* because of the lack of characteristic elements (*Geum reptans* and *Oxyria digyna*), all the identified differential species are typically constant or dominant of this association (Grabherr & Mucina, 1993). We thus hypothesize that *Sieversio-Oxyrietum digynae* is nevertheless the most plausible representative association of silicate supraglacial debris of the Alps in general. Anyway, more data should be collected from other areas to perform a comprehensive syntaxonomic overview of both the iceless moraines and supraglacial debris vegetation located below the treeline.

Syntaxonomic scheme

VACCINIO MYRTILLI-PICEETEA ABIETIS Br.-Bl. in Br.-Bl., Sissingh & Vlieger 1939
PICEETALIA EXCELSAE Pawłowski in Pawłowski, Sokołowski & Wallisch 1928
Piceion excelsae Pawlowski in Pawlowski, Sokolowski & Wallisch 1928
Astrantio minoris-Laricetum deciduae Andreis, Armiraglio, Caccianiga & Cerabolini 2009

BETULO CARPATICAE-ALNETEA VIRIDIS Rejmánek in Huml, Lepš, Prach & Rejmánek 1979
ALNETALIA VIRIDIS Rübel 1933
Alnion viridis A. Schnyd. 1930
Rhododendro ferruginei-Alnetum viridis Boscutti, Poldini & Buccheri 2014

MULGEDIO ALPINI-ACONITETEA VARIEGATI Hadac & Klika in Klika & Hadac 1944
ADENOSTYLETALIA ALLIARIAE Br.-Bl. 1931

THLASPIETEA ROTUNDIFOLII Br.-Bl. 1948
ANDROSACETALIA ALPINAE Br.-Bl. in Br.-Bl. & Jenny 1926
Androsacion alpinae Br.-Bl. in Br.-Bl. & Jenny 1926
Agrostio rupestris-Trifolietum pallescentis Caccianiga & Andreis 2004
Sieversio-Oxyrietum digynae Friedel 1956 em. Englisch, Valachovič, Mucina, Grabherr & Ellmauer in Grabherr & Mucina 1993

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Appendix: Sporadic species

Tab. 1 – Rel 411B: Centaurea nervosa subsp. nervosa +, Sedum alpestre +, Trifolium alpinum +; Rel 412A: Festuca nigrescens 1, Alchemilla gr. Vulgaris +, Carex curvula subsp. curvula +, Hieracium pilosum +; Rel 412C: Viola biflora +; Rel 415C: Maianthemum bifolium +; Rel 415B: Rubus idaeus 1, Streptopus amplexifolius +; Rel 414C: Thesium alpinum +; Rel 414A: Chaerophyllum hirsutum +, Corallorhiza trifida +; Rel 414B: Dactylorhiza maculata +, Polypodium vulgare +, Polystichum lonchitis +; Rel 425B: Rhinanthus alpinus +; Rel 425C: Epilobium nutans +; Rel 423C: Saxifraga oppositifolia subsp. oppositifolia +; Rel 424C: Galium anisophyllon +, Hieracium staticifolium +; Rel 434B: Epilobium alsinifolium +; Rel 435A: Ranunculus glacialis +; Rel 435C: Betula pendula +; Rel 433C: Gnaphalium supinum +.

Tab. 1 - Analytic table of relevés.

Cluster	1. Stable slope															2. Iceless moraine															3. Supraglacial debris														
Code	411C	411A	411B	413B	413A	413C	412A	412B	412C	415C	415A	415B	414C	414A	414B	425B	425A	425C	421A	421B	421C	422C	422A	422B	423B	423A	423C	424C	424A	424B	434B	434A	431A	431C	434C	432A	432B	432C	435B	431B	435A	435C	433B	433A	433C
Date	27.07.2014	27.07.2014	27.07.2014	27.07.2014	27.07.2014	27.07.2014	27.07.2014	27.07.2014	27.07.2014	27.07.2014	27.07.2014	27.07.2014	27.07.2014	27.07.2014	27.07.2014	21.07.2014	21.07.2014	21.07.2014	02.07.2014	02.07.2014	02.07.2014	21.07.2014	21.07.2014	21.07.2014	21.07.2014	21.07.2014	21.07.2014	21.07.2014	21.07.2014	21.07.2014	19.07.2014	19.07.2014	03.07.2014	03.07.2014	19.07.2014	19.07.2014	19.07.2014	19.07.2014	19.07.2014	03.07.2014	19.07.2014	19.07.2014	19.07.2014	19.07.2014	19.07.2014
Coordinates	N45 57.106 E7 55.262	N45 57.096 E7 55.266	N45 57.097 E7 55.263	N45 57.538 E7 55.285	N45 57.536 E7 55.281	N45 57.542 E7 55.288	N45 57.414 E7 55.157	N45 57.420 E7 55.164	N45 57.424 E7 55.170	N45 58.006 E7 55.435	N45 57.996 E7 55.417	N45 58.000 E7 55.421	N45 57.881 E7 55.271	N45 57.864 E7 55.272	N45 57.871 E7 55.256	N45 58.027 E7 55.329	N45 58.026 E7 55.324	N45 58.029 E7 55.339	N45 57.135 E7 54.911	N45 57.126 E7 54.911	N45 57.122 E7 54.907	N45 57.484 E7 54.849	N45 57.475 E7 54.840	N45 57.480 E7 54.842	N45 57.642 E7 55.083	N45 57.649 E7 55.089	N45 57.638 E7 55.079	N45 57.743 E7 55.229	N45 57.743 E7 55.214	N45 57.745 E7 55.218	N45 57.785 E7 55.264	N45 57.789 E7 55.259	N45 57.167 E7 54.694	N45 57.164 E7 54.709	N45 57.779 E7 55.266	N45 57.486 E7 54.708	N45 57.486 E7 54.698	N45 57.487 E7 54.688	N45 58.086 E7 55.269	N45 57.165 E7 54.699	N45 58.080 E7 55.274	N45 58.091 E7 55.264	N45 57.685 E7 54.925	N45 57.693 E7 54.921	N45 57.680 E7 54.924
Landform	Stable slope	Stable slope	Stable slope	Stable slope	Stable slope	Stable slope	Stable slope	Stable slope	Stable slope	Stable slope	Stable slope	Stable slope	Stable slope	Stable slope	Stable slope	Iceless moraine	Iceless moraine	Iceless moraine	Iceless moraine	Iceless moraine	Iceless moraine	Iceless moraine	Iceless moraine	Iceless moraine	Iceless moraine	Iceless moraine	Iceless moraine	Iceless moraine	Iceless moraine	Iceless moraine	Supraglacial debris	Supraglacial debris	Supraglacial debris	Supraglacial debris	Supraglacial debris	Supraglacial debris	Supraglacial debris	Supraglacial debris	Supraglacial debris	Supraglacial debris	Supraglacial debris	Supraglacial debris	Supraglacial debris	Supraglacial debris	Supraglacial debris
Elevation (m a.s.l.)	2135	2135	2135	2055	2055	2055	2075	2075	2075	1875	1885	1880	1930	1930	1935	1895	1895	1895	2125	2125	2125	2055	2065	2060	2005	2005	2005	1955	1960	1960	1920	1920	2115	2120	1915	2055	2055	2055	1890	2120	1890	1890	2015	2015	2010
Aspect (°)	260	260	260	300	305	320	300	315	315	350	350	340	5	10	20	330	325	320	270	260	280	120	45	80	300	305	305	150	150	155	70	55	10	180	80	45	50	45	70	15	60	45	95	30	130
Slope (°)	40	30	35	20	30	25	25	20	20	25	20	20	35	30	30	35	35	30	35	15	15	30	25	25	15	0	0	30	25	35	20	15	10	25	15	5	10	10	10	5	10	10	15	5	10
Arboreous cover (%)	0	0	0	0	0	0	0	0	0	30	40	60	50	60	60	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
High-shrubs cover (%)	0	0	0	60	70	80	0	0	0	5	5	0	30	60	60	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Low-shrubs cover (%)	50	65	60	20	25	40	70	70	75	30	80	80	90	50	30	15	10	10	0	0	0	0	5	5	15	35	25	10	25	15	0	0	0	0	0	0	0	0	0	0	0	5	5	0	5
Herbaceous cover (%)	75	80	60	75	75	65	50	60	50	80	30	50	25	70	50	55	50	50	20	20	20	20	10	20	10	10	10	15	10	5	5	0	5	5	5	10	5	10	5	5	10	10	10	10	10
Bryophytes and lichens cover (%)	0	5	10	10	15	5	10	5	10	5	10	5	0	20	15	5	10	5	5	5	5	10	5	5	0	0	0	0	0	0	0	0	0	0	0	5	5	5	0	5	0	5	5	5	5
Outcrops cover (%)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Debris cover (%)	0	5	10	0	0	0	20	10	25	0	0	0	5	25	20	25	30	35	75	75	75	70	80	70	75	55	65	75	65	80	95	100	95	95	95	85	90	85	95	90	90	80	80	85	80
Soil cover (%)	5	0	5	0	0	0	10	0	5	15	15	10	5	20	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Number of species	23	26	30	14	14	12	27	21	26	20	19	23	24	33	33	12	16	16	16	19	22	18	18	19	23	23	28	18	22	20	11	10	7	6	9	8	10	9	10	12	12	16	12	14	17
Diff. stable slope																																													
Rhododendron ferrugineum	2	1	2	1	1	2	3	3	3	1	4	3	4	2	2	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.
Vaccinium myrtillus	1	1	1	1	1	1	2	1	2	.	1	1	1	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Dryopteris dilatata	.	.	.	1	1	1	1	+	1	2	1	+	1	1	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Astrantio minoris-Laricetum deciduae																																													
Astrantia minor	1	1	1	.	.	.	1	+	1	.	.	.	+	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Gentiana purpurea	+	+	.	+	1	1	1	+	+	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Prenanthes purpurea	.	.	.	.	.	.	.	.	.	1	1	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Vaccinio myrtilli-Piceetea abietis, *Piceetalia excelsae* and *Piceion excelsae*																																													
Avenella flexuosa	1	2	1	1	1	1	1	1	1	1	1	1	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Homogyne alpina	1	1	+	+	1	+	1	+	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Calamagrostis villosa	2	.	.	4	4	3	1	.	.	4	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Sorbus aucuparia	.	.	.	.	.	.	.	.	.	1	+	+	+	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Melampyrum sylvaticum	.	.	.	.	.	.	.	.	.	+	.	.	1	2	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Pyrola minor	.	.	.	.	.	.	.	.	.	.	.	.	+	1	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Mulgedio alpini-Aconitetea variegati and *Adenostyletalia alliariae*																																													
Veratrum album subsp. lobelianum	.	.	.	1	1	1	1	+	1	1	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Athyrium distentifolium	.	.	.	.	1	1	.	+	1	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Rumex alpestris	.	.	.	1	1	1	+	+	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Luzula sieberi	.	.	.	+	.	.	1	1	1	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Peucedanum ostruthium	.	.	.	.	.	.	.	.	.	1	1	.	.	1	1	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Achillea macrophylla	.	.	.	.	.	.	.	.	.	1	+	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Adenostyles alliariae	.	.	.	.	.	.	.	.	.	1	+	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Geranium sylvaticum	.	.	.	.	.	.	.	.	.	1	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Stellaria nemorum subsp. nemorum	.	.	.	.	1	.	.	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cicerbita alpina	.	.	.	.	.	.	.	.	.	.	1	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Milium effusum	.	.	.	.	.	.	.	.	.	1	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Diff. iceless moraine																																													
Epilobium fleischeri	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	+	+	+	+	+	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Poa alpina	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	+	+	1	.	+	+	+	+	+	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.
Trifolium pratense subsp. nivale	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	+	.	.	.	+	+	.	+	+	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Saxifraga aspera	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	+	+	+	+	+	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Agrostio rupestris-Trifolietum pallescentis																																													
Trifolium pallescens	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	+	.	+	+	1	+	1	+	+	+	+	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Achillea erba-rotta subsp. moschata	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	+	+	+	+	+	.	+	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Festuca halleri	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	+	+	+	.	.	.	+	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Euphrasia minima	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	+	+	+	.	.	.	.	.	.	.	.	+	.	+	.	.	+	.	.	.	.	.	.	.	.	.	.	.	+	+
Agrostis rupestris	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.	.	.	.	.	+	+	.	.	.	.	.	.	+	+	+	+	+	+	.	+	.	+	+	+	+
Diff. supraglacial debris																																													
Poa laxa	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	+	.	.	.	.	.	.	.	.	.	1	+	+	+	+	1	+	1	+	+	+	+	1	1	1
Cerastium pedunculatum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	.	.	.	.	.	.	.	.	.	+	+	+	+	+	+	+	+	+	+	+	.	+	+	+
Leucanthemopsis alpina	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	+	.	.	+	.	.	.	.	.	.	+	.	.	.	.	.	+	+	.	+	+	+	+	+
Luzula alpinopilosa subsp. alpinopilosa	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	+	.	+	.	+	+	+	+	+	+
Campanula excisa	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	+	+	.	+
Saxifraga stellaris	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	+	.	.	+	.	.	+
Androsacetalia alpinae and *Androsacion alpinae*																																													
Silene rupestris	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	1	.	+	+	1	+	+	+	+	+	+	+	+	.	+	.	.	+	.	+	+	+	.	+	+	+	+	+
Cardamine resedifolia	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	+	+	+	+	+	+	+	+	.	.	+	+	.	.	.	.	.	+	+	+	+	+	+	+	.	.	+
Sagina saginoides	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	+	.	.	.	+	.	+	.	.	.	+	.	.	.	+	.	.	.	.	.	+	+	.	.	.
Saxifraga bryoides	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	+	.	.	.	.	+	.	.	.	.	.	.	.	.
Oxyria digyna	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	+	.	.	.	.	.
Thlaspietea rotundifolii																																													
Rumex scutatus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	1	+	+	+	+	+	+	+	+	+	+	1	+	+	.	+	+	.	+	.	.	.	.	.	+	+	.	+	+
Linaria alpina subsp. alpina	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	+	+	.	+	.	+	+	.	.	.	+	+	+	+	+	.	.	.	+	+	.	.	.	+	.
Arabis alpina subsp. alpina	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Subalpine woody species																																													
Salix appendiculata	.	.	.	.	.	.	.	.	.	.	.	.	2	3	3	+	+	1	+	+	+	+	+	+	1	+	+	1	1	1	+	+	.	+	+	+	+	+	+	+	+	1	+	+	+
Larix decidua	.	.	.	.	.	.	.	.	.	2	2	3	3	3	3	1	1	1	.	.	.	.	+	+	+	+	+	+	1	.	+	.	.	.	.	.	.	.	.	.	.	+	+	+	+
Salix helvetica	1	1	1	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	+	+	+	+	+	.	1	.	+	+	.	.	.	.	.	.	.	.	.	+	.	.	+	.	+
Alnus viridis	.	.	.	3	4	4	.	.	.	.	.	.	.	.	.	1	1	.	.	.	.	.	.	.	1	2	1	+	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Vaccinium gaultherioides	1	2	2	.	.	.	2	1	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Juniperus communis subsp. alpina	1	1	+	.	.	.	.	.	.	1	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Companion species																																													
Agrostis stolonifera	1	1	+	+	1	1	1	1	1	.	.	.	1	1	1	2	2	2	1	1	1	1	1	1	+	+	1	1	1	1	+	+	+	+	+	+	+	.	+	+	1	1	+	1	+
Festuca gr. varia	.	1	1	.	.	.	1	.	.	.	.	+	1	1	+	1	1	+	.	.	.	+	.	.	+	1	+	+	+	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Juncus trifidus	1	+	1	.	.	.	.	+	1	.	.	.	.	.	.	.	.	.	+	+	+	+	+	+	+	.	+	+	+	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Anthoxanthum alpinum	1	1	2	+	.	.	1	2	2	.	.	.	.	1	1	.	.	.	1	1	1	.	+	.	.	+	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Luzula lutea	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	+	+	+	+	+	+	+	+	+	.	+	.	.	.	.	.	.	+	+	.	.	.	.	.	.	+	+
Sempervivum montanum subsp. montanum	.	+	+	.	.	.	.	.	.	.	.	.	+	+	+	.	.	.	.	.	.	+	+	+	+	.	+	+	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Silene vulgaris subsp. vulgaris	+	.	.	1	1	.	1	.	+	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	+	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Silene exscapa	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	+	.	+	.	.	.	+	+	.	.	.	.	.	.	.	.	.	+	.	+	.	+	.
Cerastium arvense subsp. strictum	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	+	.	.	.	+	.	+	+	+	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Lotus alpinus	.	.	.	.	.	.	.	.	.	.	.	.	+	+	+	1	1	1	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.
Phyteuma betonicifolium	1	1	+	.	.	.	.	.	.	.	.	.	.	1	+	.	.	.	.	.	.	.	.	.	.	+	+	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cystopteris fragilis	.	.	.	.	.	.	.	.	.	+	+	+	.	+	.	.	.	+	.	.	.	.	.	.	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Leontodon helveticus	+	1	+	.	.	.	1	+	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Campanula scheuchzeri	.	+	+	.	.	.	.	.	.	.	+	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Solidago virgaurea subsp. virgaurea	1	1	+	.	.	.	.	.	.	.	.	.	1	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Campanula barbata	+	.	+	.	.	.	.	.	.	.	.	+	.	1	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Ligusticum mutellina	.	.	.	.	.	.	+	+	1	.	.	.	+	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Phleum alpinum	.	.	.	.	.	.	.	+	1	.	.	.	.	1	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Dryopteris filix-mas	.	.	.	.	.	.	.	.	.	.	.	+	1	1	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Arnica montana	1	1	1	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Bartsia alpina	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Helictotrichon versicolor	+	1	1	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Myosotis alpestris	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	+	+	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Nardus stricta	1	+	1	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Soldanella alpina	.	+	.	.	.	.	.	.	.	.	.	+	.	1	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hieracium murorum	1	.	.	.	.	.	.	.	.	1	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
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Alchemilla gr. alpina	.	.	.	.	.	.	1	+	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
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Potentilla aurea	.	+	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
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Sporadic species	0	0	3	0	0	0	4	0	1	1	0	2	1	2	3	1	0	1	0	0	0	0	0	0	0	0	1	2	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	1

Debris-covered glaciers as habitat and warm-stage refugia for cold-adapted plants and arthropods

Running title: debris-covered glaciers as habitat and refugia

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Abstract

Debris-covered glaciers are glaciers with the ablation zone covered by a debris layer. Recent papers showed that such landforms are able to support plant and arthropod life and could act as warm-stage refugia for cold-adapted species due to their microclimate features and thermal inertia. However, integrated research comparing debris-covered glaciers with surrounding landforms to outline their ecological peculiarities are absent. We analyzed the abiotic (ground surface temperature and humidity, soil physical and chemical parameters) and biotic features (plant and arthropod communities) of a debris-covered glacier (Belvedere, western Italian Alps), comparing them with the surrounding landforms as reference sites (control slope and iceless moraine). Our data show remarkable differences between control slopes and debris-featured landforms as a whole. The iceless moraine and the supraglacial debris show similar soil features, but supraglacial debris differs for lower ground surface temperature and the occurrence of cold-adapted species; such differences can be likely attribute to the thermal effect of underlying ice. According with previous studies, the thermal contrast with the surrounding landforms and the ability to descend below the climatic treeline make debris-covered glaciers potential warm-stage refugia for cold-adapted species. However, some limitation can be imposed by the glacial dynamics, especially by periodic extreme events like surge-type movements able to prevent the colonization of low-dispersal taxa.

Key-words: carabid beetles, climate change, flora, moraines, spiders, refugia, vegetation.

Introduction

The increasing debris cover on glacier surfaces is one of the most relevant effects of the current climate change on many mountain landscapes of the world, with noteworthy implications both by the glaciological (Diolaiuti et al., 2003; Mihalcea et al., 2006, 2008; Azzoni et al., 2016) and biological viewpoints (Fickert et al. 2007; Gobbi et al. 2011; Caccianiga et al. 2011; Pelfini et al., 2012; Azzoni et al., 2015). The phenomenon is due on the one hand to the progressive exposure of englacial debris with ice melting, on the other hand to the increasing occurrence of rock-falls from the slopes ice-freed by glacier thinning and thus exposed to gelivation processes (Kirkbride and Warren, 1999; Mattson, 2000; Diolaiuti et al., 2003; Stokes et al., 2007). If a thin debris layer promotes further ablation through its thermal conductivity, over a thickness threshold of 1-2 cm the ablation rate decreases logarithmically as a consequence of thermal insulation, allowing glaciers to prevent further mass loss in spite of the ongoing climate warming (Mattson et al., 1993; Nakawo and Rana, 1999). Therefore, over a transition from a cold-climatic stage to a warm-climatic one, glacier systems are able to turn from a debris-free state to a debris-covered one, a new metastable equilibrium characterized by less negative mass balance, smaller amplitude of frontal fluctuations and tongue descending to lower altitudes (Kirkbride, 2000; Diolaiuti et al., 2003; Deline, 2005).

In some cases, debris-covered glaciers are able to support plant and arthropod life. Vegetation on these landforms was observed since the first decades of 20th century (e.g. Negri, 1935, 1942; Valbusa, 1937; Birks, 1980), but were only recently in-depth analyzed by the ecological viewpoint. Plants that most successfully colonize supraglacial debris are pioneer species with an extensive and shallow root system, even though shrubs and trees can frequently occur (Fickert et al., 2007; Caccianiga et al., 2011; Pelfini et al., 2012). Arthropod species can establish as well on supraglacial debris, especially predatory taxa (carabid beetles and spiders) that likely take nutrition from incoming aeroplankton (aphids and springtails) and flying insects (flies) (Gobbi et al. 2006a, 2011). To our knowledge, Miage glacier (Monte Bianco, Western Italian Alps) is the only debris-covered glacier analyzed by the botanical (Caccianga et al., 2011) and zoological viewpints (Gobbi et al., 2011); plant and arthropod species assemblage and species richness on its surface resulted to be affected by ground stability as a function of ice flow velocity and by ground surface temperature as a function of debris thickness. Interestingly, these landform can host cold-adapted high alpine taxa below their normal altitudinal distribution side by side with typical subalpine ones, a phenomenon observed in many biogeographical contexts of the world and generally attributed to the thermal effect of underlying ice (Fickert et al. 2007; Gobbi et al. 2011; Caccianiga et al. 2011).

The importance of geomorphological heterogeneity at landscape level to safeguard biodiversity in spite of the climate changes is known, since specific landforms can locally preserve suitable microclimate conditions for stenotherm species even when the macroclimate became adverse (Ashcroft et al., 2012; Birks and Willis, 2008; Dobrowski, 2011; Stewart et al., 2010; Gentili et al., 2015). In the matter of that, the role of debris-covered glacier was already debated.

Fickert et al. (2007) proposed such landforms as refugia and dispersal pathways during the ice ages, calling into question the ice ages themselves as periods of biogeographical isolation. Other authors interpreted debris-covered glaciers as potential warm-stage refugia for cold-adapted plant (Caccianiga et al. 2011) and arthropod species (Gobbi et al. 2011), as a consequence of the microclimate features due to the ice presence and the thermal inertia due to the debris cover. Since supraglacial debris occurs during warm-climatic stages rather than cold-climatic ones, it may provide a new suitable habitat for cold-adapted species right when they are most threatened by the upshift of altitudinal belts (Theurillat and Guisan, 2001; Pauli et al., 2003; Thuiller et al., 2005; Dullinger et al., 2012, Pizzolotto et al., 2014).

Studies about geomorphological (e.g. Diolaiuti et al., 2003; Deline, 2005), botanical (e.g. Fickert et al., 2007; Caccianiga et al., 2011) and zoological features (e.g. Gobbi et al., 2011; Azzoni et al., 2015) of debris-covered glaciers were already performed, but no studies integrated multidisciplinary data about climate, soil, plants and arthropods at the same time. The ecological variability within debris-covered glaciers as a function of glaciological parameters (e.g. ice flow velocity and supraglacial debris thickness) was already analyzed both from the plants (Caccianiga et al., 2011) and arthropods viewpoint (Gobbi et al., 2011), but no studies compared debris-covered glaciers with the surrounding landforms as reference sites and clearly contextualized debris-covered glaciers with respect to the altitudinal zonation of mountain ecosystems (e.g. with respect to the climatic treeline).

In the present paper we analyze the abiotic (glacial dynamics, ground surface temperature and humidity, soil physical and chemical parameters) and biotic features (plant and arthropod communities) of an Alpine debris-covered glacier (Belvedere glacier, Monte Rosa, Western Italian Alps), comparing them with those of the surrounding landforms as reference sites (control slope and iceless moraine).

Our hypotheses are: 1) the debris-covered glacier differs from the surrounding landforms for (a) ground surface temperature/humidity and (b) soil physical/chemical parameters; 2) the debris-covered glacier differs from the surrounding landforms for (a) plant/arthropod species richness/abundance, (b) plant/arthropod cold-adapted species.

We finally aim to infer the arrangement of debris-covered glaciers with respect to the climatic treeline as lower limit of the alpine belt (Körner 2003), to improve the discussion about such landforms as potential warm-stage refugia for cold-adapted species.

Data collection

Study area

The present study was performed on Belvedere glacier (Wester Italian Alps, N45 57.685 E7 54.925) (fig. 1), one of the most well known debris-covered glaciers of the Alps (e.g. Monterin, 1923). Its fame is partially due to its interesting and hazardous dynamics, like the several outburst floods recorded from 1868 to 1979 and the surge-type movement performed between the summers 2001 and 2002 (Haeberli et al., 2002; Mortara and Tamburini, 2009).

The glacier is c. 3400 m long and 700 m wide, covering a total surface of c. 4.53 km^2. It takes origin from the confluence of four main tongues descending from the ice cap of Monte Rosa (4633 m a.s.l.) and reaches 1785 and 1820 m a.s.l. with two divergent frontal lobes; such altitudes make Belvedere the lowest glacier of the Italian Alps after Brenva (1440 m a.s.l.) and Miage (1730 m a.s.l.). The glacier surface is almost completely covered by a debris layer whose thickness ranges from c. 5 cm in the upper tongue to 20-30 cm in the frontal lobes, with peak levels of c. 80 cm in the depressions (Diolaiuti et al., 2003). Two moraine systems delimit the glacier: an external one deposed in the Little Ice Age (at present consolidated and fully covered by vegetation) and an internal more recent one (still unconsolidated and with lower plant cover) (Mortara and Tamburini, 2009). The area is characterized by a substrate of gneiss and schists (Mattirolo et al., 1951) and a sub-oceanic climate regime (Mortara and Tamburini, 2009; Tampucci et al., 2016).

The climatic treeline resulted to be located at c. 2215 m a.s.l., c. 430 m below the glacier front. It was estimated as follows: seven years (2008-2014) of mean daily temperature at 1360, 2075 and 2820 m a.s.l. were used to calculate the monthly mean altitudinal temperature lapse rate; fifteen years (2000-2014) of mean daily temperature at 1360 m a.s.l. were used to get the altitude of the climatic treeline following Paulsen and Körner (2014) (data provided by ARPA Piemonte).

Sampling design

We selected three adjacent landforms, corresponding to three different ecological conditions: 1) control slope (stable slope not involved in Holocene glacial dynamics, supposed to have the potentiality for the full development of soil and biocoenoses), 2) iceless moraine (debris-featured landform without underlying ice, deposed after the Little Ice Age and still unconsolidated), 3) supraglacial debris (debris-featured landform with underlying ice).

A data-logger (Tinytag TGP-4500) was placed at each landform (at 2075, 2060 and 2055 m a.s.l., respectively) in order to analyze the patterns of mean daily ground surface temperature and mean daily ground surface humidity during the period October 2014–15. The devices were placed between stones at a depth ranging from 10 to 15 cm, in order to shield them from direct solar radiation. The recording was set at one-hour interval; the temperature data have an accuracy of ± 0.20°C from 0 to 50°C and a resolution of 0.25°C at 0°C; the humidity data have an accuracy of ± 3% at 25°C and a resolution ≥ 0.5%.

We selected 5 plots for each landform (fig. 1) and 3 sampling points for each plot, randomly placed at least c. 10 m far from each other. Soil samples were taken at the surface for physical and chemical analysis: at each plot a sample of c. 1 kg was taken for particle size distribution analysis; at each sampling point a sample of c. 200 g was taken to measure soil pH (in 1:2.5 soil:water) and organic matter content (Walkley-Black method). At each sampling point, plant and arthropod community data were collected as follows: plant species surveys of 25m^2 were performed, estimating the percentage of bare soil surface and each plant species cover with a resolution of 5%; arthropod species sampling was performed placing a pitfall trap, a plastic cup buried up to the edge and filled with approximately 20 ml of wine-vinegar and salt solution (Gobbi et al., 2011). Pitfall traps were collected and re-set every 20 days during the snow-free season (July–October 2014). The analysis concerned ground beetles (Coleoptera: Carabidae) and spiders (Arachnida: Araneae), since they are two taxa well known by the ecological viewpoint (Brandmayr et al., 2003; Thaler, 2003) and extensively used as bioindicators of climate change in high latitude-altitude ecosystems (e.g. Bråten et al., 2012; Gobbi et al., 2006, 2007).

Concerning glaciological analyses, at each plot a 2 m long ablation stake was installed to quantify the ice ablation rate and the ice flow velocity in the period 4th July–28th September 2014. Each position was registered through a Leica ATX1230 GNSS GPS receiver at the beginning and at the end of the period. At each plot, remote-sensing analysis of thermal data from Landsat 8 (100 m resolution) were used to estimate ground surface temperature in 27th August and 12th September 2014. At each sampling point supraglacial debris thickness was measured. Glaciological data were used to perform a comparative analysis with Miage Glacier, a nearby debris-covered glacier for which plant and arthropod data are available (Caccianiga et al., 2011; Gobbi et al., 2011).

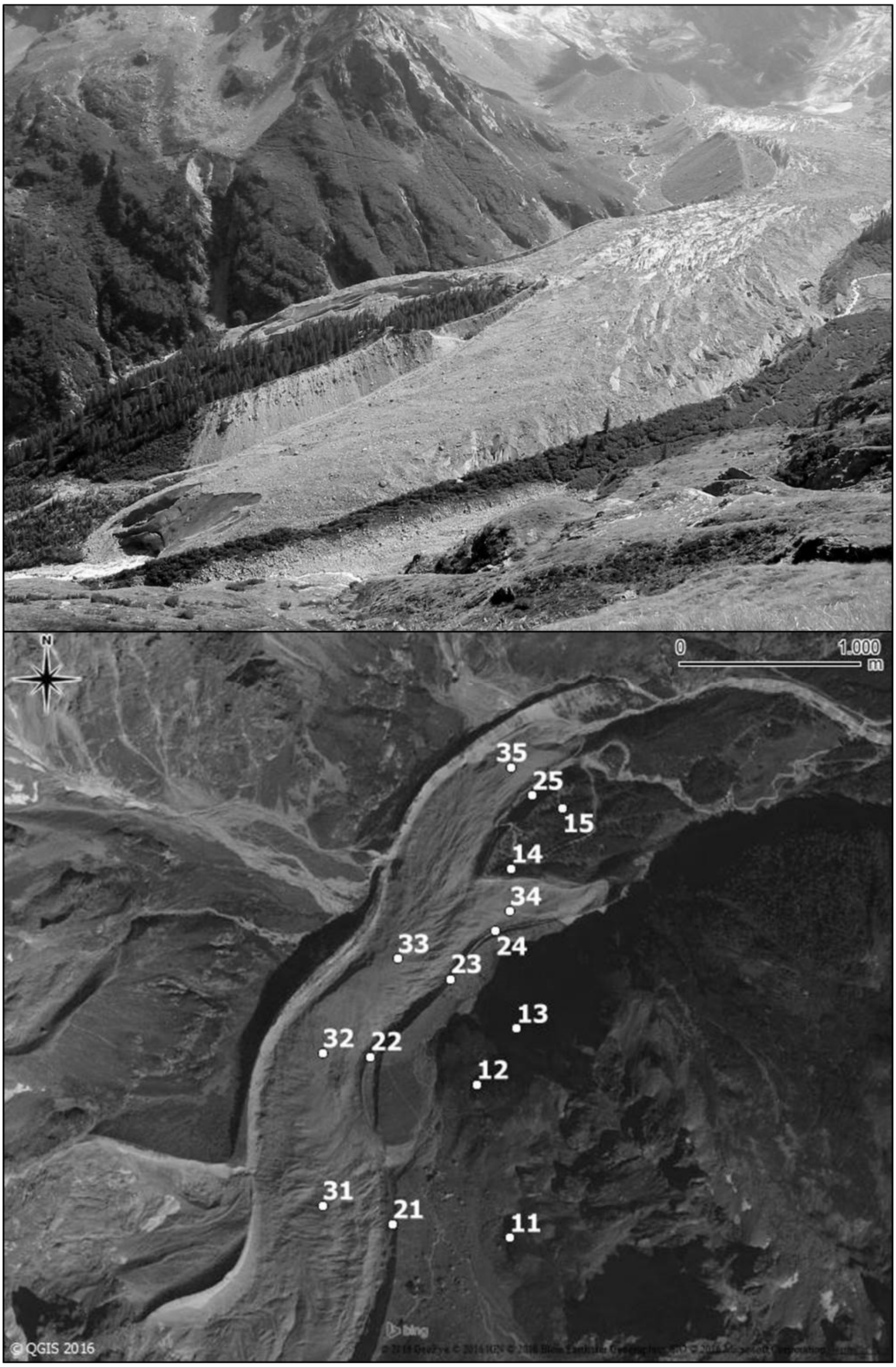

Fig. 1. Belvedere glacier with plots position (photo by Lindsey Nicholson).

Environmental and community variables

The observations were recorded in a dataset of 45 rows (one for each sampling point) and 181 columns, including: the landform, four soil variables, four community variables and abundance for 117 plant species and 55 arthropod species.

The landform was considered as a categorical variable in three classes (control slope, iceless moraine, supraglacial debris). The following soil variables were considered: bare soil surface (expressed in percentage), coarse debris fraction (sum of gravel and sand fractions expressed in percentage), soil pH, organic matter content (expressed in g/kg). The following community variables were considered: plant species richness (number of plant species), plant total cover (sum of every plant species cover expressed in percentage), arthropod species richness (number of ground beetle species plus number of spider species), arthropod total activity density (sum of ground beetle and spider activity density: ratio among number of captured specimens and number of days of trap activity). Each plant species abundance was expressed as cover percentage with a resolution of 5%; each arthropod species abundance was expressed as activity density.

Species nomenclature refers to Landolt et al. (2010) for plants, Vigna Taglianti (2013) for ground beetles and World Spider Catalog (2016) for spiders. We define "cold-adapted species" all the species strictly linked to the alpine belt (e.g. above the climatic treeline in Körner, 2003). Concerning plants, we consider like that all 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 based on the available descriptive literature about the requirement of each identified taxa (e.g. Magistretti, 1965; Casale et al., 1982; Brandmayr and Zetto Brandmayr, 1988; Pantini and Isaia, 2016).

Descriptive statistics (median, minimum and maximum values) of the following glaciological variables were reported: ice ablation rate (expressed in cm of water equivalent/day), ice flow velocity (expressed in m/day), ground surface temperature (mean between ground surface temperature estimated for 27th August and 12th September 2014 expressed in °C), supraglacial debris thickness (expressed in cm).

Data analysis

To compare the landforms in terms of microclimate features, descriptive statistics (mean value and standard deviation) of ground surface temperature and ground surface humidity were calculated for the period October 2014–15. Following Schmid et al. (2012), two distinct periods of the year were distinguished: the snow-cover period (period with daily ground surface temperature standard deviation < 0.2°C on the basis of 1 hour sampling rate) and the snow-free period (period with daily ground surface temperature standard deviation > 0.2°C on the basis of 1 hour sampling rate). The snow cover period included the zero-curtain one, which is the period affected by the latent heat effect in maintaining ground surface temperature of freezing or thawing soils near 0°C (Outcalt et al., 1990) (period with ground surface temperature ranging from -0.25 to 0.25°C in Gubler et al., 2011). Air temperature at 2075 m a.s.l. was also reported as reference climate parameter (data provided by ARPA Piemonte).

To compare the landforms in terms of soil and community variables, regression methods were used: each variable was included in a regression model as response variable, except the landform, which was included as explicative one. For all soil variables and plant total cover, Quantile Regression Models (QRM) (Cade and Noon, 2003) were used, thus the median values of each variable were compared among landforms. To account for the correlation among sampling points within each plot, a random effect with Laplace distribution was included in each model (Geraci and Bottai, 2014).

For the remaining community variables (plant species richness, arthropod species richness and activity density), Generalized Linear Models (GLM) with Poisson error were used. To account for the correlation among sampling points within each plot (Gobbi and Brambilla, 2016), the models were estimated with Generalized Estimating Equation methods (Zeger et al., 1988), using an exchangeable working covariance matrix. Results from all the models were reported in terms of estimated differences among medians (QRM) and mean ratios (GLM) among different landforms, with respective 95% Confidence Intervals. The Confidence Intervals were adjusted for multiple comparisons with the Bonferroni rule.

To identify characteristic plant and arthropod species of each landform, Indicator Species Analysis (ISA) (Dufrêne and Legendre, 1997) was used; the IndVal index for abundance data was used to quantify the association between species and the three landforms. Once identified the species with the highest association for each landform, such associations were assessed through permutation tests (number of permutations: 9999). In order to control for the "block effect" of plots, a restricted permutation scheme was adopted, in which sampling points within each plot permute, but cannot be exchanged with sampling points outside the plot.

All the analyses were performed with the R software (R Core Team 2015), with the packages FactoMineR (Husson et al., 2016), vegan (Oksanen et al., 2015), lqmm (Geraci, 2014), geepack (Højsgaard et al., 2006) and indicspecies (De Caceres and Legendre, 2009).

Results

All the investigated landforms showed a peculiar thermal regime (fig. 2, table 1). Mean daily ground surface temperature during the snow-cover period showed the main difference between control slope and debris-featured landforms as a whole: on the first it remained slightly above 0°C (0.11°C), while on the second it slightly oscillated around lower values (-0.75 and -0.90°C on the iceless moraine and the supraglacial debris, respectively). By contrast, mean daily ground surface temperature during the snow-free period showed the main difference between supraglacial debris and iceless landforms as a whole, being more constant and lower on the first (5.80°C) than on control slope (8.81°C) and iceless moraine (9.31°C) (fig. 2, table 1). Ground surface humidity reached the constant value of c. 100% on all the landforms during the snow-cover period, while during the snow-free one it oscillated between c. 80 and 90% depending on the landform, with the highest value on the iceless moraine (90.94%), the mid one on the control slope (84.98%) and the lower one on the supraglacial debris (80.25%) (table 1).

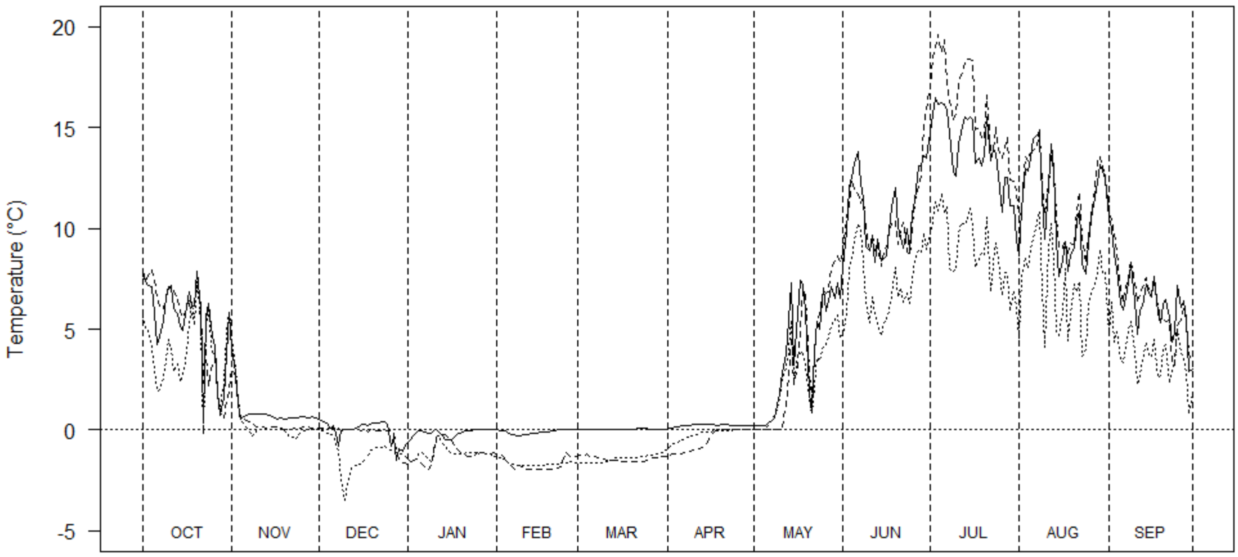

Fig. 2. Patterns of mean daily ground surface temperature of the investigated landforms over the period October 2014–15: control slope (continuous line), iceless moraine (dashed lines) and supraglacial debris (dotted lines).

Landform	Altitude (m a.s.l.), Aspect (°), Slope (°)	Period	Length (days)	Ground surface temperature (°C)	Ground surface humidity (%)
1. Control slope	2075, 315, 20	Snow-cover	186	0.11 (0.35)	99.98 (0.19)
		Snow-free	179	8.81 (3.90)	84.98 (13.31)
		Year	365	4.38 (5.14)	92.62 (11.96)
2. Iceless moraine	2060, 80, 25	Snow-cover	189	-0.75 (0.78)	100.00 (0.00)
		Snow-free	176	9.31 (4.50)	90.94 (10.05)
		Year	365	4.10 (5.95)	95.63 (8.31)
3. Supraglacial debris	2055, 50, 10	Snow-cover	186	-0.90 (0.73)	99.81 (1.47)
		Snow-free	179	5.80 (2.70)	80.25 (17.81)
		Year	365	2.38 (3.88)	90.64 (15.65)
Air	2075	Snow-cover	-	-1.40 (4.28)	-
		Snow-free	-	8.44 (3.98)	-
		Year	365	3.42 (6.43)	-

Table 1. Ground surface temperature and ground surface humidity recorded during the period October 2014–15 on each landform. Results were reported in terms of mean value (with standard deviation in brackets) for the snow-cover and snow-free periods and for the whole year.

The control slope differed from debris-featured landforms as a whole for lower coarse debris-fraction and higher organic matter content (fig. 3, table 2). Bare soil surface and soil pH differed among all the landforms: bare soil surface reached the lowest and highest values on control slope and supraglacial debris, respectively; soil pH reached the higher and lower values on the iceless moraine and the control slope, respectively (fig. 3, table 2).

Plant and arthropod species richness showed similar patterns, since supraglacial debris differed from the surrounding landforms for lower species richness. By contrast, plant and arthropod species abundance showed different patterns: plant total cover was different on each landform, reaching the highest and lowest values on the control slope and supraglacial debris, respectively; arthropod activity density was lower on the iceless moraine than on the surrounding landforms (fig. 3, table 2).

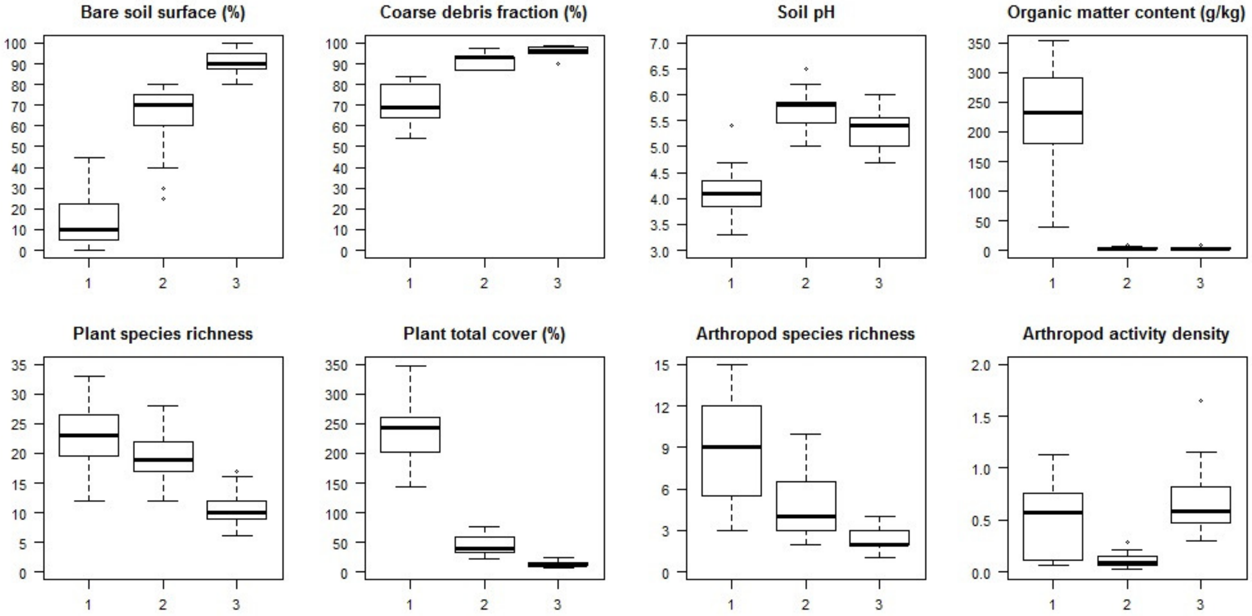

Fig. 3. Boxplot of each variable for the investigated landforms: control slope (1), iceless moraine (2), supraglacial debris (3).

	3 vs 2	3 vs 1	2 vs 1
Bare soil surface (%)	18.45 (12.92, 28.06)	76.05 (61.61, 87.73)	57.60 (46.01, 69.65)
Coarse debris fraction (%)	-0.08 (-3.02, 11.58)	26.02 (15.32, 34.39)	26.11 (7.26, 30.99)
Soil pH	-0.40 (-0.87, -0.03)	1.23 (0.78, 1.55)	1.62 (1.05, 2.15)
Organic matter content (g/kg)	-0.03 (-3.39, 1.74)	-224.74 (-315.42, -172.21)	-224.71 (-315.44, -171.78)
Plant species richness *	0.56 (0.41, 0.74)	0.47 (0.33, 0.67)	0.84 (0.61, 1.11)
Plant total cover (%)	-25.94 (-44.01, -17.30)	-233.22 (-250.95, -188.06)	-207.28 (-227.78, -155.42)
Arthropod species richness *	0.5 (0.30, 0.82)	0.28 (0.17, 0.45)	0.55 (0.30, 1.11)
Arthropod total activity density *	6.11 (3.32, 11.02)	1.32 (0.67, 2.72)	0.22 (0.10, 0.50)

Table 2. Results of the multiple comparisons of variables among landforms: control slope (1), iceless moraine (2), supraglacial debris (3). All the comparisons were carried out with QRM, except plant species richness, arthropod species richness and arthropod total activity density, which were carried out with GLM (Poisson distribution) (*). Results were reported as Est (95% C.I.).

One hundred-seventeen plant species were found (table 4); 85 plant species were found on the control slope, 51 on the iceless moraine and 31 on the supraglacial debris. The ISA (table 4) selected 76 species (65% of the flora) best-fitting on the control slope, 27 (23%) on the iceless moraine and 14 (12%) on the supraglacial debris. Seven species resulted significantly linked to the control slope: *Rhododendron ferrugineum* (IndVal 1.00, p=0.0012), *Avenella flexuosa* (IndVal 0.97, p=0.0012), *Vaccinium myrtillus* (IndVal 0.97, p=0.0012), *Dryopteris dilatata* (IndVal 0.89, p=0.0102), *Gentiana purpurea* (IndVal 0.77, p=0.0117), *Calamagrostis villosa* (IndVal 0.73, p=0.0149) and *Anthoxanthum alpinum* (IndVal 0.73, p=0.0238). Six species resulted significantly linked to the iceless moraine: *Trifolium pallescens* (IndVal 0.97, p=0.0009), *Rumex scutatus* (IndVal 0.88, p=0.0009), *Achillea moschata* (IndVal 0.82, p=0.0009), *Luzula lutea* (IndVal 0.77, p=0.0090), *Festuca halleri* (IndVal 0.73, p=0.0096) and *Silene rupestris* (IndVal 0.80, p=0.0238). Three species resulted significantly linked to the supraglacial debris: *Cerastium pedunculatum* (IndVal 0.90, p=0.0009), *Poa laxa* (IndVal 0.96, p=0.0021) and *Luzula alpinopilosa* (IndVal 0.69, p=0.0235).

Fifty-five arthropod species were found (14 carabid beetles and 41 spiders) (table 4); 41 arthropod species were found on the control slope (10 carabid beetles and 31 spiders), 31 on the iceless moraine (9 carabid beetles and 22 spiders) and six on the supraglacial debris (all spiders). The ISA (table 4) selected 33 species (60% of the fauna) best-fitting on the control slope, 20 (36%) best-fitting on the iceless moraine and two (4%) best-fitting on the supraglacial debris. Five species resulted significantly linked to the control slope: *Pterostichus multipunctatus* (IndVal 0.89, p=0.0030), *Leistus nitidus* (IndVal 0.73, p=0.0102), *Centromerus pabulator* (IndVal 0.58, p=0.0102), *Tenuiphantes jacksoni* (IndVal 0.74, p=0.0117) and *Robertus truncorum* (IndVal 0.84, p=0.0182). One species resulted significantly linked to the iceless moraine: *Coelotes rudolfi* (IndVal 0.72, p=0.0247). Two species resulted significantly linked to the supraglacial debris: *Oedothorax agrestis* (IndVal 1.00, p=0.0009) and *Pardosa saturatior* (IndVal 0.83, p=0.0030).

Each glaciological variable shows a quite high variability and a more or less clear distributional patterns along the glacier tongue. Ice ablation rate ranged from -0.11 to -2.53 w.e./day (median: -1.86 w.e./day) showing no clear distributional patterns along the glacier tongue. Ice flow velocity ranged from 0.02 to 0.06 m/day (median: 0.05 m/day), slightly decreasing from the upper to the lower zones. GST ranged from 13.7 to 17.5 °C (median: 15.30 °C), slightly increasing from the upper to the lower zones. Supraglacial debris thickness ranged from 6 to 38 cm (median: 20 cm) showing no clear distributional pattern.

Discussion

Ecology of debris-covered glaciers and surrounding landforms

Supraglacial debris was remarkably different from the surrounding landforms for thermal regime and species assemblage, while its soil features were similar to those of the iceless moraine.

The ground surface temperature of the control slope follows the typical pattern expected in normal condition at the considered altitude. During the snow-cover period, both debris-featured landforms show lower temperature than control slope: on the iceless moraine likely as a consequence of the rougher surface (e.g. coarse boulders and high acclivity) which prevent a thick and continuous snow cover able to insulate the ground from air temperature; on the supraglacial debris likely also as a consequence of the thermal effect of underlying ice, similarly to active rock glaciers (Hoelzle et al., 1999). Coherently, during the snow-free period the ground surface temperature of the iceless moraine does not differ from that of the control slope, while that of the supraglacial debris maintains lower values. Therefore, according to our hypothesis, the debris-covered glacier differs from the surrounding landforms for ground surface temperature, particularly during the snow-free period which is the period of highest biological activity.

The soil of control slope can be likely considered as more developed than those of debris-featured landforms, since organic matter content is higher while bare soil surface, coarse debris fraction and soil pH are lower. Debris-featured landforms differ each other only in terms of bare soil surface being the iceless moraine much more covered by vegetation than supraglacial debris, but can be considered substantially equal in terms of coarse debris fraction, organic matter content and pH. Therefore, according to our hypothesis, the debris-covered glacier differs from the control slope for soil physical and chemical parameters; by contrast, it does not differs from the iceless moraine.

The control slope is characterized by high values of richness and abundance both for plant and arthropod species, with typical plants of acidophilous conifer woodlands like *Rhododendron ferrugineum*, *Vaccinium myrtillus* and *Calamagrostis villosa* (Grabherr and Mucina, 1993; Oberdorfer, 1998; Andreis et al., 2009) and arthropods generally expected in such habitat like the carabid beetle *Pterostichus multipunctatus* (Brandmayr and Zetto Brandmayr, 1988; Gobbi et al., 2007) and the spider *Robertus truncorum* (Nentwig et al., 2016). The iceless moraine overall shows similar species richness but lower abundance with respect to the control slope, with pioneer but not cold-adapted plants like *Trifolium pallescens*, *Rumex scutatus* and *Silene rupestris* and lacks characteristic arthropod species. Some species affinities with the control slope (e.g. woody plants like *Larix decidua* and *Alnus viridis*, carabid beetles like *Pterostichus cribratus* and *Carabus concolor*, spiders like *Coelotes pickardi* and *Robertus arundineti*) suggest that such community may represent a successional stage toward the potential biocoenosis of the area. On the supraglacial debris, while plant total cover is rather low, arthropod total activity density reaches very high values due to the large population of the ballooner spider *Oedothorax agrestis* (Weyman et al., 2002; Bell et al., 2005; Blandenier et al., 2009). The community is characterized by few but almost exclusive species, especially pioneer cold-adapted ones normally widespread above the climatic treeline, like the plants *Cerastium pedunculatum*, *Poa laxa* and *Luzula alpinopilosa* and the spider *Pardosa saturatior*. Therefore, according to our hypotheses, the debris-covered glacier differs from the surrounding landforms for species richness and abundance (particularly for plants) and for the occurrence of cold-adapted plant and arthropod species.

Summarizing, the community of the iceless moraine appears as a pioneer stage over the subalpine primary succession; by contrast, the supraglacial debris seems more selective as a consequence of both the higher ground instability due to the glacial dynamic (e.g. ice ablation rate and ice flow velocity) and the lower ground temperature due to the underlying ice. Such features thus likely prevents the subalpine primary succession development and promotes the persistence of cold-adapted species in an adverse altitudinal context.

The supraglacial debris of Belvedere seems to be overall harsher than Miage as habitat for plant and arthropod life, due to the slightly lower supraglacial debris thickness and ground surface temperature and above all to the remarkable higher ice flow velocity. The higher ice flow velocity of Belvedere may explain the overall lower species richness, since likely excludes species most demanding in terms of ground stability. However, the most surprising difference between the two glaciers lies in the absence of carabid beetles on Belvedere, in spite of the high values of species richness and activity density in the area. Cold-adapted carabid beetles (e.g. *Oreonebria* spp.) are able to tolerate comparable supraglacial debris thickness (e.g. down to 24 cm on Miage glacier in Gobbi et al., 2011) and much lower mean annual ground surface temperature (e.g. down to -2.3°C on active rock glaciers in Gobbi et al., 2014), thus their absence is not imputable to microclimatic limitation. The supraglacial debris permanently supports both spider and carabid species with similar trophic requirements (Gobbi et al., 2006, 2011; Tenan et al., 2016), so carabid beetles absence is neither imputable to trophic factors. Therefore, the absence of carabid beetles could be due to the higher surface instability due to the higher ice flow velocity.

Besides the current ecological factors, we probably have to take into account also past events which may have affected the actual biological features. The surge-type movement of 2001-02 achieved extraordinary ice flow velocity up to 200 m/year (Haeberli et al., 2002; Mortara and Tamburini, 2009), likely erasing both plant and arthropod supraglacial communities. The potential community, probably including carabid beetles, could not have established yet. The occurrence of spiders supports this hypothesis, because spiders are characterized by much higher dispersal ability (Weyman et al., 2002; Bell et al., 2005; Blandenier et al., 2009) allowing them to colonize the supraglacial debris before carabid beetles. The Miage glacier, without recent surge-type movements, could thus better represent the real potentiality of Alpine debris-covered glaciers as habitat for plant and arthropod life.

Glacier	**Belvedere**	**Miage**
Altitudinal range (m a.s.l.)	1890-2120	1815-2230
Ice ablation rate (w.e./day)	-1.86 (-2.53, -0.11)	N.A.
Ice flow velocity (m/day)	0.05 (0.02, 0.06)	0.01 (0.00, 0.04)
Ground surface temperature (°C)	15.3 (13.7, 17.5)	17.5 (15.1, 19.7)
Supraglacial debris thickness (cm)	20 (6, 38)	37 (10, 56)
Total plant species richnes	31	45
Total arthropod species richness	6	12
Carabid beetles species richness	0	2
Spider species richness	6	10

Table 3. Comparison between Belvedere and Miage glaciers in terms of glaciological and biological parameters. Glaciological parameters were reported as median values (with minimum and maximum values in brackets); biological variables were reported as total values at landform level.

Debris-covered glaciers as warm-stage refugia?

Our results, together with previous ones (Caccianiga et al., 2011; Gobbi et al., 2011), show that debris-covered glaciers as habitat have all the ecological requirements to act as warm-stage refugia for cold-adapted species. Such landforms occurs especially during warm-climatic stages and likely persist during them thanks to the thermal insulation provided by the supraglacial debris and to the continuous ice supply from the accumulation zone which compensates the ice losses in the ablation one. The microclimate due to the underlying ice provides suitable habitat for cold-adapted species, allowing them to live below their normal altitudinal distribution (in our study case, c. 430 m below the climatic treeline). Further, the glacial dynamic contributes to prevent the development of the normal primary succession at this elevation, promoting the long-lasting persistence of species which would be otherwise replaced by those of the surrounding environments.

However, the refugium role of debris-covered glaciers is probably limited to pioneer cold adapted species and not to those linked to stable sites; furthermore, extraordinary events like surge movements may cause local extinction of species right within their refugia. Finally, some questions advanced by Fickert et al. (2007) still remain as crucial matters both for the cold- and warm-stage refugia hypotheses, particularly: 1) if species are able to close their life cycle before calving off the glacier as a consequence of the ice flow; 2) if propagules are then able to recolonize the upper zones of the glacier to restart a new life cycle. Further studies are thus needed to implement the discussion about debris-covered glaciers as warm-stage refugia for cold-adapted species.

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Table S1. Synoptic table at landform level: soil and community variables were expressed as median values (minimum and maximum values in brackets), followed by total values at landform level (for community variables only). Plant species cover were expressed as mean value of cover in percentage (Ab); arthropod species abundances were expressed as sum of activity density (Ab) (ara = spider, car = carabid beetles). For each species were reported: cold-adaptation (C), IndVal for each landform (IndVal), best-fitting landform (BFL), significance of the association with the best-fitting landform (p-value, with * for significantly association).

	Landform	**1. Control slope**		**2. Iceless moraine**		**3. Supraglacial debris**				
	Bare soil surface (%)	10.00 (0.00, 45.00)		70.00 (25.00, 80.00)		90.00 (80.00, 100.00)				
	Coarse debris fraction (%)	69.08 (53.80, 84.02)		92.86 (86.91, 97.68)		96.40 (90.26, 98.71)				
	Soil pH	4.10 (3.30, 5.40)		5.80 (5.00, 6.50)		5.40 (4.70, 6.00)				
	Organic matter content (g/kg)	231.70 (38.56, 354.50)		2.26 (0.33, 8.95)		1.73 (9.47, 1.73)				
	Plant species richness	23.00 (12.00, 33.00), 85		19.00 (12.00, 28.00), 51		10.00 (6.00, 17.00), 31				
	Plant total cover	243.00 (144.00, 347.00), 233.27		39.00 (22.00, 77.00), 45.27		12.00 (6.00, 24.00), 13.53				
	Arthropod species richness	9.00 (3.00, 15.00), 41		4.00 (2.00, 10.00), 31		2.00 (1.00, 4.00), 6				
	Arthropod total activity density	0.57 (0.06, 1.13), 7.27		0.09 (0.03, 0.28), 1.71		0.59 (0.30, 1.65), 10.28				
	Plant cold-adapted indices									
	Plant high-dispersal indices									
	Arthropod cold-adapted indices									
	Arthropod high-dispersal indices									
C	**Plant species**	**Ab**	**IndVal**	**Ab**	**IndVal**	**Ab**	**IndVal**	**BFL**	**p-value**	**Sig.**
	Rhododendron ferrugineum	39,33	1,00	0,13	0,02	0,07	0,01	1	0,0012	*
	Avenella flexuosa	11,67	0,97	0,00	0,00	0,00	0,00	1	0,0012	*
	Vaccinium myrtillus	13,00	0,97	0,00	0,00	0,00	0,00	1	0,0012	*
	Dryopteris dilatata	8,20	0,89	0,00	0,00	0,00	0,00	1	0,0102	*
	Gentiana purpurea	2,67	0,77	0,00	0,00	0,00	0,00	1	0,0117	*
	Calamagrostis villosa	22,67	0,73	0,07	0,01	0,00	0,00	1	0,0149	*
	Anthoxanthum alpinum	11,07	0,73	1,27	0,22	0,00	0,00	1	0,0238	*
	Astrantia minor	2,27	0,77	0,00	0,00	0,00	0,00	1	0,0623	
	Luzula sieberi	2,07	0,58	0,00	0,00	0,00	0,00	1	0,0634	
	Homogyne alpina	2,27	0,77	0,00	0,00	0,00	0,00	1	0,0651	
	Veratrum lobelianum	3,13	0,73	0,00	0,00	0,00	0,00	1	0,0686	
	Athyrium distentifolium	3,40	0,63	0,07	0,04	0,00	0,00	1	0,0686	
	Campanula barbata	0,60	0,58	0,00	0,00	0,00	0,00	1	0,0694	
	Juniperus nana	1,80	0,58	0,00	0,00	0,00	0,00	1	0,0694	
	Soldanella alpina	0,53	0,52	0,00	0,00	0,00	0,00	1	0,0694	
	Hieracium murorum aggr.	1,33	0,45	0,00	0,00	0,00	0,00	1	0,0694	

Silene vulgaris	1,60	0,63	0,27	0,20	0,00	0,00	1	0,0853
Ligusticum mutellina	0,93	0,58	0,00	0,00	0,00	0,00	1	0,2509
Phleum rhaeticum	1,13	0,50	0,07	0,06	0,00	0,00	1	0,2509
Huperzia selago	0,13	0,37	0,00	0,00	0,00	0,00	1	0,2509
Sorbus aucuparia	0,67	0,63	0,00	0,00	0,00	0,00	1	0,2541
Larix decidua	20,00	0,60	2,07	0,25	0,33	0,07	1	0,2541
Dryopteris filix-mas	0,80	0,52	0,00	0,00	0,00	0,00	1	0,2541
Melampyrum sylvaticum	3,40	0,52	0,00	0,00	0,00	0,00	1	0,2541
Peucedanum ostruthium	1,33	0,50	0,07	0,06	0,00	0,00	1	0,2541
Geranium sylvaticum	0,47	0,45	0,00	0,00	0,00	0,00	1	0,2541
Rumex alpestris	2,13	0,63	0,00	0,00	0,00	0,00	1	0,2580
Leontodon helveticus	1,53	0,63	0,00	0,00	0,00	0,00	1	0,2615
Vaccinium gaultherioides	11,33	0,63	0,00	0,00	0,00	0,00	1	0,2615
Helictotrichon versicolor	0,80	0,52	0,00	0,00	0,00	0,00	1	0,2615
Nardus stricta	1,40	0,52	0,00	0,00	0,00	0,00	1	0,2615
Geum montanum	0,47	0,45	0,00	0,00	0,00	0,00	1	0,2615
Phyteuma hemisphaericum	0,20	0,45	0,00	0,00	0,00	0,00	1	0,2615
Primula hirsuta	0,20	0,45	0,00	0,00	0,00	0,00	1	0,2615
Potentilla aurea	0,13	0,37	0,00	0,00	0,00	0,00	1	0,2615
Stellaria nemorum	0,80	0,45	0,00	0,00	0,00	0,00	1	0,2647
Solidago virgaurea	1,13	0,56	0,07	0,06	0,00	0,00	1	0,2654
Phyteuma betonicifolium	1,13	0,53	0,20	0,17	0,00	0,00	1	0,2654
Arnica montana	1,73	0,52	0,00	0,00	0,00	0,00	1	0,2654
Salix helvetica	4,67	0,46	1,13	0,32	0,20	0,08	1	0,2654
Festuca varia	1,80	0,50	1,47	0,54	0,07	0,04	1	0,3014
Campanula scheuchzeri	0,27	0,42	0,13	0,21	0,00	0,00	1	0,3429
Juncus trifidus	1,13	0,44	0,73	0,53	0,07	0,05	1	0,3889
Cystopteris fragilis	0,27	0,39	0,20	0,29	0,00	0,00	1	0,5677
Alnus viridis	14,00	0,37	6,07	0,40	0,00	0,00	1	0,6994
Festuca arundinacea	1,67	0,45	0,00	0,00	0,00	0,00	1	0,7014
Poa nemoralis	0,73	0,45	0,00	0,00	0,00	0,00	1	0,7014
Pyrola minor	0,80	0,45	0,00	0,00	0,00	0,00	1	0,7014
Salix appendiculata	10,00	0,38	3,00	0,46	1,20	0,28	1	0,7014
Ranunculus montanus aggr.	0,13	0,37	0,00	0,00	0,00	0,00	1	0,7014
Chaerophyllum hirsutum	0,07	0,26	0,00	0,00	0,00	0,00	1	0,7014
Corallorhiza trifida	0,07	0,26	0,00	0,00	0,00	0,00	1	0,7014
Dactylorhiza maculata	0,07	0,26	0,00	0,00	0,00	0,00	1	0,7014
Polypodium vulgare	0,07	0,26	0,00	0,00	0,00	0,00	1	0,7014
Polystichum lonchitis	0,07	0,26	0,00	0,00	0,00	0,00	1	0,7014
Thesium alpinum	0,07	0,26	0,00	0,00	0,00	0,00	1	0,7014
Alchemilla alpina aggr.	0,73	0,45	0,00	0,00	0,00	0,00	1	0,7049

	Pseudorchis albida	0,13	0,37	0,00	0,00	0,00	0,00	1	0,7049	
	Alchemilla vulgaris aggr.	0,07	0,26	0,00	0,00	0,00	0,00	1	0,7049	
x	*Carex curvula*	0,07	0,26	0,00	0,00	0,00	0,00	1	0,7049	
	Festuca nigrescens	0,33	0,26	0,00	0,00	0,00	0,00	1	0,7049	
	Hieracium morisianum	0,07	0,26	0,00	0,00	0,00	0,00	1	0,7049	
	Viola biflora	0,07	0,26	0,00	0,00	0,00	0,00	1	0,7049	
	Carex sempervirens	1,67	0,45	0,00	0,00	0,00	0,00	1	0,7096	
	Centaurea nervosa	0,07	0,26	0,00	0,00	0,00	0,00	1	0,7096	
	Sedum alpestre	0,07	0,26	0,00	0,00	0,00	0,00	1	0,7096	
	Trifolium alpinum	0,07	0,26	0,00	0,00	0,00	0,00	1	0,7096	
	Achillea macrophylla	1,40	0,45	0,00	0,00	0,00	0,00	1	0,7111	
	Adenostyles alliariae	0,73	0,45	0,00	0,00	0,00	0,00	1	0,7111	
	Oxalis acetosella	1,40	0,45	0,00	0,00	0,00	0,00	1	0,7111	
	Prenanthes purpurea	0,73	0,45	0,00	0,00	0,00	0,00	1	0,7111	
	Cicerbita alpina	0,40	0,37	0,00	0,00	0,00	0,00	1	0,7111	
	Milium effusum	1,33	0,37	0,00	0,00	0,00	0,00	1	0,7111	
	Maianthemum bifolium	0,07	0,26	0,00	0,00	0,00	0,00	1	0,7111	
	Rubus idaeus	0,33	0,26	0,00	0,00	0,00	0,00	1	0,7111	
	Streptopus amplexifolius	0,07	0,26	0,00	0,00	0,00	0,00	1	0,7111	
	Trifolium pallescens	0,00	0,00	1,80	0,97	0,00	0,00	2	0,0009	*
	Rumex scutatus	0,00	0,00	1,53	0,88	0,47	0,33	2	0,0009	*
x	*Achillea moschata*	0,00	0,00	0,67	0,82	0,00	0,00	2	0,0009	*
	Luzula lutea	0,00	0,00	0,80	0,77	0,27	0,26	2	0,0090	*
	Festuca halleri	0,00	0,00	0,53	0,73	0,00	0,00	2	0,0096	*
	Silene rupestris	0,00	0,00	1,47	0,80	0,67	0,46	2	0,0238	*
	Cardamine resedifolia	0,00	0,00	0,80	0,69	0,53	0,46	2	0,0545	
	Epilobium fleischeri	0,00	0,00	0,60	0,77	0,00	0,00	2	0,0680	
	Poa alpina	0,07	0,07	0,80	0,68	0,07	0,07	2	0,0694	
	Trifolium pratense	0,13	0,17	0,47	0,60	0,00	0,00	2	0,0845	
	Cerastium strictum	0,13	0,18	0,40	0,55	0,00	0,00	2	0,0938	
x	*Silene exscapa*	0,00	0,00	0,40	0,52	0,20	0,26	2	0,0969	
	Saxifraga aspera	0,00	0,00	0,47	0,64	0,07	0,09	2	0,1086	
	Agrostis stolonifera	6,47	0,51	11,47	0,76	1,73	0,29	2	0,1662	
	Bartsia alpina	0,00	0,00	0,27	0,52	0,00	0,00	2	0,2544	
	Pedicularis tuberosa	0,00	0,00	0,13	0,37	0,00	0,00	2	0,2566	
	Sempervivum montanum	0,33	0,36	0,53	0,57	0,00	0,00	2	0,3178	
	Myosotis alpestris	0,07	0,13	0,20	0,39	0,00	0,00	2	0,4232	
	Euphrasia minima	0,07	0,09	0,33	0,43	0,20	0,26	2	0,4723	
	Lotus alpinus	0,20	0,12	2,40	0,49	0,07	0,04	2	0,5356	
	Sagina saginoides	0,00	0,00	0,33	0,43	0,27	0,34	2	0,5759	
	Galium anisophyllon	0,00	0,00	0,07	0,26	0,00	0,00	2	0,7002	

	Hieracium staticifolium	0,00	0,00	0,07	0,26	0,00	0,00	2	0,7002	
	Epilobium nutans	0,00	0,00	0,07	0,26	0,00	0,00	2	0,7018	
	Rhinanthus alpinus	0,00	0,00	0,07	0,26	0,00	0,00	2	0,7018	
x	*Saxifraga oppositifolia*	0,00	0,00	0,07	0,26	0,00	0,00	2	0,7045	
	Arabis alpina	0,00	0,00	0,13	0,37	0,00	0,00	2	0,7059	
x	*Cerastium pedunculatum*	0,00	0,00	0,13	0,13	0,93	0,90	3	0,0009	*
x	*Poa laxa*	0,00	0,00	0,20	0,12	2,60	0,96	3	0,0021	*
x	*Luzula alpinopilosa*	0,00	0,00	0,07	0,09	0,53	0,69	3	0,0235	*
	Campanula excisa	0,00	0,00	0,00	0,00	0,33	0,58	3	0,0660	
	Saxifraga stellaris	0,00	0,00	0,00	0,00	0,33	0,58	3	0,0714	
x	*Leucanthemopsis alpina*	0,00	0,00	0,20	0,23	0,53	0,62	3	0,0885	
	Linaria alpina	0,00	0,00	0,47	0,47	0,53	0,53	3	0,3807	
x	*Saxifraga bryoides*	0,00	0,00	0,07	0,15	0,13	0,30	3	0,5553	
x	*Agrostis rupestris*	0,67	0,23	0,27	0,21	0,73	0,57	3	0,6861	
	Epilobium alsinifolium	0,00	0,00	0,00	0,00	0,07	0,26	3	0,6972	
x	*Gnaphalium supinum*	0,00	0,00	0,00	0,00	0,07	0,26	3	0,7041	
	Betula pendula	0,00	0,00	0,00	0,00	0,07	0,26	3	0,7053	
x	*Ranunculus glacialis*	0,00	0,00	0,00	0,00	0,07	0,26	3	0,7053	
x	*Oxyria digyna*	0,00	0,00	0,00	0,00	0,13	0,37	3	0,7092	

C	**Arthropod species**	**Ab**	**IndVal**	**Ab**	**IndVal**	**Ab**	**IndVal**	**BFL**	**p-value**	**Sig.**
	Pterostichus multipunctatus (car)	3,80	0,89	0,08	0,05	0,00	0,00	1	0,0030	*
	Leistus nitidus (car)	0,16	0,73	0,00	0,00	0,00	0,00	1	0,0102	*
	Centromerus pabulator (ara)	0,11	0,58	0,00	0,00	0,00	0,00	1	0,0102	*
x	*Tenuiphantes jacksoni (ara)*	0,12	0,74	0,01	0,07	0,00	0,00	1	0,0117	*
	Robertus truncorum (ara)	0,72	0,84	0,08	0,08	0,02	0,06	1	0,0182	*
	Pterostichus spinolae (car)	0,58	0,58	0,00	0,00	0,00	0,00	1	0,0623	
	Calathus micropterus (car)	0,13	0,58	0,00	0,00	0,00	0,00	1	0,0651	
x	*Oreonebria castanea (car)*	0,16	0,55	0,05	0,18	0,00	0,00	1	0,1633	
x	*Coelotes pickardi (ara)*	0,20	0,51	0,11	0,31	0,00	0,00	1	0,2294	
	Pterostichus cribratus (car)	0,23	0,56	0,11	0,29	0,00	0,00	1	0,2464	
	Cybaeus intermedius (ara)	0,03	0,37	0,00	0,00	0,00	0,00	1	0,2541	
	Walckenaeria cuspidata (ara)	0,02	0,37	0,00	0,00	0,00	0,00	1	0,2580	
	Pardosa mixta (ara)	0,07	0,58	0,00	0,00	0,00	0,00	1	0,2615	
	Gnaphosa badia (ara)	0,10	0,45	0,00	0,00	0,00	0,00	1	0,2615	
	Micrargus apertus (ara)	0,04	0,45	0,00	0,00	0,00	0,00	1	0,2647	
	Pardosa blanda (ara)	0,23	0,58	0,04	0,14	0,00	0,00	1	0,4245	
	Lepthyphantes nodifer (ara)	0,02	0,30	0,00	0,00	0,01	0,15	1	0,6994	
	Bolyphantes alticeps (ara)	0,01	0,26	0,00	0,00	0,00	0,00	1	0,6994	
	Centromerus subalpinus (ara)	0,01	0,26	0,00	0,00	0,00	0,00	1	0,6994	
	Mughiphantes mughi (ara)	0,01	0,26	0,00	0,00	0,00	0,00	1	0,6994	

	Pardosa ferruginea (ara)	0,01	0,26	0,00	0,00	0,00	0,00	1	0,7049	
	Pelpecopsis radicicola (ara)	0,01	0,26	0,00	0,00	0,00	0,00	1	0,7049	
	Trichotichnus laevicollis (car)	0,01	0,26	0,00	0,00	0,00	0,00	1	0,7049	
	Haplodrassus signifer (ara)	0,03	0,37	0,00	0,00	0,00	0,00	1	0,7096	
x	*Incestophantes frigidus (ara)*	0,03	0,37	0,00	0,00	0,00	0,00	1	0,7096	
	Micaria aenea (ara)	0,01	0,26	0,00	0,00	0,00	0,00	1	0,7096	
	Palliduphantes pallidus (ara)	0,01	0,26	0,00	0,00	0,00	0,00	1	0,7096	
	Xysticus desidiosus (ara)	0,02	0,26	0,00	0,00	0,00	0,00	1	0,7096	
	Xysticus ulmi (ara)	0,01	0,26	0,00	0,00	0,00	0,00	1	0,7096	
	Pterostichus unctulatus (car)	0,06	0,37	0,00	0,00	0,00	0,00	1	0,7111	
	Walckenaeria obtusa (ara)	0,01	0,26	0,00	0,00	0,00	0,00	1	0,7111	
	Rugathodes bellicosus (ara)	0,04	0,17	0,02	0,12	0,03	0,15	1	0,7993	
	Anguliphantes monticola (ara)	0,01	0,18	0,01	0,18	0,00	0,00	1	0,9183	
x	*Coelotes rudolfi (ara)*	0,01	0,05	0,29	0,72	0,00	0,00	2	0,0247	*
	Drassodex drescoi (ara)	0,00	0,00	0,06	0,37	0,00	0,00	2	0,2544	
	Theridion petraeum (ara)	0,00	0,00	0,04	0,37	0,00	0,00	2	0,2544	
	Cicindela gallica (car)	0,00	0,00	0,03	0,45	0,00	0,00	2	0,2566	
	Drassodes lapidosus (ara)	0,00	0,00	0,03	0,45	0,00	0,00	2	0,2566	
	Cychrus cordicollis (car)	0,00	0,00	0,03	0,37	0,00	0,00	2	0,2622	
x	*Diplocephalus helleri (ara)*	0,00	0,00	0,06	0,37	0,00	0,00	2	0,2622	
	Platynus depressus (car)	0,00	0,00	0,02	0,37	0,00	0,00	2	0,2622	
x	*Pardosa nigra (ara)*	0,01	0,05	0,17	0,53	0,10	0,41	2	0,3059	
x	*Mughiphantes handschini (ara)*	0,02	0,21	0,04	0,30	0,00	0,00	2	0,3424	
	Carabus concolor (car)	0,08	0,34	0,10	0,51	0,00	0,00	2	0,3706	
	Robertus arundineti (ara)	0,03	0,29	0,04	0,28	0,00	0,00	2	0,6083	
	Tenuiphantes tenuis (ara)	0,00	0,00	0,05	0,37	0,00	0,00	2	0,7018	
	Carabus depressus (car)	0,04	0,27	0,07	0,29	0,00	0,00	2	0,7018	
	Walckenaeria capito (ara)	0,00	0,00	0,01	0,26	0,00	0,00	2	0,7018	
	Xysticus audax (ara)	0,00	0,00	0,03	0,26	0,00	0,00	2	0,7018	
	Amara erratica (car)	0,00	0,00	0,01	0,26	0,00	0,00	2	0,7059	
	Caracladus avicula (ara)	0,00	0,00	0,01	0,26	0,00	0,00	2	0,7059	
	Troglohyphantes lucifuga (ara)	0,06	0,25	0,07	0,27	0,00	0,00	2	0,7062	
	Zelotes subterraneus (ara)	0,01	0,18	0,01	0,18	0,00	0,00	2	0,9219	
	Oedothorax agrestis (ara)	0,00	0,00	0,01	0,01	9,79	1,00	3	0,0009	*
x	*Pardosa saturatior (ara)*	0,00	0,00	0,02	0,09	0,33	0,83	3	0,0030	*

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Plant and arthropod colonisation of a glacier foreland in a peripheral mountain range

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Primary successions along glacier forelands are perfect examples of the changing climate upon high mountain ecosystems. Peripheral mountain ranges deserve particular attention, given they are characterised by high numbers of species and endemism and are considered to be particularly susceptible to climate change. We analysed thermal regime, soil parameters and plant/arthropod primary succession along a glacier foreland located in such a context, comparing it with those previously studied in the inner Alps. The overall patterns of the investigated primary succession agree with those of the inner Alps at the same elevation, but stands out for a delayed plant and arthropod colonisation which promotes the long-lasting persistence of pioneer cold-adapted species. In light of the results obtained, and considering the glaciological features of peripheral mountain ranges (glaciers persistence at low elevation), this paper asserts the hypothesis that glacial landforms of these areas may act as warm-stage refugia for pioneer cold-adapted species.

Keywords: primary succession; climate change; refugia; cold-adapted species; carabid beetles; spiders

Introduction

After the Little Ice Age (LIA; sixteenth–nineteenth centuries), Alpine glaciers were subjected to a generalised retreat temporarily interrupted by short periods of advance. Ecological successions along the terrain freed by glacier retreat (glacier forelands) represent an effect of changing climate on high mountain ecosystems (Matthews 1992). Along a chronosequence of glacier retreat, early-successional species assemblages are progressively replaced by mid- and late-successional ones (Kaufmann 2001; Raffl et al. 2006). Time since deglaciation is the chief factor driving such processes, although the role of local ecological conditions at small scale is not negligible (Burga et al. 2010; Schlegel and Riesen 2012).

Plant succession and soil development along glacier forelands have been analysed in depth since the beginning of the twentieth century and summarised in several reviews (e.g. Matthews 1992; Miles and Walton 1993). Within the Alps, such dynamics were investigated in a wide range of geographical situations (e.g. Burga et al. 2010; Caccianiga and Andreis 2004; Lüdi 1955, 1958; Pirola and Credaro 1993; Raffl et al. 2006). Arthropod successions were also investigated, even though the studies are fewer and more recent (e.g. Gereben, Krenn, and Strodl 2011; Gobbi et al. 2006a, 2010; Kaufmann 2001, 2002; Schlegel and Riesen 2012). However, almost all the previous works were performed on glacier forelands located in the inner massifs of the Alpine chain, while knowledge about peripheral mountain ranges is still poor due to the scarcity of glaciers.

Nevertheless, in the context of climate change, peripheral mountain ranges of any mountain system deserve particular attention for at least three reasons: (1) they display plausible future scenarios for the whole chain and allow to directly test the fate of high mountain ecosystems, as the relatively low elevation makes them particularly susceptible to climate change (Bona et al. 2013; Pauli, Gottfried, and Grabherr 2003); (2) they are presently characterised by high values of species richness and endemism, since they were largely ice-free during glacial periods and acted as refugia for many plant (Martini et al. 2012; Schönswetter et al. 2005) and arthropod species (Latella, Verdari, and Gobbi 2012; Lohse, Nicholls, and Stone 2011); (3) their spatial arrangement causes remarkable climatic differences with respect to the inner massifs, affecting the altitudinal distribution of glaciers and their response to climate change (Scotti, Brardinoni, and Crosta 2014), as well as the elevation of vegetation belts (Caccianiga et al. 2008; Pirola and Credaro 1977).

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The Orobian Alps (maximum elevation: 3050 m above sea level (a.s.l.)) are a west–east oriented peripheral mountain range of the central Alps, south of the inner and higher Rhaetian Alps (maximum elevation: 4049 m a.s.l.). They are characterised by oceanic climate regime (mean annual precipitation: 1200–2000 mm/y), in sharp contrast with the continental Rhaetian Alps (mean annual precipitation: 650–1200 mm/y) (Ceriani and Carelli 2000). The high winter precipitation causes Orobian glaciers to be supply-limited rather than controlled by ablation, so they are able to persist at lower elevation and retreat comparatively less than the Rhaetian ones (Scotti, Brardinoni, and Crosta 2014). As consequence, high alpine plant species can live at lower altitudes (Caccianiga, Ravazzi, and Zubiani 1993; Pirola and Credaro 1977), sometimes below the potential treeline (Caccianiga et al. 2008). The Orobian Alps were often indicated as refugia during the glacial periods, which explains the high number of species and endemism (Lohse, Nicholls, and Stone 2011; Martini et al. 2012). However, the lower altitudinal distribution of glaciers and vegetation belts could result in a refugium role also during warm climatic stages (Gentili et al. 2015).

This paper aims to analyse the primary succession along a glacier foreland located in such a context, considering both the abiotic (thermal regime and soil parameters) and the biotic variables (plant and arthropod communities). Afterwards, we compared the investigated colonisation pattern with those previously observed in the inner Alps. Our hypotheses are: (1) plant and arthropod colonisation follows the same pattern along the primary succession; (2) plant and arthropod colonisation patterns differ from those of the inner Alps at the same elevation.

Methods

Study area

Trobio glacier was selected as the chief study site, due to the remarkable documented fluctuations which have occurred since the LIA. The glacier probably reached its maximal extension in the early nineteenth century, leaving a well-preserved moraine system. The following period was characterised by a general retreat, interrupted by four short advances: during the last years of nineteenth century, the 1920s, 1960s and 1980s. From the LIA to the 1990s, the glacier lost about 70% of its surface and split into three parts: Eastern, Central and Western Trobio (Bonardi et al. 2012; Caccianiga, Ravazzi, and Zubiani 1993). Our study was performed along the glacier foreland of the Western Trobio glacier and on the terrain outside the LIA moraine, likely ice-free since the Late Glacial (LG) and not involved in the Holocene glacial dynamic. Currently, the glacier foreland is about 1.2 km long and ranges from 2550 m a.s.l. (Western Trobio front) to 2350 m a.s.l. (LIA moraine). The bedrock is composed by siltstones, sandstones and conglomerates (Jadoul et al. 2000).

Sampling design

Six plots were selected, each corresponding to a specific deglaciation stage, as in Caccianiga, Ravazzi, and Zubiani (1993):

1. Terrain close to the present front of the glacier (ice-free since <30 years).
2. Terrain within the area marked by the glaciological mark of 1985 (c. 30 years).
3. Terrain within the moraine of the 1920s (c. 95 years).
4. Terrain on the roche moutonnée ice-free since the beginning of the twentieth century (c. 115 years).
5. Terrain within the LIA moraine, ice-free in the early nineteenth century (c. 150 years).
6. Terrain external to the LIA moraine, ice free since the LG and not involved in Holocene glacial dynamics (c. 10,000 years).

Two data-loggers (Tinytag TGP-4500) were placed between stones, protected from direct sunlight, at the plots 1 (2500 m a.s.l.) and 5 (2375 m a.s.l.) respectively, to analyse the thermal regime at ground level along the glacier foreland over one year (15 August 2013–15 August 2014, recording interval: 60 min). Five sampling points for each plot were selected and randomly placed about 10 m apart from each other. Substrate samples were taken at the surface for physical and chemical analysis: a sample of about 1 kg was taken at every plot for particle size distribution analysis; a sample of about 200 g was taken at each sampling point to obtain soil pH (in 1:2.5 soil:water), calcium carbonate content (Dietrich–Fruhling calcimeter) and organic matter content (Walkley–Black method). Vegetation surveys were performed on 25 m^2 surfaces at each sampling point. The percentage cover of rock outcrop, debris, soil, total plant cover and of every plant species were estimated with a resolution of 5%. Arthropods data were collected through pitfall traps: plastic cups buried up to the edge and filled with approximately 20 ml of vinegar and salt solution. We placed a pitfall trap at each sampling point, collected and re-set every 20 days during the snow-free season (July–October 2013–14). Since several pitfall traps were destroyed by marmots, we integrated this method with capture by hand (one-hour long catching activity in each plot on 12 September and 2 October 2014). The analysis on arthropod assemblages concerned carabid beetles (Coleoptera: Carabidae) and spiders (Arachnida: Araneae), the most abundant ground-dwelling arthropods; these two taxa are well known by the ecological viewpoint (Brandmayr et al. 2003; Thaler 2003) and are widely used as bioindicators of climate change at high latitude/elevation ecosystems (e.g. Bråten et al. 2012; Gobbi, Fontaneto, and De Bernardi 2006b; Pizzolotto, Gobbi, and Brandmayr 2014).

Statistical analysis

We report descriptive statistics (minimum and maximum values, median and interquartile range) of the distribution of soil parameters (soil pH, calcium carbonate content, organic matter content, total plant cover) along the glacier foreland. The correlation among such variables was assessed through Spearman's monotone correlation coefficient rho. The patterns of correlation were evaluated by a principal component analysis (PCA) on the ranks of the variables. Soil parameters entered as active variables; total plant cover was plotted on the plane of the principal components as a passive variable to evaluate the relationships between soil and vegetation.

Patterns of plant species distribution along the glacier foreland were described through detrended correspondence analysis (DCA) (Hill and Gauch 1980) carried out on a matrix of plant species cover percentages of 29 sampling points for 55 species (17 species out of 72 were omitted since occurring in only one sampling point; one sampling point was omitted since no plant species was recorded in it). A cluster analysis was performed to identify groups of sampling points with homogeneous vegetation patterns. For determining the clusters we used only the coordinates of sampling points on the first canonical axis of the DCA, since it represented the main ordination trend of vegetation. Two clustering algorithms were used: in a first step hierarchical clustering was performed with Euclidean distance metric and Ward linkage; then, k-means clustering was used for 'consolidating' the clusters previously determined (Husson, Lê, and Pagès, 2010).

The results of cluster analysis were used to study the relationships between plant assemblages and soil parameters and species richness. For each variable, a generalised linear regression model (GLM) was fitted including the variable as response and the cluster as explicative categorical variable. The Gaussian distribution was assumed for the response in each case except for species richness, for which the Poisson distribution was the proper one. To achieve a satisfactory approximation to the Gaussian distribution, the arcsin transformation $f(x) = \arcsin(\sqrt{x})$ was applied to total plant cover and the natural logarithm transformation to organic matter content. In order to account for the potential correlation of observations within each plot, the GLM models were fitted by the generalising estimating equations (GEE) method (Zeger, Liang, and Albert 1988). For each model, an exchangeable working covariance structure was specified, in which observations within the same plot were assumed to be correlated. The results were reported in terms of: (1) global test (chi-square) evaluating the null hypothesis of no overall difference among the clusters; (2) multiple comparison between means for all the possible pairs of clusters (Wald test); the *p*-values were adjusted using the Bonferroni correction.

Concerning the arthropod species, since a quantitative sampling method (pitfall traps) and a qualitative one (capture by hand) were integrated, we chose to base the analysis only on the presence/absence species matrix (6 plots for 20 species). Before performing the analysis we tested the accuracy of our sampling design and methods estimating the theoretical total species richness according to an index based on observed data: the incidence-based coverage estimator (ICE) (Colwell et al. 2012). ICE estimates the overall number of species that may live in the study area, on the basis of the observed number of species and the frequency of their occurrence in the plots (Hortal, Borges, and Gaspar 2006). Canonical correspondence analysis (CCA) (Ter Braak 1986) was performed to describe the patterns of presence/absence of species and their relationships with the soil parameters. As the ratio between number of soil parameters in CCA and the number of samples should be kept low to avoid potential biases of the results, only pH and total plant cover were used. However, this restriction did not severely affect the results, since pH is highly correlated with the soil parameters not included in the analysis (calcium carbonate content and organic matter content).

Following Vater (2012) and Vater and Matthews (2013, 2015), plant and arthropod colonisation patterns along the chronosequence were analysed calculating three community parameters for each deglaciation stage (plot): (1) total species richness (number of species at plot level); (2) species first appearances (number of species appearing for the first time along the succession, including first-and-last appearances); (3) species last appearances (number of species appearing for the last time along the succession, including first-and-last appearances). Herein, we define 'cold-adapted species' all the species strictly linked to alpine and nival belts, thus characterised by a limited range of tolerance in altitudinal distribution. Concerning plants, we consider like that all 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 based on the available descriptive literature about the ecological requirement of each identified taxon (Casale, Sturani, and Vigna Taglianti 1982; Isaia et al. 2007). All analyses except ICE were performed with the R software (R Core Team 2014), with the packages vcd, vegan, FactoMineR, nnet and geepack added. ICE was calculated with the EstimateS 9.1.0 software (Colwell et al. 2012).

Comparative analysis

The pattern of total species richness, species first appearances and species last appearance along the Trobio glacier foreland was compared with those of three glacier forelands of the Rhaetian Alps for which both plant and arthropod data were available: (1) Morteratsch glacier, Swiss Alps, below the potential treeline (1900–2100 m a.s.l.) (Burga 1999; Schlegel and Riesen 2012); (2) Rotmoos glacier, Austrian Alps, near the potential treeline (2280–2450 m a.s.l.) (Kaufmann 2001; Marcante, Schwienbacher, and Erschbamer 2009); (3) Cedec glacier, Italian Alps, above the potential treeline (2694–2726 m a.s.l.) (Gobbi et al. 2010). Four common deglaciation stages were recognised: (1) pioneer (c. 1–30 years since deglaciation); (2) early (c. 31–100 years since deglaciation); (3) mid (c. 101–150 years since deglaciation); (4) late (c. 10,000 years old, ice-free since the LG). The comparison concerns plants and carabid beetles, while spiders were omitted because of data unavailability for some glacier forelands. In the area of Morteratsch glacier, five vegetation surveys of 400 m^2 were performed by one of the Authors (DT) to integrate the missing data about the vegetation of the terrain ice free since the LG (12 September 2015).

Results

Primary succession along the glacier foreland

The glacier foreland was characterised by a gradient of increasing mean annual temperature (from 0.5 to 1.3 °C) and decreasing snow cover persistence (from 225 to 160 days) from the glacier front to the LIA moraine (supplementary Figure 1). The difference in altitude between the latter allows for an estimation of a yearly altitudinal temperature lapse rate of -0.69 °C $(100\ \mathrm{m})^{-1}$ on the investigated landform. All soil parameters were correlated to each other (supplementary Table 1) and varied along the glacier foreland following a more or less clear trend (supplementary Figure 2), except grain size distribution (supplementary Figure 3). The main soil gradient occurring from the glacier front to the terrain ice-free since the LG consists of a progressive decrease of pH and calcium carbonate content and a corresponding increase of organic matter content and total plant cover (supplementary Figure 4).

Seventy-two plant species were recorded (Table 1), among which the most frequent were *Poa alpina* and *Silene acaulis* (occurring in 83% of the sampling points), followed by *Saxifraga oppositifolia* (70%), *Androsace alpina*, *Artemisia genipi*, *Festuca quadriflora* and *Oxyria digyna* (50%). Twenty-nine of the identified plant species were ‘cold-adapted’. Twenty arthropod species (6 carabid beetles and 14 spiders) were recorded (Table 1), among which the most frequent were the carabid *Carabus castanopterus* and the spiders *Coelotes pickardi tirolensis* and *Entelecara media* (occurring in 83% of the plots), followed by the carabid *Pterostichus lombardus* and the spiders *Diplocephalus helleri*, *Drassodex heeri* and *Mughiphantes pulcher* (67%). All the identified arthropod species were ‘cold-adapted’, except *Carabus castanopterus* (the carabid beetle is able to descend below the potential treeline) (Casale, Sturani, and Vigna Taglianti 1982) and *Agyneta rurestris* (the high-dispersal spider is distributed on a wide altitudinal range) (Isaia et al. 2007).

The primary succession along the glacier foreland developed in three main steps, each characterised by distinct vegetation and soil features (supplementary Figure 5 and Table 2). The first step lasted about 95 years (plots 1, 2, 3, corresponding to pioneer and early-successional stages). It showed basic substrate (average pH 7.82) with relatively high calcium carbonate content (2.64%) and low organic matter content (1.57 g/kg). Total plant cover was highly variable but generally scarce (27.3%), with few pioneer and cold-adapted species (e.g. *Androsace alpina* and *Saxifraga oppositifolia*). The second step lasted 90 years at least (we are able to observe the succession only since LIA) (plots 4 and 5, corresponding to mid-successional stages). It was characterised by neutral soil (pH 6.96) with an intermediate content of calcium carbonate (0.55%) and organic matter (13.32 g/kg). Total plant cover reached a mean value of 42% and included mainly graminoids (e.g. *Luzula alpinopilosa* and *Poa alpina*) and cushion species (e.g. *Saxifraga bryoides* and *Silene acaulis*). The last step occurred on terrain ice free since LG and not involved in Holocene glacial dynamics (plot 6, corresponding to late-successional stages). It displays acid soil reaction (pH 4.82), very low calcium carbonate content (0.28%) and high organic matter content (118.30 g/kg). Total plant cover reached the highest values (60.9%) including typical species of acidophilous alpine grasslands (e.g. *Carex curvula* and *Carex sempervirens*). Plant species richness (Figure 1a) regularly increased from pioneer to mid-successional stages, to decrease in the late-successional ones. The number of species appearing for the first time was quite uniform along the whole chronosequence (c. 9 first appearances for each plot on average), while the number of species occurring for the last time increased from early-successional stages.

Two main arthropod assemblages were recognisable (supplementary Figure 6): a pioneer one (including species like *Oreonebria soror tresignore* and *Agyneta rurestris*) which gradually disappears over the succession and a late-successional one (including species like *Oreonebria lombarda* and *Gnaphosa petrobia*) which simultaneously increases. Early- and mid-successional stages lacked a specific arthropod community and were rather characterised by the overlapping of species belonging to the

Table 1. Species distribution along Trobio glacier foreland. Plant species frequencies at plot level were indicated in percentage; arthropod species presences were indicated with "+" ("ara" = Araneae; "car" = Carabidae); cold-adapted plant and arthropod species were indicated with "*". Sporadic plant species (with relative plot): * *Achillea nana* (2), *Agrostis alpina* (6), *Festuca halleri* (6), *Festuca scabriculmis* (3), *Gentiana acaulis* (6), *Gentiana verna* (4), *Helictotrichon versicolor* (4), * *Lloydia serotina* (3), *Luzula spicata* (5), * *Minuartia sedoides* (4), *Myosotis alpestris* (4), * *Oreochloa disticha* (6), *Pseudorchis albida* (4), *Rhodiola rosea* (4), * *Saxifraga exarata* (3), * *Saxifraga seguieri* (5), *Trifolium pallescens* (5). Plant species nomenclature follows Landolt et al. (2010).

	Plot	1	2	3	4	5	6
ID	Age (years)	< 30	c. 30	c. 95	c. 115	c.150	c. 10,000
Li.a	*Linaria alpina*	20	40	20	.	.	.
Th.c	* *Thlaspi corymbosum*	.	20	20	.	.	.
Ar.g	* *Artemisia genipi*	20	80	100	100	.	.
Pr.a	* *Pritzelago alpina*	20	100	40	20	.	.
Ox.d	* *Oxyria digyna*	20	100	40	100	40	.
An.a	*Androsace alpina*	20	100	80	60	40	.
Ge.r	* *Geum reptans*	20	60	20	60	100	.
Sa.o	* *Saxifraga oppositifolia*	80	100	100	100	40	.
Po.a	*Poa alpina*	40	100	100	100	100	60
Si.a	* *Silene acaulis*	20	100	100	100	100	80
Sa.p	*Saxifraga paniculata*	20	100	.	80	20	.
Pa.a	*Papaver aurantiacum*	.	20	.	60	20	.
Ar.a	*Arabis alpina*	.	40	80	20	40	.
Fe.q	*Festuca quadriflora*	.	80	100	100	20	.
Ra.g	* *Ranunculus glacialis*	.	80	20	20	100	.
Sa.b	* *Saxifraga bryoides*	.	40	20	60	100	.
Ce.u	* *Cerastium uniflorum*	.	40	.	20	.	.
Sa.a	*Saxifraga aizoides*	.	100	.	20	.	.
Ar.c	* *Arabis caerulea*	20	.	60	80	.	.
Dr.a	*Draba aizoides*	.	.	40	20	.	.
Ca.co	*Campanula cochleariifolia*	.	.	20	.	20	.
Po.n	*Potentilla nitida*	.	.	60	.	.	.
Ca.cu	* *Carex curvula*	.	.	.	.	.	100
Ca.s	*Carex sempervirens*	.	.	.	.	.	100
Ho.a	*Homogyne alpina*	.	.	.	.	.	80
Hu.a	*Huperzia selago*	.	.	.	.	.	80
Lo.p	*Loiseleuria procumbens*	.	.	.	.	.	60
So.a	*Soldanella alpicola*	.	.	.	.	.	60
Va.g	*Vaccinium gaultherioides*	.	.	.	.	.	80
Ba.a	*Bartsia alpina*	.	.	20	20	20	100
Er.u	* *Erigeron uniflorus*	.	.	60	80	40	20
Eu.m	*Euphrasia minima*	.	.	40	80	40	40
Pr.l	*Primula latifolia*	.	.	20	20	20	40
Ta.a	*Taraxacum alpinum* s.l.	.	.	60	40	80	20
Ve.a	*Veronica alpina*	.	.	20	60	100	20
Bo.l	*Botrychium lunaria*	.	.	40	20	20	.
Lu.a	* *Luzula alpinopilosa*	.	.	.	40	100	60
An.c	*Antennaria carpatica*	.	.	.	20	20	40
Ca.r	*Cardamine resedifolia*	.	.	.	20	40	20
Hi.g	* *Hieracium glanduliferum*	.	.	.	20	40	60
Ph.h	*Phyteuma hemisphaericum*	.	.	.	20	20	100
Pr.d	*Primula daonensis*	.	.	.	20	60	100
Sa.h	* *Salix herbacea*	.	.	.	60	60	100
Co.v	*Coeloglossum viride*	.	.	.	20	20	.
Sa.a	* *Saxifraga androsacea*	.	.	.	20	20	.
Po.v	*Polygonum viviparum*	.	.	.	60	.	100
Sa.r	*Salix retusa*	.	.	.	60	.	40
Do.g	*Doronicum grandiflorum*	.	.	.	.	40	40
Ag.r	*Agrostis rupestris*	.	.	.	.	80	100
Gn.s	* *Gnaphalium supinum*	.	.	.	.	20	20
Le.h	*Leontodon helveticus*	.	.	.	.	40	100
Le.a	* *Leucanthemopsis alpina*	.	.	.	.	100	100
Pe.k	* *Pedicularis kerneri*	.	.	.	.	60	100
Se.c	* *Senecio carniolicus*	.	.	.	.	40	80
Se.a	*Sedum alpestre*	.	.	.	.	80	.

(*continued*)

Table 1. (*Continued*)

ID	Plot Age (years)	1 < 30	2 c. 30	3 c. 95	4 c. 115	5 c.150	6 c. 10,000
Agy.ru	*Agyneta rurestris (ara)*	+	+	.	.	.	.
Ore.so	* *Oreonebria soror tresignore (car)*	+	+	.	.	.	.
Mug.pu	* *Mughiphantes pulcher (ara)*	+	+	.	+	+	.
Tre.in	* *Trechus insubricus (car)*	.	+	.	+	+	.
Ach.pe	* *Acantholycosa pedestris (ara)*	.	+	.	+	.	.
Mec.br	* *Mecynargus brocchus (ara)*	.	.	.	.	+	.
Wal.vi	* *Walckenaeria vigilax (ara)*	.	.	.	.	+	.
Gna.pe	* *Gnaphosa petrobia (ara)*	.	.	.	.	+	+
Ore.lo	* *Oreonebria lombarda (car)*	.	.	.	.	+	+
Agy.gu	* *Agyneta gulosa (ara)*	.	.	.	.	.	+
Bem.rh	* *Bembidion rhaeticum (car)*	.	.	.	.	.	+
Ore.mo	* *Oreoneta montigena (ara)*	.	.	.	.	.	+
Wal.ca	* *Walckenaeria capito (ara)*	.	.	.	.	.	+
Sit.lo	* *Sitticus longipes (ara)*	.	.	+	.	.	+
Pte.lo	* *Pterostichus lombardus (car)*	.	.	+	+	+	+
Dra.he	* *Drassodex heeri (ara)*	.	.	+	+	+	+
Dip.he	* *Diplocephalus helleri (ara)*	.	+	+	.	+	+
Car.ca	*Carabus castanopterus (car)*	.	+	+	+	+	+
Coe.pi	* *Coelotes pickardi tirolensis (ara)*	.	+	+	+	+	+
Ent.me	* *Entelecara media (ara)*	+	+	+	.	+	+
	Plant species richness	11	18	25	36	37	31
	Arthropod species richness	4	9	7	7	12	13

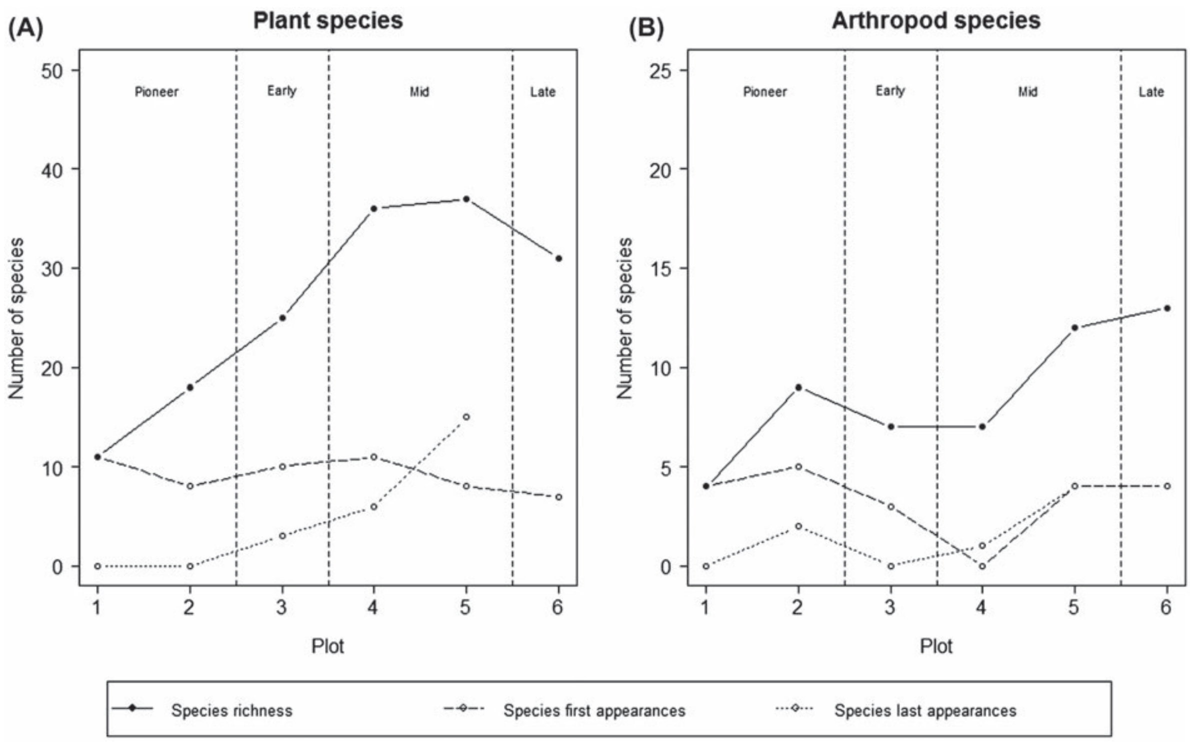

Figure 1. Patterns of plant (A) and arthropod (B) species richness, species first appearances and species last appearances through the six deglaciation stages (plots) identified on Trobio glacier foreland. Dotted lines separate the four deglaciation stages as defined for the comparative analysis: pioneer (c. 1–30 years since deglaciation); early (c. 31–100 years since deglaciation); mid (c. 101–150 years since deglaciation); late (c. 10.000 years old, ice-free since the LG).

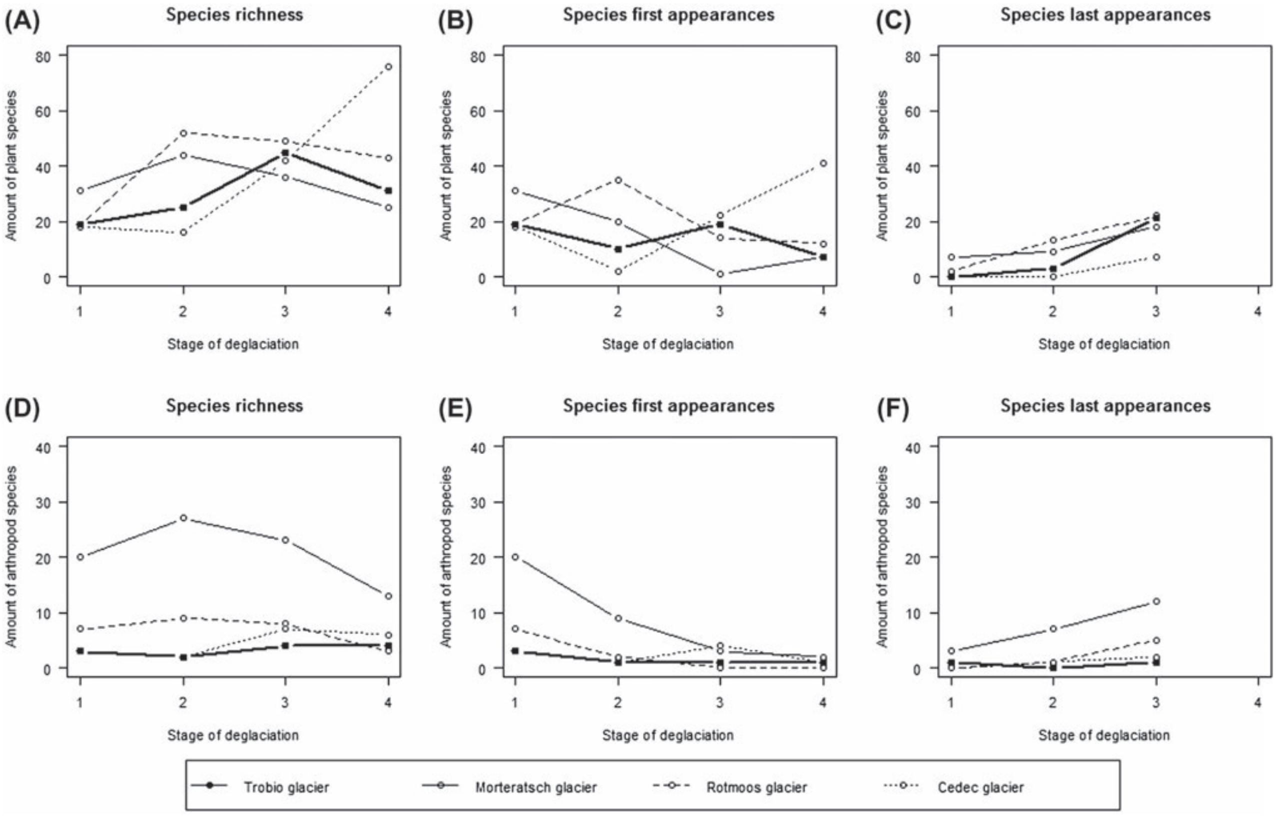

Figure 2. Patterns of plant and arthropod species richness, species first appearances and species last appearances on the compared glacier forelands. Stages of deglaciation: (1) pioneer (c. 1–30 years since deglaciation); (2) early (c. 31–100 years since deglaciation); (3) mid (c. 101–150 years since deglaciation); (4) late (c. 10.000 years old, ice-free since the LG).

pioneer and late-successional assemblages, as well as by the presence of ubiquitous species (e.g. *Carabus castanopterus* and *Coelotes pickardi tirolensis*). Arthropod species richness (Figure 1b) generally increased along the chronosequence, but was characterised by two distinct peaks: a first one in pioneer stages and a second in late-successional ones. First and last species appearances followed a similar trend, being both characterised by a severe drop in mid- and early-successional stages, respectively.

Comparison with the glacier forelands of inner mountain ranges

The colonisation patterns of Trobio glacier foreland showed important differences with respect to that of the inner Alpine ones, both for plant and arthropod species.

The pattern of plant species richness (Figure 2a) on Trobio chronosequence was characterised by a later maximum (mid-successional stages) with respect to Morteratsch and Rotmoos glaciers (early-successional stages), while Cedec showed a monotonic increase from early-successional stages. Trobio glacier foreland was characterised by a rather uniform number of species first appearances throughout the primary succession (Figure 2b), while species entrances on inner Alpine chronosequences reached the maximum in different stages depending on the glacier elevation: pioneer on Morteatsch, early-successional on Rotmoos and late-successional on Cedec. Species last appearances (Figure 2c) showed an overall similarity among the investigated glacier forelands, with the maximum number of last appearances in mid-successional stages; however, on Morteratsch and Rotmoos glaciers species loss occurred at the beginning of the succession (some species showed their first-and-last appearance in the pioneer stages), while on Cedec and Trobio no species disappeared in pioneer stages.

Two main trends of arthropod species richness were recognisable (Figure 2d): the one of Morteratsch and Rotmoos glaciers was characterised by an early maximum and a later decrease, while those of Cedec and Trobio reached the maximum in mid-successional stages. Species first appearances (Figure 2e) reached its maximum right as the beginning of the succession on Morteratsch and Rotmoos glaciers and in mid-successional stages on Cedec glacier, while the trend was rather uniform along the Trobio chronosequence. Species last appearances (Figure 2f) were quite similar through the investigated glacier forelands being always characterised by a later maximum, but the trend appeared again more uniform along Trobio glacier foreland.

Discussion

Primary succession along the glacier foreland

The overall development and the environmental drivers of primary succession generally agree with those previously observed in the inner Alps, since plant and arthropod species distribution depends on time since deglaciation and its related soil parameters. Plant succession develops in three distinct steps: a first one on recently deglaciated terrain, a mid-successional one on the terrain ice free between 100 years ago and LIA and a late-successional one on the terrain ice free since LG, in agreement with Caccianiga and Andreis (2004). Arthropod colonisation seems to follow a more gradual pattern where two main arthropod assemblages (a pioneer and a late-successional ones) seamlessly overlap in the intermediate stages, in agreement with Kaufmann (2001). Therefore, plant and arthropod species follow different colonisation patterns, even if species richness generally increases for both along the succession. Our result contrast with those of Gobbi et al. (2010), where plant and arthropod species richness vary in steps along the chronosequence. Our hypothesis (1) is thus not supported by our data.

Comparison with the glacier forelands of inner mountain ranges

Despite the overall affinities with the patterns previously observed in the inner Alps, the investigated primary succession stands out for noteworthy differences in temporal patterns. The colonisation of Rhaetian glacier forelands differs depending on the elevation: according to Vater and Matthews (2013), a typical 'replacement change model' prevails below the treeline (Morteratsch glacier), an 'addition and persistence model' prevails above the treeline (Cedec glacier) and an intermediate pattern characterised the glacier foreland near the treeline (Rotmoos glacier). Trobio glacier stands at an elevation similar to that of Rotmoos, but lies above the potential treeline, which is locally depressed as a consequence of the oceanic climate (Caccianiga, Ravazzi, and Zubiani 1993; Caccianiga et al. 2008). Coherently, its colonisation pattern shows an intermediate trend between those of Rotmoos and the higher Cedec glacier. In particular, from pioneer to mid-successional stages, the trends match better with that of Cedec glacier for three main features: late species richness maximum, constant first appearances along the chronosequence, few first-and-last appearances in pioneer stages. On the other hand, with the transition from mid- to late-successional stages, the trend of Trobio detaches from that of Cedec to become more similar to that of the lower glacier forelands (a phenomenon more evident for plant than for arthropod species). More evidence of the 'addition and persistence model' seems thus to occur on Trobio glacier foreland than on the inner Alpine ones at the same elevation. Being the climate the main environmental difference between Orobian and Rhaetian Alps, we suppose that oceanic regime may affect the colonisation patterns of ice free terrain in the same way elevation does within a climatically homogeneous area. Our hypothesis (2) is thus supported by our data.

Slower plant colonisation on the Orobian Alps was previously observed and attributed to the more severe environmental condition imposed by the oceanic climate regime (Caccianiga and Andreis 2004; Caccianiga, Ravazzi, and Zubiani 1993), as long-lasting snow cover and long-lasting temperatures around zero occurring in spring (Caccianiga et al. 2008). Such phenomenon promotes the long-lasting persistence of species that otherwise are considered typically as 'pioneer'. For example, cold-adapted plants generally restricted to pioneer stages (e.g. *Androsace alpina* and *Saxifraga oppositifolia*) (Caccianiga and Andreis 2004) in our study area are able to persist even in the terrain ice-free since the LIA. In a similar way, cold-adapted carabid beetles that usually live near the glacier front (e.g. genus *Oreonebria*) (Gobbi et al. 2007; Kaufmann 2001) occur here along the whole chronosequence.

Taxonomical and biogeographical overview

Besides the colonisation processes, an important difference between peripheral and inner mountain ranges lies in the taxonomical and biogeographical features. The investigated flora counts some noteworthy peculiarities, such as the presence of an endemic species (*Primula daonensis*) and the occurrence of Western-Alpine (e.g. *Achillea nana* and *Primula latifolia*) as well as Eastern-Alpine elements (e.g. *Potentilla nitida* and *Senecio carniolicus*). However, the most interesting data comes from the arthropod species.

All the collected carabid beetles (except *Bembidion rhaeticum*) are steno-endemic species of the Orobian Alps. Particularly interesting is the finding of *Oreonebria soror tresignore*, recently described by Szallies and Huber (2014) as endemic subspecies of Pizzo Tre Signori (western Orobian Alps). Our findings in the eastern chain indicates that this subspecies should be now considered as endemic of the whole Orobian range. This data furtherly clarified the biogeographical arrangement of *Oreonebria soror* in the central-eastern Italian Alps, with two distinct subspecies in two different geographical contexts: *Oreonebria soror soror* as endemic subspecies of the Adamello-Presanella Massif (Szallies and Huber 2014) and *Oreonebria soror tresignore* as endemic subspecies of the Orobian Alps. On the other hand, no steno-endemic spiders were found: the most circumscribed distribution was that of *Drassodex heeri* and *Coelotes pickardi tirolensis*, both occurring on the central Alps. Carabid beetles are thus supposed to be more sensitive markers of biogeographical events than spiders, probably as a consequence of different dispersal abilities.

Peripheral mountain ranges as warm-stage refugia?

Cold-adapted species are supposed to be the first threatened by climate change, due to the progressive reduction of their habitat with temperature increase and the upshift of altitudinal belts (Dullinger et al. 2012). However, recent works highlighted the importance of warm-stage refugia: sites that locally preserve suitable condition in spite of large scale climate change (Birks and Willis 2008; Gentili et al. 2015; Stewart et al. 2010). Glacial and periglacial landforms have been recently proposed as potential warm-stage refugia for cold-adapted species, due to their microclimate features and thermal inertia (Caccianiga et al. 2011; Gentili et al. 2015; Gobbi et al. 2014; Gobbi, Isaia, and De Bernardi 2011; Millar et al. 2013).

Cold-adapted species do not necessarily decrease along the primary succession of Trobio glacier foreland; some cold-adapted species are in fact late-successional ones (e.g. *Carex curvula* and *Salix herbacea* for plants or *Oreonebria lombarda* and *Gnaphosa petrobia* for arthropods) and are thus not threatened by glacier retreat, which on the contrary causes an extension of suitable surfaces to colonise. On the other hand, pioneer but not strictly cold-adapted species (e.g. *Arabis alpina*, *Linaria alpina* or *Agyneta rurestris*) may be locally affected by glacier retreat as the ongoing colonisation induces a competition with late-successional species; however, such species are likely able to find available habitat on a wide altitudinal range, as they are not forced to up-shift with temperature increase, but can down-shift or persist at the current elevation in other habitats. Therefore, the most threatened species are those characterised by the conjunction of cold-adapted and pioneer strategies (e.g. *Androsace alpina, Saxifraga oppositifolia* or *Oreonebria soror tresignore*). According to Erschbamer et al. (2007), the potential loss of cold-adapted species with climate change seems to be induced by temperature increase, but mainly mediated by interspecific competition. Since cold-adapted species are homogeneously distributed along the glacier foreland and the thermal gradient appears substantially coherent with the yearly altitudinal temperature lapse rate at regional scale (-0.58 °C $(100\ \text{m})^{-1}$ in Rolland 2003), our results suggest a marginal role of glacier microclimate in enhancing cold-adapted species distribution. On the other hand, a more important role could be played by the outstanding long-lasting snow cover near the glacier front.

The glacier persistence at lower elevation and the slower colonisation of ice free terrains could result in an advantage for pioneer cold-adapted species, providing them long-lasting suitable conditions in spite of the climate change at large scale. Therefore, given the climate requirements for glacier formation at regional scale, we suppose that peripheral mountain ranges of any mountain system may offer more survival chance for pioneer cold-adapted species than inner massifs at the same elevation. We thus advance the hypothesis that glacial landforms of peripheral mountain ranges (e.g. glacier forelands and recent moraines) could act as warm-stage refugia. Our suggestion is to consider the potential role of glacial landforms as plausible alternative hypothesis to explain part of the present biogeographical arrangement of these chains. More data should be collected in other geographical and climatic context to test our hypothesis.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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Plant and arthropod colonization of a glacier foreland in a peripheral mountain range

Supplemental material - ecological features of the primary succession

Trobio glacier foreland (Orobian Alps, Italy)

Thermal regime

The thermal regime of the glacier foreland over one year was reported (Fig. 1). A mean annual temperature of 0.5 °C and a range of 10.8 °C (Min –3.2 °C, Max 7.6 °C) were recorded at plot 1, while plot 5 was characterized by a mean annual temperature of 1.3 °C and a range of 18.4 °C (Min –6.5 °C, Max 11.9 °C). Two hundred and twenty-five consecutive days (02 January 2014–15 August 2014) with mean daily temperature between -1 and 0 °C were recorded at plot 1 likely as consequence of snow cover, while one hundred and sixty consecutive days (20 January 2014–28 June 2014) with the same features were recorded at plot 5. Temperature at plot 5 generally exceed those of plot 1 for the whole year (0.86 °C higher on average), except for the period between the end of November and the end of December. On the basis of the difference in altitude between the plots 1 and 5 (125 m), a yearly altitudinal temperature lapse rate of -0.69 °C $(100\ \text{m})^{-1}$ was estimated on the investigated landform. However, the anomalous persistence of snow cover over the whole summer 2015 at plot 1 highly affects data lowering mean temperature and thus likely brings to overestimate such value.

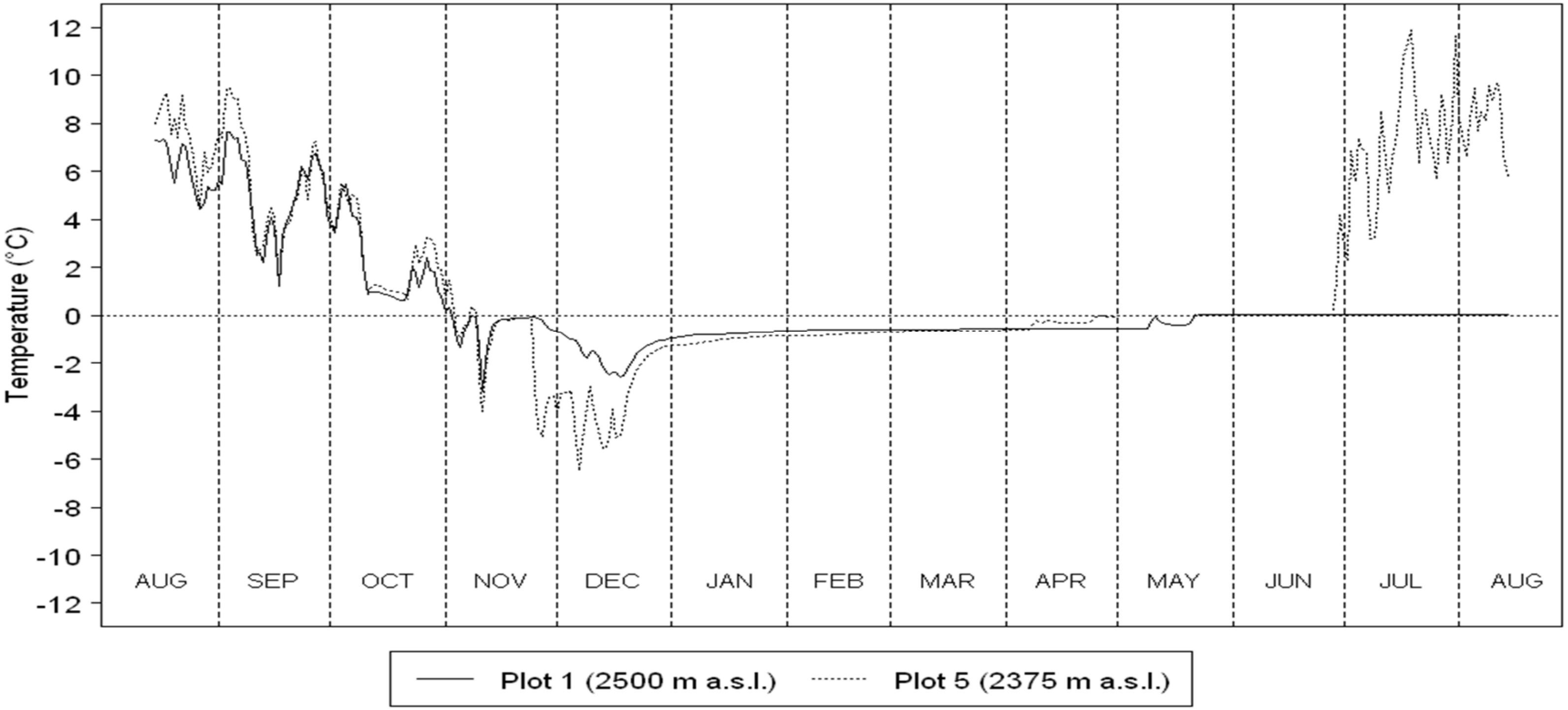


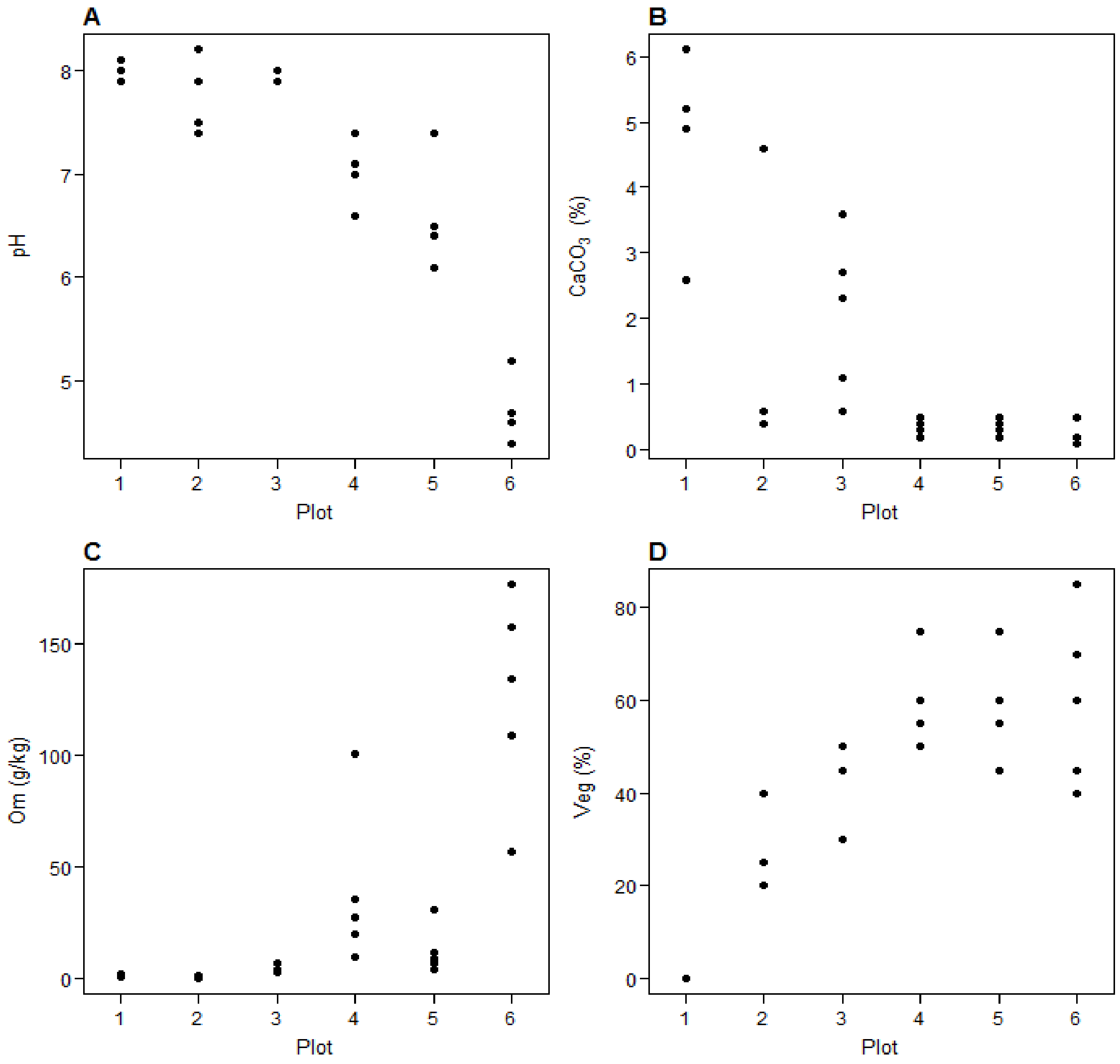
Fig. 1. Mean daily temperatures of the Plots 1 and 5 from 15 August 2013 to 15 August 2014.

Soil parameters

Soil pH varied from 4.4 (6A) to 8.2 (2D) (median: 7.4; IQR: 1.5), calcium carbonate content varied from 0.06% (6A) to 6.11% (1A) (median: 0.54%; IQR: 2.21%), organic matter content varied from 0.17 (2A) to 176.56 g/kg (6A) (median: 5.54 g/kg; IQR: 28.36 g/kg), total plant cover varied from 0 (1C) to 85% (6D) (median: 45%; IQR: 35.00%). All the soil parameters except grain size distribution were correlated each other (Table 1) and varied along the glacier foreland following a more or less clear trend (Fig. 2): soil pH decreased progressively along the primary succession, with a moderate variability within plots; calcium carbonate is relatively abundant in the first plots, although with high variability, while sharply decreased in the last plots; organic matter content and total plant cover regularly increased. The distribution of grain size along the glacier foreland did not show any evident trend and was characterized by a general prevalence of coarse debris (gravel and sand) (Fig. 3). A high positive correlation emerged between pH and calcium carbonate content, while both resulted negatively correlated with organic matter content; total plant cover showed a positive relationship with organic matter content and therefore a negative correlation with soil pH and calcium carbonate content (Fig. 4).

	pH	**$CaCO_3$**	**Om**	**Veg**
pH	1.00	0.84	-0.78	-0.69
$CaCO_3$	0.84	1.00	-0.69	-0.63
Om	-0.78	-0.69	1.00	0.78
Veg	-0.69	-0.63	0.78	1.00

Table 1. Correlation among environmental variables: soil reaction (pH), calcium carbonate content (CaCO3), organic matter content (Om), total plant cover (Veg). Results are reported in terms of Spearman's index of monotone correlation (rho).



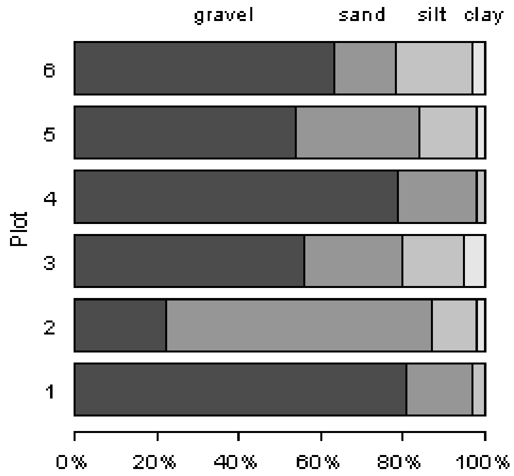


Fig. 3. Grain size distribution for each plot.

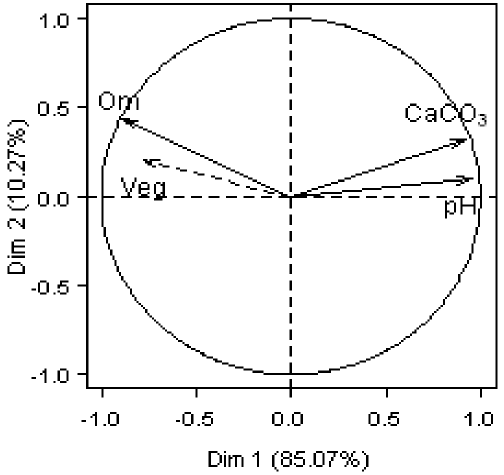


Fig. 2. Sample distribution of environmental variables for each plot: (A) soil reaction (pH), (B) calcium carbonate content (CaCO3), (C) organic matter content (Om), (D) total plant cover (Veg).

Fig. 4. PCA diagram showing the mutual correlations among the environmental variables: soil reaction (pH), calcium carbonate content (CaCO3), organic matter content (Om), total plant cover (Veg).

Plant species

The first two axis of DCA (Fig. 5) explained 38.6% of the total explained inertia (27.6% and 11.0% for the first and second axis, respectively). The low percentages of explained variability could be attributed to the sparsity of the data matrix. The first axis progressively separated the plant assemblages of pioneer and early-successional stages (plots 1, 2 and 3) from those of late-successional ones (plot 6). The second axis separated from each other the plant assemblages of mid-successional stages (plots 4 and 5). Cluster analysis gathered the plant assemblages into three groups: (1) pioneer and early-successional (sampling points of the plots 1, 2 and 3, except the sampling point 3C); (2) mid-successional (sampling points of the plots 4 and 5, plus the sampling point 3C); (3) late-successional (sampling points of the plot 6). The global test evidenced significant differences between clusters for each variable (Table 2). The Wald tests indicated significant differences between each pair of clusters for all soil parameters except for the calcium carbonate content, for which no significant differences was found between clusters 2 and 3. No difference at the 0.05% significance level emerged for total plant cover, despite the global test indicated a significant difference among the three clusters. Concerning species richness, a significant difference emerged only between early- and late-successional plant assemblages.

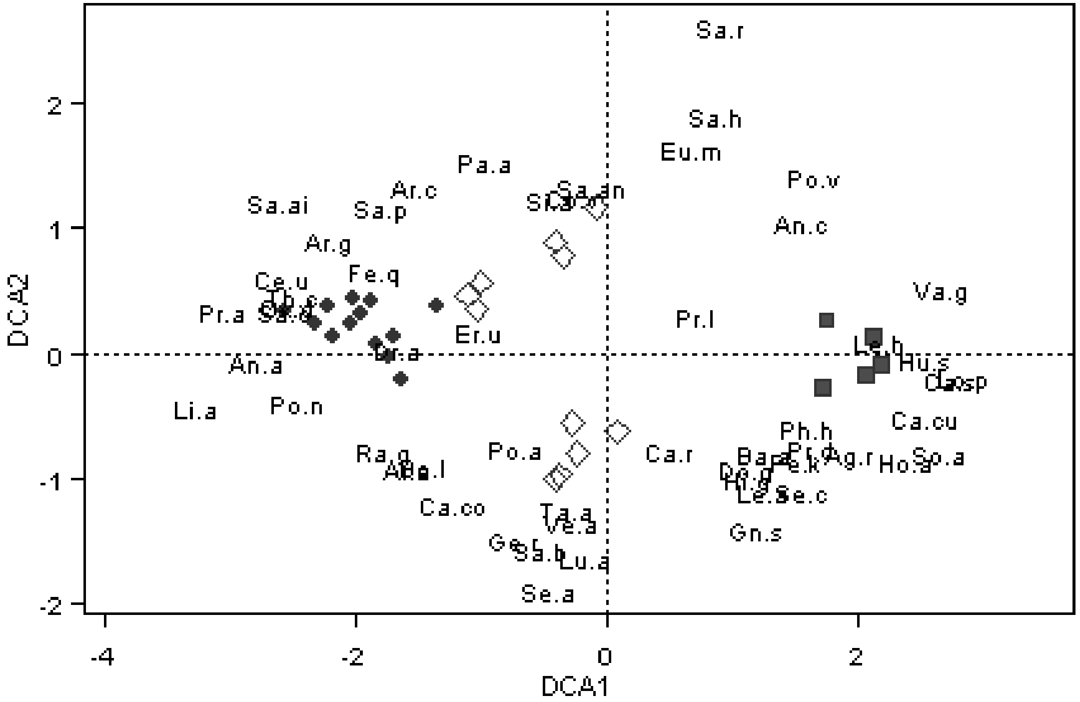


Fig. 5. DCA ordination plot of plant species. Sampling points were labeled according to their cluster membership: black diamonds correspond to pioneer and early-successional plant assemblages (cluster 1), white diamonds to mid-successional plant assemblages (cluster 2); grey squares to late-successional plant assemblages. Species labels are reported in Table 1 of the paper.

Variable	Expected cluster means:			Global test: p-value	Multiple comparisons		
	Cluster 1	Cluster 2	Cluster 3		Effect	Z	p>z
pH	7.82	6.96	4.82	<2e-16 *	cluster 2 vs cluster 1	15.1	0.000303 *
					cluster 3 vs cluster 1	2116.7	<2e-16 *
					cluster 3 vs cluster 2	95.0	<2e-16 *
$CaCO_3$	2.64	0.55	0.28	0.011 *	cluster 2 vs cluster 1	8.00	0.0141 *
					cluster 3 vs cluster 1	9.05	0.0079 *
					cluster 3 vs cluster 2	1.62	0.6093
Om (log transformed)	0.45	2.59	4.77	<2e-16 *	cluster 2 vs cluster 1	11.8	1.78e-03 *
					cluster 3 vs cluster 1	113.9	0.00e+00 *
					cluster 3 vs cluster 2	32.6	3.46e-08 *
Veg (arcsin transformed)	1.10	1.41	1.79	0.029099 *	cluster 2 vs cluster 1	0.624	1.0000
					cluster 3 vs cluster 1	4.724	0.0892
					cluster 3 vs cluster 2	2.530	0.3350
Species richness	11.75	16.30	21.80	0.003418 *	cluster 2 vs cluster 1	1.19	0.82443
					cluster 3 vs cluster 1	6.52	0.03205 *
					cluster 3 vs cluster 2	3.66	0.16752

Table 2. Assessment of the association between plant assemblages and environmental variables and species richness. The mean values within each cluster of surveys estimated on the basis of the GLM model are shown in columns 2-4 (expected cluster means). The p-value for evaluating the null hypothesis of no overall difference among the clusters is shown in column 5 (global test). Multiple comparisons are shown in columns 6-8. Comparisons were not carried out for E-evenness, since no significant difference among the clusters emerged.

Arthropod species

ICE estimator of species richness produced 24.4 species, thus 82% of estimated species richness was recorded confirming the good accuracy of the sampling methods applied. The first two axis of CCA (Fig. 6) explained 59.7% of the total explained inertia (37.1% and 22.6% for the first and second axis, respectively). The first axis separated the species assemblages of pioneer stages (plots 1 and 2) from the later ones, while the second axis separated the species assemblages of pioneer and late-successional stages (plots 1 and 6) from the others. The first axis of CCA was totally correlated with total plant cover (Pearson r index = 0.99), while a high negative association was found with pH (Pearson r index = -0.79).

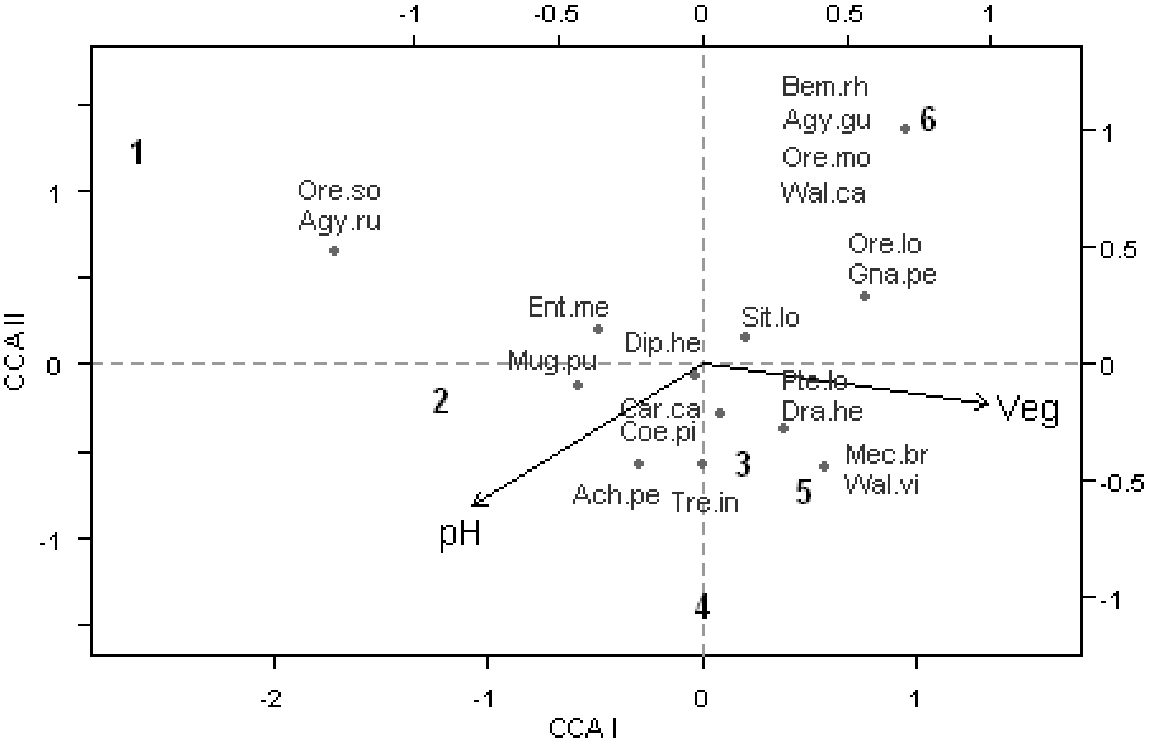


Fig. 6. CCA ordination plot of arthropod species. Plots were represented by numbers (1-6). Species labels are reported in Table 1 of the paper. The environmental variables are soil reaction (pH) and total plant cover (Veg).

Distributional pattern of cold-adapted plants and arthropods in a peripheral mountain range: cold- and warm-stage refugia should be considered

Running title: distribution of cold-adapted species and refugia

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Abstract

The geographical isolation due to the ice-sheets expansion in cold-climatic stages was traditionally involved to explain the present patchy distribution of some plants and arthropods in mountain regions; summits emerging from the ice-sheet were thus interpreted as cold-stage refugia. More recently, the areal contraction during warm-climatic stages was also called into question; besides the highest peaks, glacial and periglacial landforms (e.g. glaciers and rock glaciers) were proposed as potential warm-stage refugia for cold-adapted species.

In the present study, we mapped by GIS-approach the distribution of ten cold-adapted plant and arthropod species with similar ecological requirements (debris-featured landforms above c. 2000 m a.s.l.) in a peripheral mountain range (Orobian Alps, Italy), in order to discuss their distributional patterns with respect to the putative position of potential cold- and warm-stage refugia.

The distributional pattern of plants seems to depend mainly on the warm-stage refugia, while that of arthropods suggests a more important role of cold-stage refugia. Our study suggests the potential role of both cold- and warm-stage refugia on the current distribution of cold-adapted species on a peripheral mountain range; these results could help to a better interpretation of those obtained by phylogeographical studies performed on taxa with distribution limited to peripheral mountain range.

Key-words: carabid beetles, climate change, endemism, glaciation, interglacial, spiders, vegetation.

Introduction

The biogeographical isolation due to the ice-sheets expansion in cold-climatic stages like the Last Glacial Maximum (LGM, c. 22.000 years BP, Antonioli and Vai, 2004) was traditionally involved to explain most of the present patchy distribution of many plant (e.g. Martini et al. 2012; Schönswetter et al. 2005) and arthropod species (e.g. Latella et al., 2012; Lohse et al., 2011) on peripheral mountain ranges. However, many species (particularly the cold-adapted ones) can be subjected to the maximum areal contraction in warm-climatic stages like the subsequent Holocene Climate Optimum (HCO, c. 8000 years BP, Antonioli and Vai, 2004), due to the progressive reduction of their habitat with temperature increase (Birks and Willis 2008; Stewart et al. 2010).

The most evident effects of temperature increase on high alpine landscapes and ecosystems are glaciers retreat (Citterio et al., 2007) and primary successions along glacier forelands (e.g. Kaufmann, 2001; Caccianiga and Andreis, 2004). Among pioneer species, the cold-adapted ones are the first to be threatened by such process, since (as pioneer) they are forced to follow the glacier retreat to avoid the competition with mid- and late-successional species, and (as cold-adapted) they are unable to withdraw on other habitats if not at higher elevation (Tampucci et al., 2015b). However, recent studies on the Alps showed that the oceanic climate of peripheral mountain range achieves: 1) slower glaciers retreat than those of the inner mountain ranges as a consequence of higher winter precipitation (Scotti et al., 2014); 2) slower colonization of ice-free terrain than those of the inner mountain ranges (Caccianiga and Andreis, 2004; Tampucci et al., 2015b) as a consequence of the more severe environmental conditions (e.g. long-lasting snow cover and temperatures around zero occurring in spring) (Caccianiga et al., 2008).

Glacier forelands and recent moraines of peripheral mountain ranges may thus promote the long-lasting persistence of pioneer cold-adapted species even at relatively low elevation, acting as warm-stage refugia besides the highest peaks (Tampucci et al., 2015b). Other studies on inner mountain ranges proposed also active rock glaciers as potential warm-stage refugia for cold-adapted species, due to their microclimate features and thermal inertia (Millar et al., 2013; Gobbi et al., 2014; Tampucci et al., 2015a). Even if active rock glaciers are scarce in peripheral mountain ranges (Scotti et al., 2013), their role as potential warm-stage refugia should be taken in account.

In the present study, we mapped the distribution of five plant and five arthropod (three carabid beetles and two spiders) cold-adapted species with similar ecological requirements (debris-featured landforms above c. 2000 m a.s.l.) in a peripheral mountain range (Orobian Alps, Italy). Our aim was to discuss the distributional pattern of such species with respect to the position of potential cold- (summits emerging from the ice-sheet during LGM) and warm-stage refugia (highest peaks, present glaciers and active rock glaciers).

Methods

Study area

The Orobian Alps are a west-east oriented peripheral mountain range delimited by Po plain to the south, Valtellina to the north, Como lake to the west and Val Camonica to the east. The northern ridge is homogeneously characterized by sub-oceanic climate (1200-2000 mm/y) and silicate substrates, while the southern massifs are all characterized by oceanic climate (1200-2500 mm/y) and carbonate substrates (Ceriani and Carelli, 2000; Jadoul et al., 2000).

During LGM the whole northern ridge of Orobian Alps was ice-free forming a continuous potential cold-stage refugium, while the southern massifs where isolated refugia emerging from the ice-sheet (Bini et al., 2009). Concerning the HCO, the Orobian highest peaks as potential warm-stage refugia are located in the central-eastern sector of the ridge (up to 3050 m a.s.l.), except few isolated summits exceeding 2500 m a.s.l. in the western sector of the ridge and in the southern massifs. We do not know whether glaciers and active rock glaciers were available during the HCO; however, 80 glaciers are currently located in the central-eastern sector of the northern ridge (Scotti et al., 2014) and 27 active rock glaciers follow a similar, despite more scattered, distributional pattern (Scotti et al., 2013).

Target species

Ten cold-adapted plants and arthropods were selected as target species. Such species are characterized by different chorology and dispersal ability, but all share the same ecological requirements (debris-featured landforms above 2000 m a.s.l.).

Five cold-adapted vascular plant species were selected: a steno-endemic species of the Orobian Alps (*Viola comollia* Massara), two alpine-endemic species (*Androsace alpina* (L.) Lam. and *Artemisia genipi* Weber) and two Arctic-Alpine species (*Ranunculus glacialis* L. and *Saxifraga oppositifolia* L.). The selected plants show different dispersal strategies: the steno-endemic *Viola comollia* shows the lowest dispersal ability, being autochory (self-dispersal by physical expulsion) and myrmecochory (dispersal by ants); the Alpine-endemic species (*Androsace alpina* and *Artemisia genipi*) and *Saxifraga oppositifolia* show an intermediate dispersal ability, being mainly boleochory (dispersal by wind gusts); the Arctic-Alpine *Ranunculus glacialis* shows the highest dispersal ability being mainly meteorochory (long-disance dispersal by air current) (Landolt et al., 2010).

Five ground-dwelling arthropod species were selected, among which three carabid beetles (Coleoptera: Carabidae) and two spiders (Arachnida: Araneae). The selected carabid beetles were the three cold-adapted species of the genus *Oreonebria* present on the study area: two steno-endemic species of the Orobian Alps (*O. lombarda* K. Daniel & J. Daniel 1890 and *O. soror tresignore* A. Szallies & C. Huber 2014) and a central-alpine endemic species (*O. castanea* Bonelli 1810). The selected spiders were two central-alpine endemic cold-adapted species (*Coelotes pickardi tirolensis* Kulczyński, 1906 and *Drassodex heeri* Pavesi 1873); no steno-endemic ground-dwelling spiders live on the Orobian Alps. The selected arthropod species are generally characterized by low dispersal ability (running on the ground), since all the carabid beetles lacks for functional wings for long-distance flight (Brandmayr, 1991) and both the spiders are unable to perform long-distance ballooning (Bell et al., 2005).

Dataset

Data were mapped by GIS approach (Software: ArcGIS 10.0 by ESRI) as follow.

The potential distribution of the target species was mapped using the contour of 2000 m a.s.l. as their lower altitudinal limit. The LGM was mapped following Bini et al. (2009), considering all the ice-free areas as potential cold-stage refugia. In order to distinguish the highest peaks as potential warm-stage refugia from the lowest ones as potential "summit traps" (Pauli et al., 2003; Sauer et al., 2011), we selected the contour of 2500 m a.s.l., which is approximately the median altitude between the lower limit of target species (2000 m a.s.l.) and the maximum altitude of the Orobian Alps (3050 m s.l.m.). Eighty glaciers were mapped following Scotti et al. (2014) and twenty-seven active rock glaciers were mapped following Scotti et al. (2013). Highest peaks, present glaciers and active rock glaciers were considered as potential warm-stage refugia.

The location of plant populations were collected on the basis of the databases of Gruppo Flora Alpina Bergamasca and Gruppo Floristico Massara (Bona et al., 2013); the location of arthropod populations were collected on the basis of the available literature (e.g. Fornasari and Villa, 2001; Pantini and Isaia, 2016) and of the collections of the Natural Sciences museums of Milano, Bergamo, Brescia and Morbegno. Further distributional data of the target plant and arthropod species were directly collected by the Authors on the field (2013–16). A total of 613 population locations were mapped (418 plants, 54 carabid beetles and 141 spiders). Since the location data cover a wide range of accuracy (from precise positions to relatively wide areas), the distribution of each species were finally represented as presence/absence in each cell of the IUCN grid with resolution of 2x2 km (Gargano, 2011).

Maps layout

The distributional map of each species was organized as follows. The orography was represented through a digital elevation model with a resolution of 25 m. The contour of 2000 m a.s.l. as lower limit of cold-adapted species was indicated as a black line. The ice-sheet extension during LGM (Bini et al., 2009) was indicated as azure areas. Peaks exceeding 2500 m a.s.l. were indicated as yellow areas. Present glaciers (Scotti et al., 2014) were indicates as blue areas, while active rock glaciers (Scotti et al., 2013) were indicates as red areas. The squares delimited by the red edges indicates the cells of the IUCN grid (Gargano, 2011); the red-filled squares of the grid indicates the target species presence.

Results and discussion

Distribution of cold- and warm-stage refugia

The contour of 2000 m a.s.l. as potential distribution of the target cold-adapted species includes the whole northern ridge and five main southern massifs apart from each other. 93% of the grid cells above 2000 m s.l.m. includes a potential cold-stage refugium, while only 28% includes a warm-stage refugium. The higher availability of cold- rather than warm-stage refugia suggest that cold-adapted species were likely subjected to the maximum areal contraction during the more recent HCO rather than the previous LGM.

Distribution of plant species

All the target plant species except *Saxifraga oppositifolia* were absent in the southern massifs and widespread on the northern ridge. Two main distributional patterns are recognizable along the latter. The first distributional pattern concerns the broadly speaking endemic species (*Viola comollia*, *Androsace alpina* and *Artemisia genipi*; fig. 1, 2 and 3) and can be summarized as follows: 1) a main core in the central-eastern sector, where highest peaks, glaciers and active rock glaciers occur; 2) a wide gap in the western sector, where highest peaks, glaciers and active rock glaciers lacks; 3) two main disjointed stands in the western sector, where highest peaks appear again. The second distributional pattern concerns the Arctic-Alpine species (*Ranunculus glacialis* and *Saxifraga oppositifolia*; fig. 4 and 5) and show a quite continuous distribution along the whole ridge, following thus the estimated potential distribution of all target species.

The absences on the carbonate southern massifs should be attributed to ecological rather than historical reasons, since all the species except the ubiquitous *Saxifraga oppositifolia* are strictly linked to silicate substrates (Aeschimann et al., 2004; Landolt et al., 2010). Concerning the northern ridge, the western gap of endemic plant species is not imputable to ecological reasons (since the whole ridge is potentially suitable for them), neither to obliteration during cold-climatic stages (since the whole ridge was ice-free during LGM); we thus advance the hypothesis that such gap is due to a fragmentation occurred in past warm-climatic stages (HCO). The disjointed stands of endemic species in the western sector suggests a wider distribution before such fragmentation, likely embracing the whole northern ridge. The ridge altitude in the western sector is not prohibitive for cold-adapted species in the current climate condition, but it may have been too low during a warmer climatic stage, acting as "summit trap" and leading to their local extinction. By contrast, the same species may have found warm-stage refugia in the central-eastern sector, due to the route escape provided by the highest peaks and to the refugia provided by glacial and periglacial landforms. By such perspective, the continuous distribution of Arctic-Alpine species (*Ranunculus glacialis* and *Saxifraga oppositifolia*) can be interpreted as a fast post-

HCO recolonization of the suitable areas, started from the same warm-stage refugia of the endemic ones and likely performed in strength of higher dispersal abilities. Considering the ecological requirements of such cold-adapted Arctic-Alpine species, the hypothesis that their present distribution still represent a LGM refugium and was not affected at all by the subsequent HCO seems unlikely.

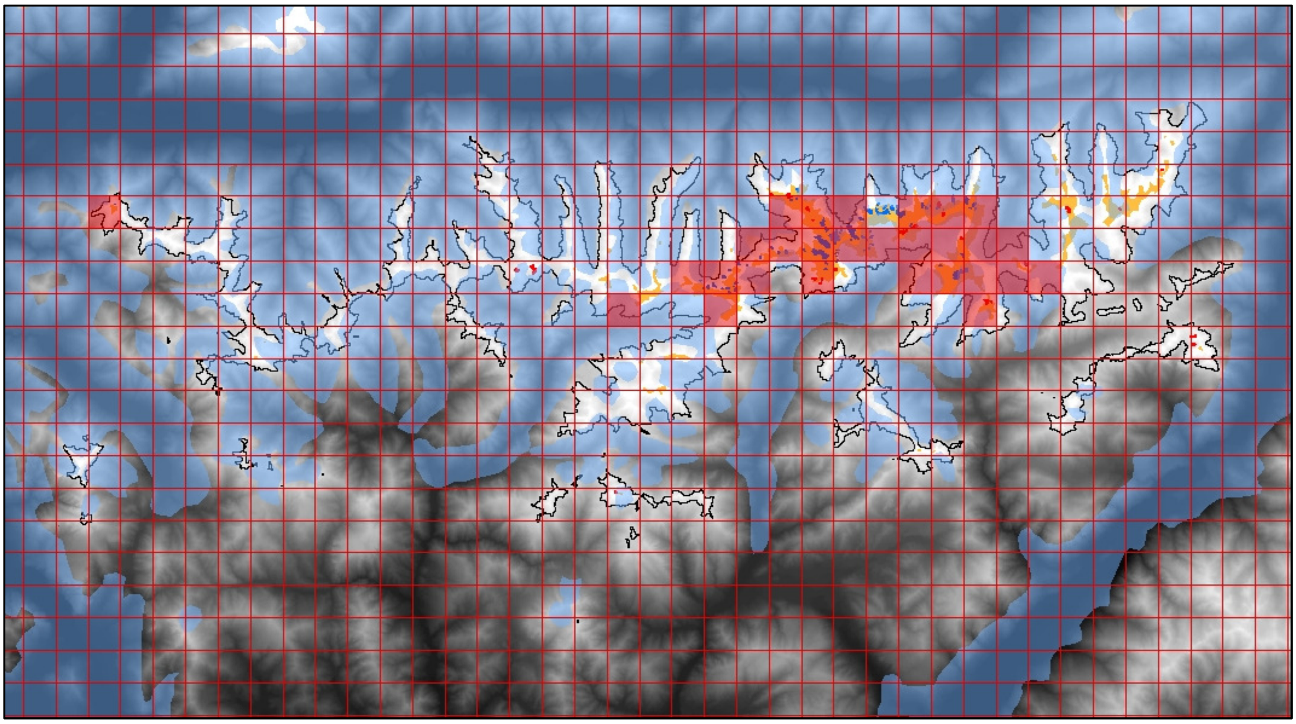

Fig. 1. Distributional pattern of *Viola comollia* on Orobian Alps (see the layout chapter for the legend).

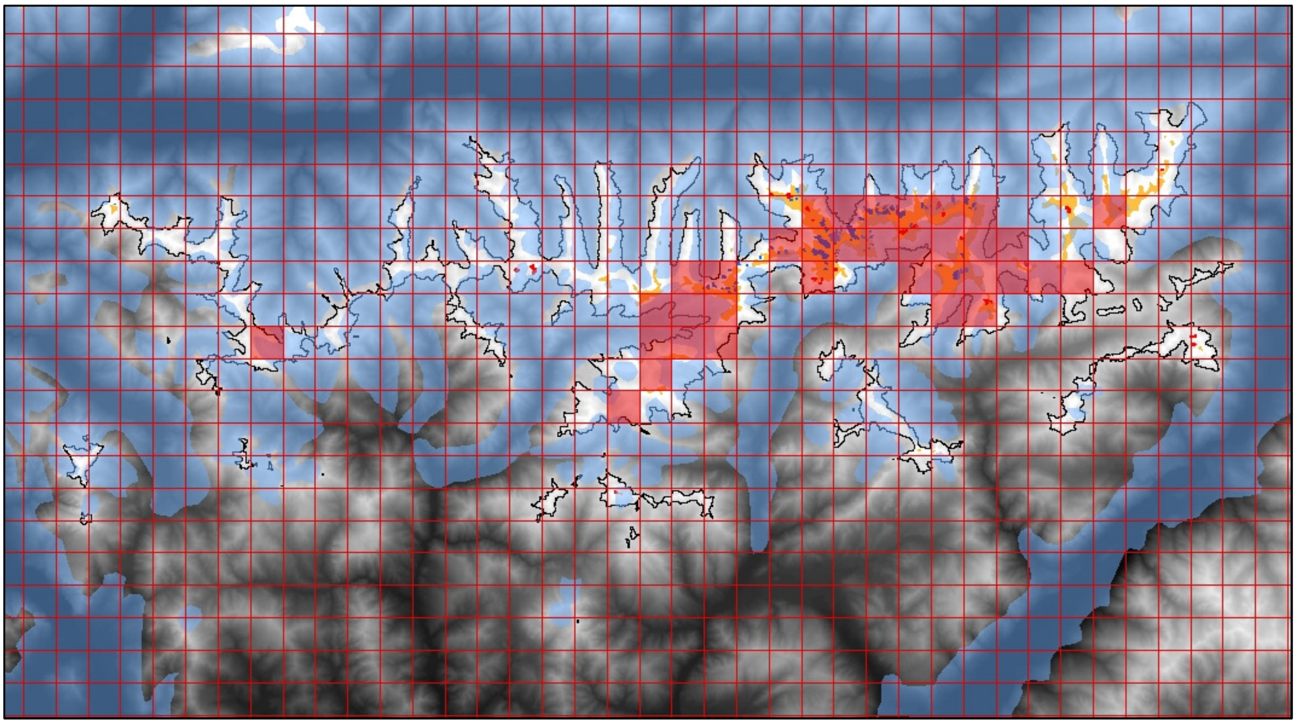

Fig. 2. Distributional pattern of *Androsace alpina* on Orobian Alps (see the layout chapter for the legend).

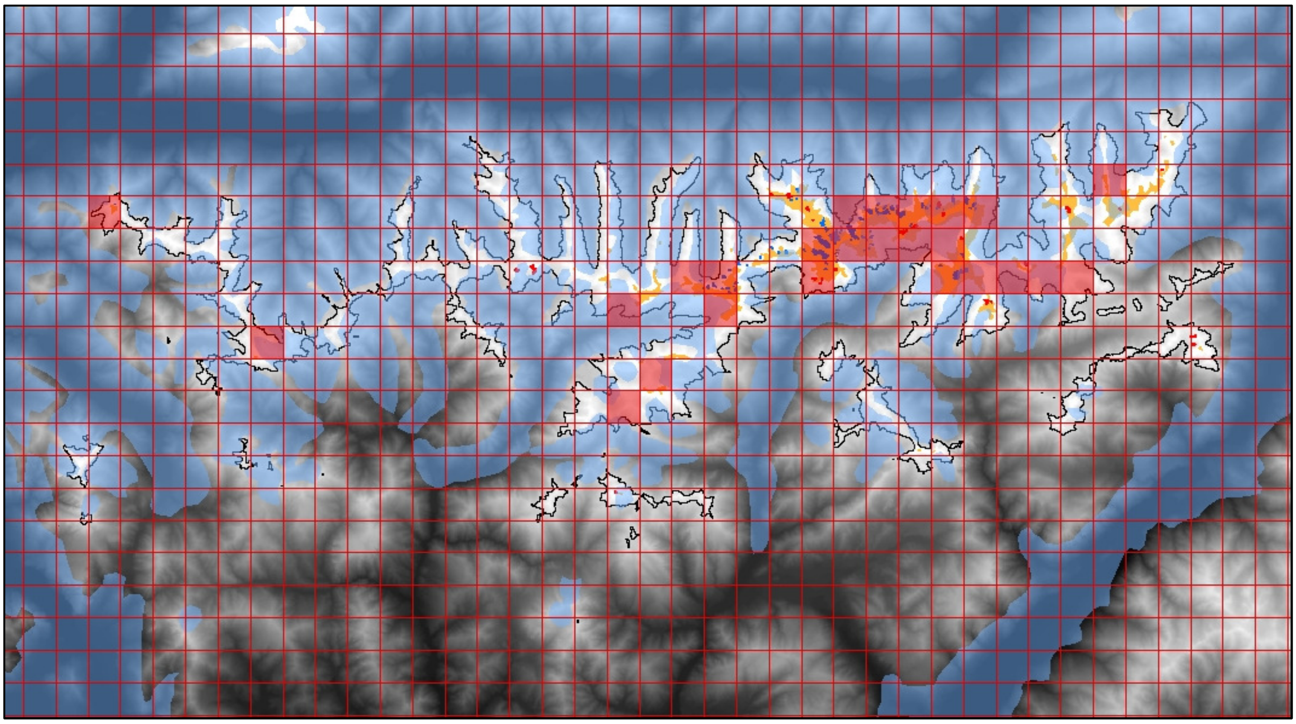

Fig. 3. Distributional pattern of *Artemisia genipi* on Orobian Alps (see the layout chapter for the legend).

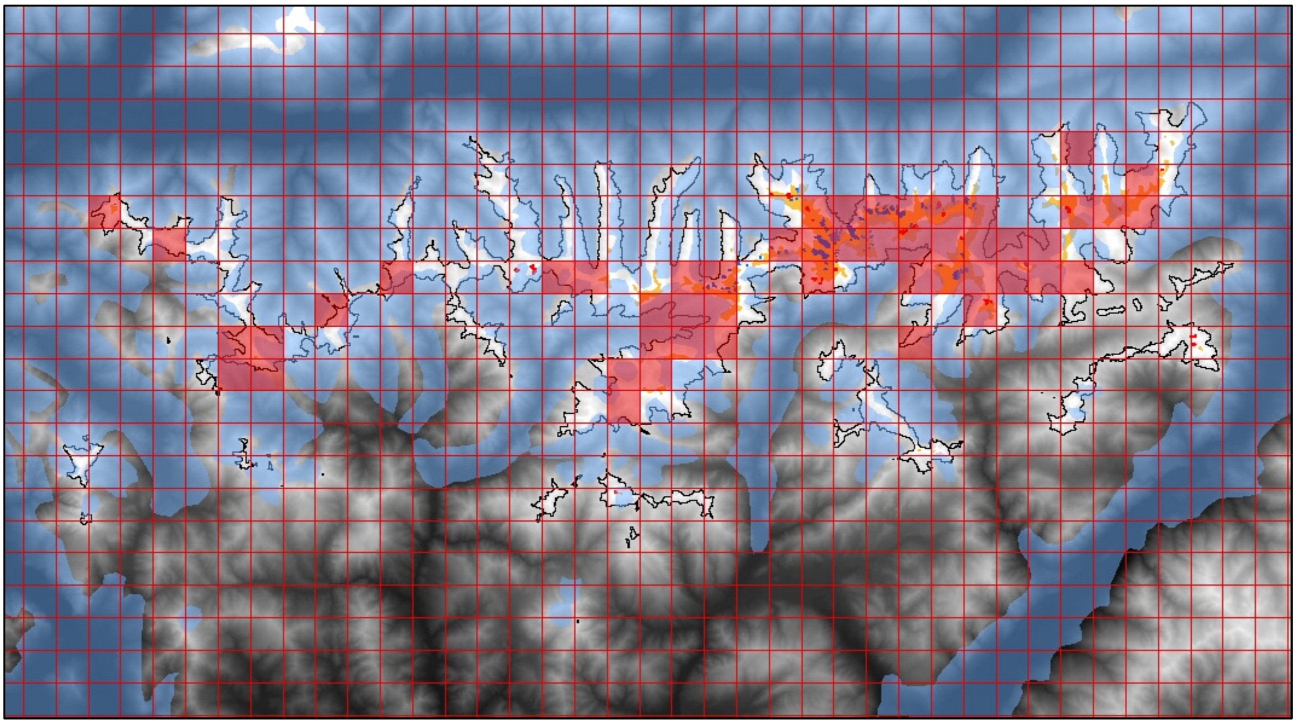

Fig. 4. Distributional pattern of *Ranunculus glacialis* on Orobian Alps (see the layout chapter for the legend).

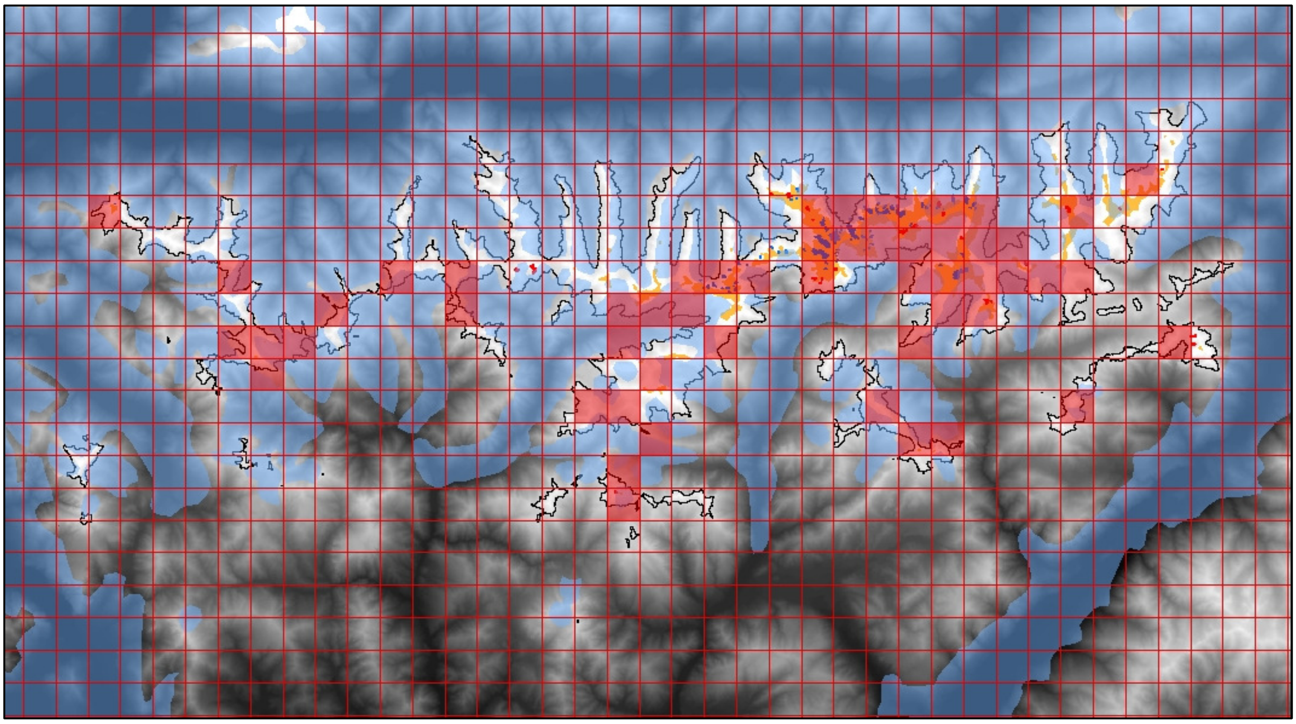

Fig. 5. Distributional pattern of *Saxifraga oppositifolia* on Orobian Alps (see the layout chapter for the legend).

Distribution of arthropod species

The distributional pattern of arthropod species for which more data are available (the carabid beetle *Oreonebria lombarda* and the spiders *Coelotes pickardi tirolensis* and *Drassodex heeri*; fig. 7, 9 and 10) suggests a main areal fragmentation during LGM rather than HCO, according with previous studies (e.g. Latella et al., 2012; Lohse et al., 2011). The hypothesis that the present distribution of arthropods represents a recent recolonization from warm-stage refugia seems unlikely, since all of them are characterized by relatively low dispersal ability. By contrast, the hypothesis of a glacial isolation of arthropods within Orobian Alps fits well with the distribution of some species of the genus *Oreonebria* in the whole central Alps. Particularly, the two endemic subspecies of *O. soror* displaced in two adjacent peripheral mountain ranges (*O. soror tresignore* in the Orobian Alps and *O. soror soror* in the Adamello-Presanella Alps) (Szallies and Huber, 2014; Tampucci et al., 2015) can be interpreted as isolated each other by the Oglio glacier during the LGM (Bini et al., 2009). Moreover, the absence of the affine *O. angustata* on both the peripheral mountain ranges and its presence on the inner Rhaetian Alps (Szallies and Huber, 2014) can be explained with the isolation performed by the Adda glacier during the LGM (Bini et al., 2009).

Our data suggest that arthropods distribution is relatively little driven by warm-climatic stages, particularly if compared with plants. Such difference can be explained with the arthropods opportunity to employ further warm-stage refugia besides the highest peaks and glacial or periglacial landforms. Indeed, karsic endogean or ipogean landforms like caves are suitable as refugia due to their microclimate features (Latella et al., 2012) and particularly widespread on the carbonate substrates of the Orobian southern massifs (Jaduol et al., 2012; Bini and Tognini, 2001).

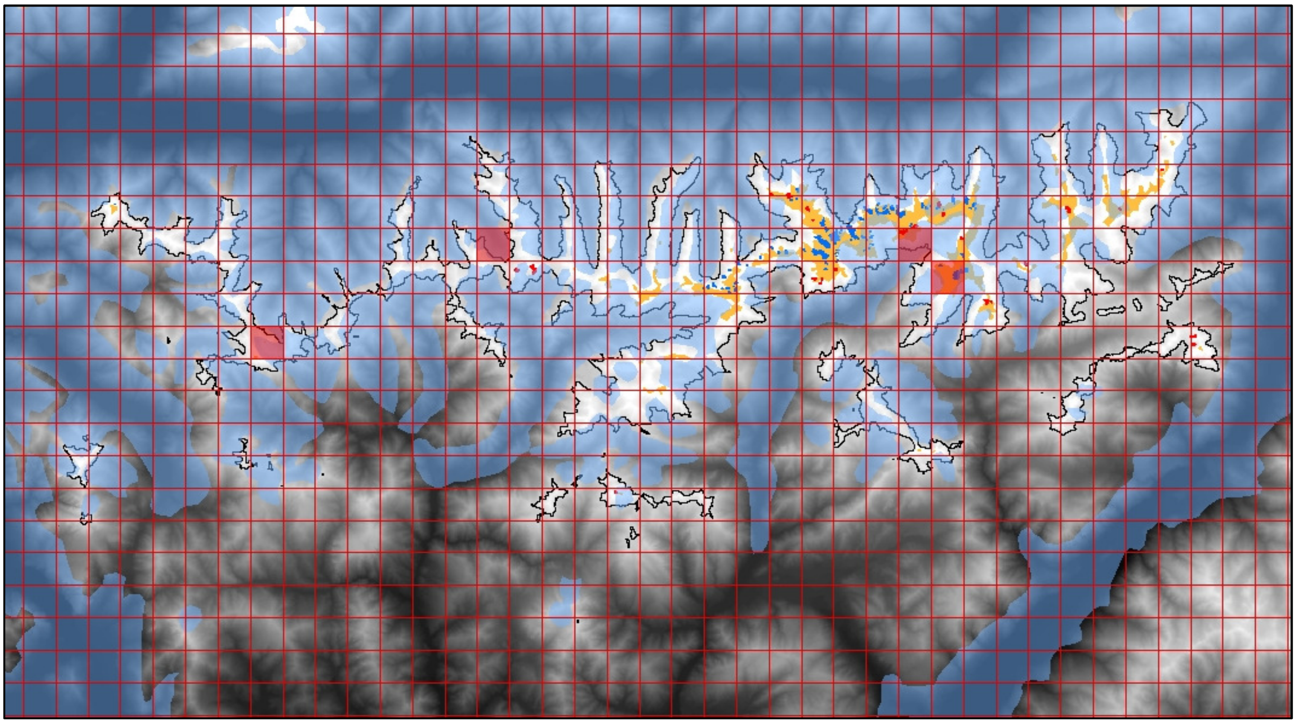

Fig. 6. Distributional pattern of *Oreonebria soror tresignore* on Orobian Alps (see the layout chapter for the legend).

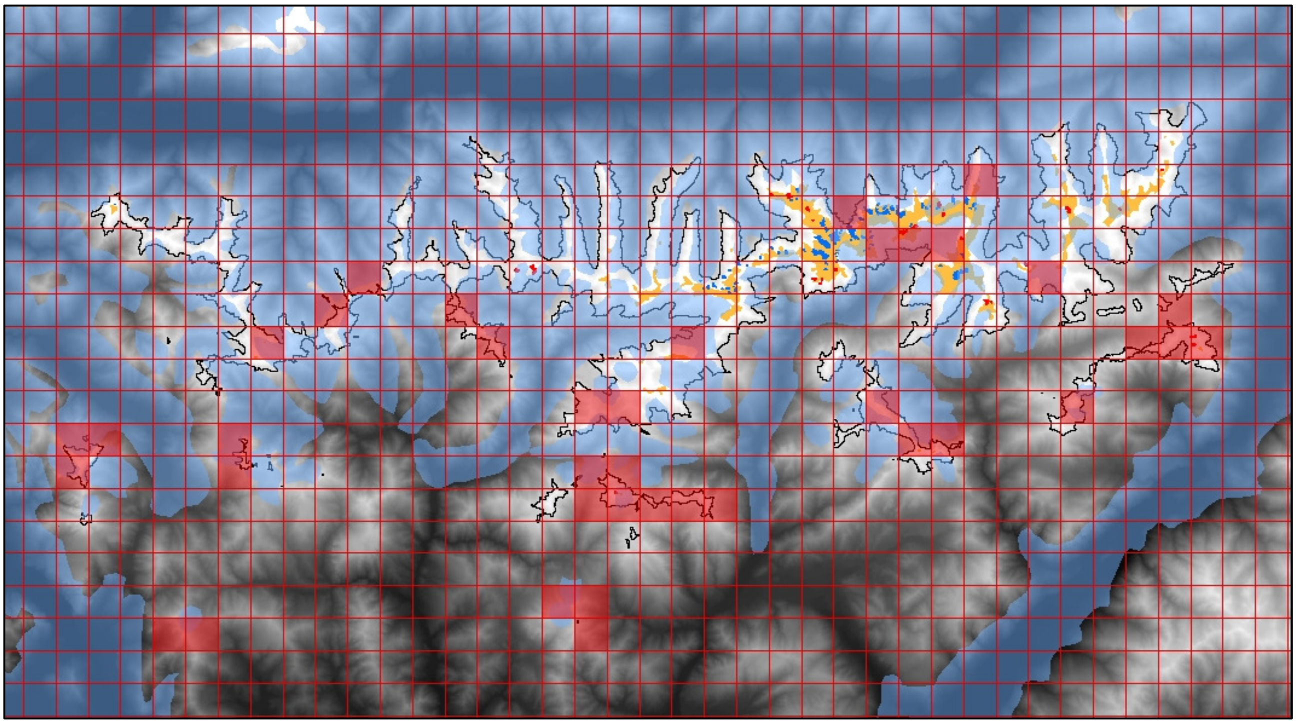

Fig. 7. Distributional pattern of *Oreonebria lombarda* on Orobian Alps (see the layout chapter for the legend).

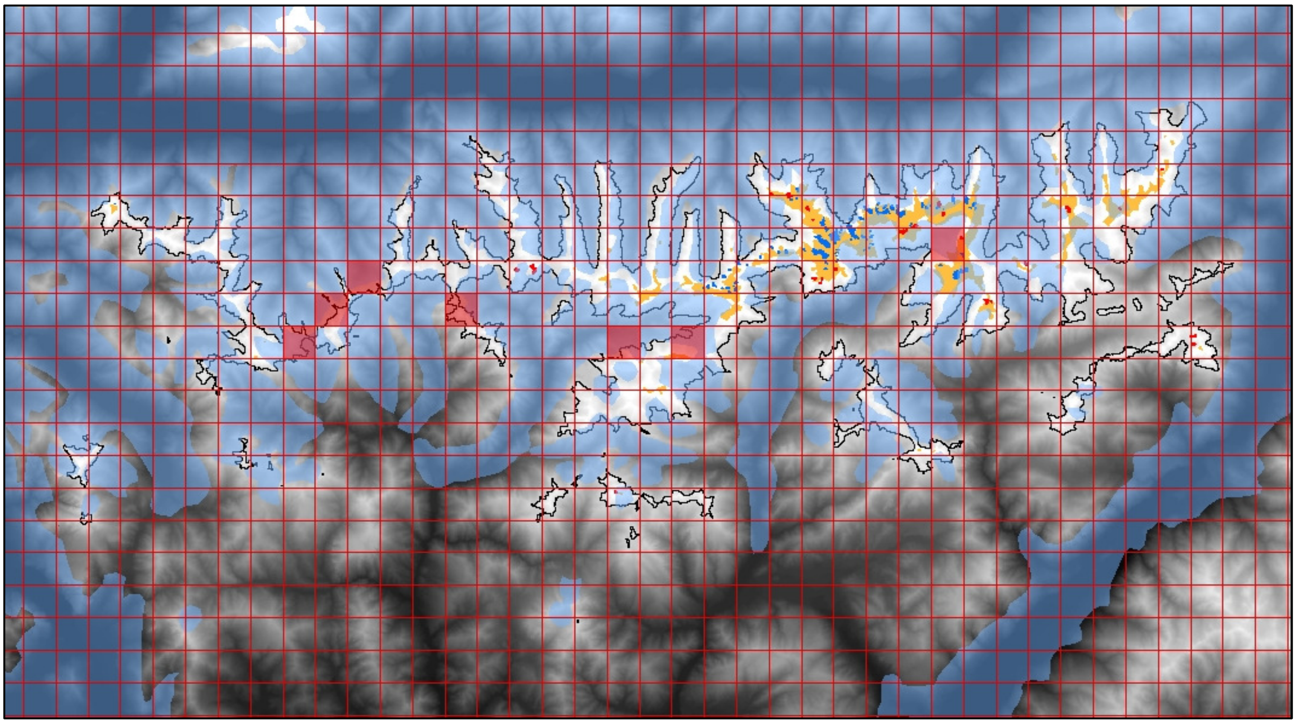

Fig. 8. Distributional pattern of *Oreonebria castanea* on Orobian Alps (see the layout chapter for the legend).

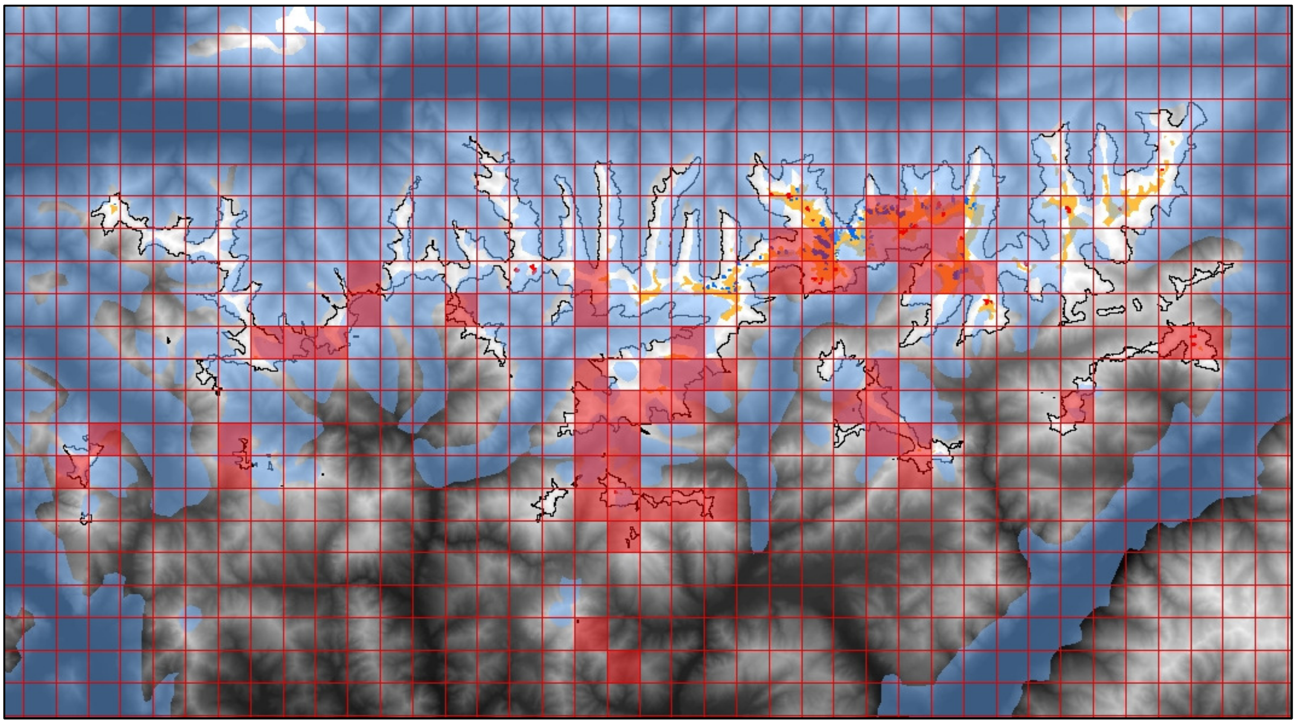

Fig. 9. Distributional pattern of *Coelotes pickardi tirolensis* on Orobian Alps (see the layout chapter for the legend).

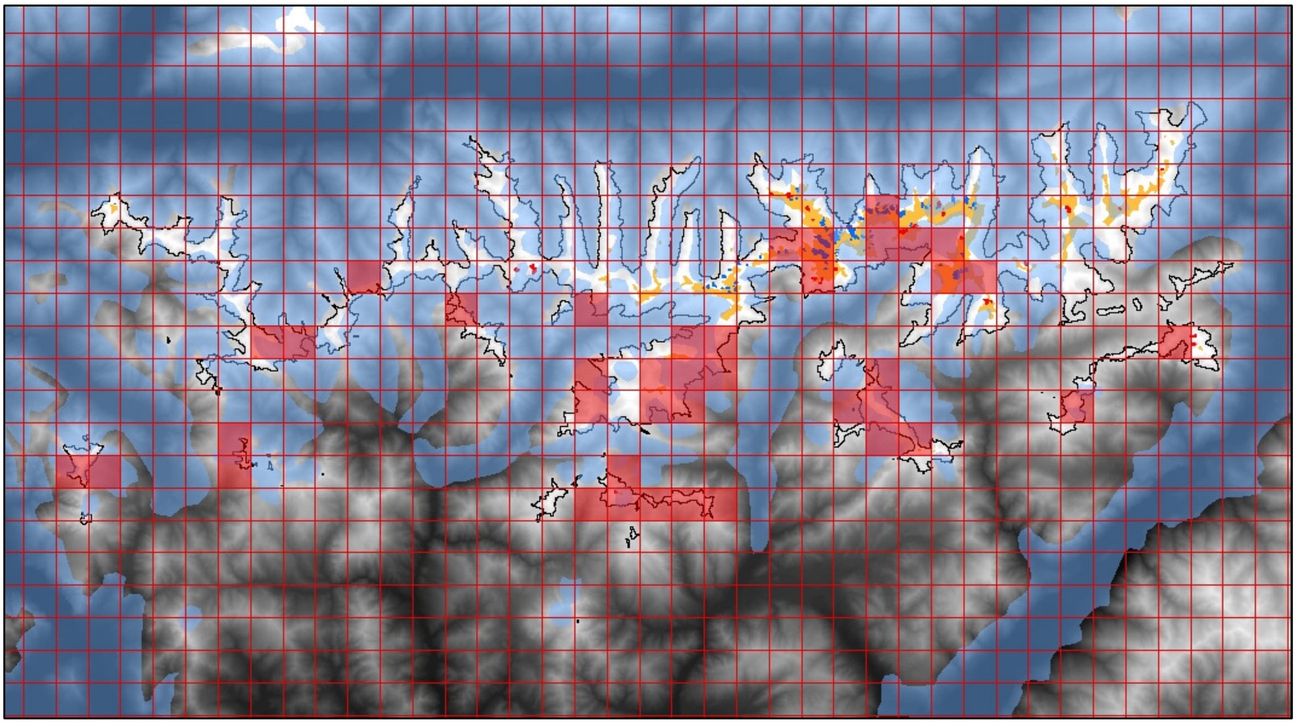

Fig. 10. Distributional pattern of *Drassodex heeri* on Orobian Alps (see the layout chapter for the legend).

Conclusions

The present distribution of ten cold-adapted plant and arthropod species on a peripheral mountain range was reconstructed and compared with the position of potential cold- and warm-stage refugia. The biogeographical evidences resulted from our study allow to advance some hypotheses on the history of such species throughout the Quaternary climate variations.

The distributional pattern of plant species seems to depend on the presence of highest peaks, glaciers and rock glaciers rather than on the summits emerging from the ice-sheet during LGM, suggesting a more important role of warm- rather than cold-stage refugia. By contrast, the distributional pattern of arthropod species seems to depend on the summits emerging from the ice-sheet during the LGM rather than on highest peaks, glaciers and rock glaciers, suggesting a more important role of cold- rather than warm-stage refugia. Such difference can be explained with the arthropods opportunity to employ further warm-stage refugia precluded for plants, as likely the endogean and ipogean environments.

These results could help to a better interpretation of those obtained by phylogeographical studies performed on taxa with distribution limited to peripheral mountain range. Genetic analysis on the target species could help to support our hypotheses. However, our suggestion is to consider the potential role of warm-stage refugia besides cold-stage ones to make light on the present biogeographical arrangement of peripheral mountain ranges. The occurrence and nature of warm-stage refugia could be of further great interest within the frame of the present warming stage.

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A global method for calculating plant CSR ecological strategies applied across biomes world-wide

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Summary

1. Competitor, stress-tolerator, ruderal (CSR) theory is a prominent plant functional strategy scheme previously applied to local floras. Globally, the wide geographic and phylogenetic

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coverage of available values of leaf area (LA), leaf dry matter content (LDMC) and specific leaf area (SLA) (representing, respectively, interspecific variation in plant size and conservative *vs*. acquisitive resource economics) promises the general application of CSR strategies across biomes, including the tropical forests hosting a large proportion of Earth's diversity.

2. We used trait variation for 3068 tracheophytes (representing 198 families, six continents and 14 biomes) to create a globally calibrated CSR strategy calculator tool and investigate strategy–environment relationships across biomes world-wide.

3. Due to disparity in trait availability globally, co-inertia analysis was used to check correspondence between a 'wide geographic coverage, few traits' data set and a 'restricted coverage, many traits' subset of 371 species for which 14 whole-plant, flowering, seed and leaf traits (including leaf nitrogen content) were available. CSR strategy/environment relationships within biomes were investigated using fourth-corner and RLQ analyses to determine strategy/climate specializations.

4. Strong, significant concordance (RV = 0·597; $P < 0{\cdot}0001$) was evident between the 14 trait multivariate space and when only LA, LDMC and SLA were used.

5. Biomes such as tropical moist broadleaf forests exhibited strategy convergence (i.e. clustered around a CS/CSR median; C:S:R = 43:42:15%), with CS-selection associated with warm, stable situations (lesser temperature seasonality), with greater annual precipitation and potential evapotranspiration. Other biomes were characterized by strategy divergence: for example, deserts varied between xeromorphic perennials such as *Larrea divaricata,* classified as S-selected (C:S:R = 1:99:0%) and broadly R-selected annual herbs (e.g. *Claytonia perfoliata*; R/CR-selected; C:S:R = 21:0:79%). Strategy convergence was evident for several growth habits (e.g. trees) but not others (forbs).

6. The CSR strategies of vascular plants can now be compared quantitatively within and between biomes at the global scale. Through known linkages between underlying leaf traits and growth rates, herbivory and decomposition rates, this method and the strategy–environment relationships it elucidates will help to predict which kinds of species may assemble in response to changes in biogeochemical cycles, climate and land use.

Key-words: community assembly, comparative ecology, Grime's CSR triangle, plant economics spectrum, plant functional type, survival strategy, universal adaptive strategy theory

Introduction

A common framework for the comparison of organism function within and between ecosystems world-wide can potentially be achieved using the continuous variation evident along spectra of functional (adaptive) traits. The main plant trait spectra evident globally represent variation in plant resource economics (a trade-off between traits conferring resource acquisition and internal conservation) and the size of plants and plant organs (Díaz *et al.* 2016). These two principal functional trait spectra can be used to assign species a position within multivariate space relative to other species and concurrently to allocate discrete ecological strategy classes (Pierce *et al.* 2013). These classes are more precise than traditional life-form or 'plant functional type' categories characterized by constant attributes (van Bodegom *et al.* 2012; Soudzilovskaia *et al.* 2013). Functional trait spectra may also better reflect the acquisition, use and cycling of energy and matter within the ecosystem. For instance, plant resource economics is a particularly important determinant of photosynthetic carbon fixation, biomass production, litter decomposition and thus ecosystem nutrient availabilities (Grime *et al.* 1997; Wright *et al.* 2004; Cornwell *et al.* 2008; Reich 2014). Ecological strategies reflect viable suites of traits that impact fitness and survival and can also provide a conceptual link between ecology and natural selection. Indeed, recent studies underline the evolutionary history of functional traits (Cornelissen & Cornwell 2014; Cornwell *et al.* 2014; Flores *et al.* 2014; Díaz *et al.* 2016) and the consistent co-occurrence of particular traits and trait values (Reich 2014; Verheijen *et al.* 2016). It is now clear that plant size and economics are the most prominent aspects of plant functional variation globally (Díaz *et al.* 2016), although there is currently no consensus on any particular ecological strategy scheme that can potentially explain *why* certain combinations of trait values are consistently observed under similar circumstances.

A prominent strategy scheme is Grime's (1974, 1977, 2001) competitor, stress tolerator, ruderal (CSR) theory (reviewed by Grime & Pierce 2012), in which the three principal strategies represent viable trait combinations arising under conditions of competition, abiotic limitation to growth or periodic biomass destruction, respectively.

Specifically, C-selected ‘competitors’ are said to survive in relatively stable, productive habitats *via* investment of resources in continued vegetative growth and rapid attainment of large individual and organ size to aid resource pre-emption. S-selected ‘stress tolerators’ protect metabolic performance in variable and resource-poor environments by investing mainly in capacity to retain resources and repair cellular components in dense, persistent tissues. They may be small or gradually accrue large size over a long life span. R-selection, or ruderalism, involves investment of a large proportion of resources not in the individual but in propagules from which the population can regenerate in the face of repeated lethal biomass destruction events, or disturbances. The world-wide leaf economics spectrum, itself a part of the ‘fast–slow’ plant economics spectrum (Reich 2014), and the leaf size spectrum are major components of CSR strategy variation (Pierce *et al.* 2012).

A number of CSR analysis methods have been developed (Grime, Hodgson & Hunt 1988; Hodgson *et al.* 1999; Pierce *et al.* 2013) and have been applied as practical tools to characterize, map and compare vegetation function (Bunce *et al.* 1999; Hunt *et al.* 2004; Schmidtlein, Feilhauer & Bruelheide 2012). They have also been used to investigate and interpret a range of community processes, such as resistance and resilience, coexistence, succession and the relationship between species richness and productivity (Lepš, Osbornová-Kosinová & Rejmánek 1982; Caccianiga *et al.* 2006; Cerabolini *et al.* 2016). However, each CSR analysis method has drawbacks, and all have been calibrated using local floras. Application of CSR analysis is therefore typically applied to herbaceous vegetation in Europe (but see Negreiros *et al.* 2014; de Paula *et al.* 2015), while the majority of plant diversity is found in tropical forests (Kreft & Jetz 2007).

Potential for a global system for comparative plant ecology lies in the fact that variation in leaf economics and leaf size is a ubiquitous phenomenon evident not just for temperate herbs but also for trees, lianas and understorey herbs in tropical forests (Santiago & Wright 2007). Indeed, other widely used traits are not applicable across life-forms: for example, plant height cannot be measured for aquatic species, whereas leaf traits allow aquatic and terrestrial species to be compared on an equal footing (Pierce *et al.* 2012). Leaf area (LA), a key determinant of capacity to intercept light, is one of the most widely available indicators of the size spectrum (Díaz *et al.* 2016). Large values of specific leaf area (SLA) and, alternatively, of leaf dry matter content (LDMC) are highly representative of the opposite extremes of the economics spectrum and are amongst the most widely available traits in the global TRY plant functional trait data base (see list at www.try-db.org/de/TabDetails.php; Kattge *et al.* 2011). Data for other key traits such as leaf nitrogen content (LNC) have a much more restricted geographic and phylogenetic coverage (Díaz *et al.* 2016).

Any generally applicable method for calculating CSR strategies must include ubiquitous traits that can represent the extremes of a trade-off between large size and conservative vs. acquisitive economics. Leaf size and economics traits are widely available, applicable to a range of life-forms and are highly representative of plant functional trade-offs. Specifically, in the European flora species characterized by high LA do not exhibit high SLA or high LDMC, species exhibiting high LDMC all have small, dense leaves and species with high SLA are small and exhibit low LDMC (Cerabolini *et al.* 2010). These trade-offs at the level of the leaf are associated with whole-plant and reproductive trade-offs (e.g. species with large leaves tend to have large seeds; Pierce *et al.* 2014a; Díaz *et al.* 2016), and it is reasonable to expect leaf-level variation to reflect a substantial portion of overall plant variation (Díaz *et al.* 2016).

The main aim of the current study was to examine the trade-off between LA, LDMC and SLA variation world-wide in order to assign combinations of leaf traits within the triangle of CSR strategies, and to use this to produce a readily applicable practical tool. This builds on the previous CSR classification system of Pierce *et al.* (2013) but upscaling of the method using a global calibration has a number of advantages. By using the absolute limits of plant functional trait spectra evident in the world flora, rather than local data ranges, the method is essentially altered from one that compares species relative to one another to become a method bounded by the entire range of plant size and economics currently known for vascular plants (i.e. species are compared against absolute limits). This means that ecologists working in biogeographically distinct contexts world-wide will have a common reference frame. As CSR theory predicts that strategies arise consistently in response to particular conditions, lessons learned in one location are potentially transferable to functionally similar vegetation found on different continents.

At local scales, an average CSR strategy for a plant community can be used to provide a ‘functional summary’ of vegetation and allow comparison of contrasting circumstances (e.g. Caccianiga *et al.* 2006). A global methodology could similarly provide functional summaries at larger scales and allow investigation of general relationships between plant functioning and broad-scale environmental parameters operating within and between biomes. There is good reason to expect that a plant functional signal should be apparent even at the scale of biomes. For example, as woody species vary between C- and S-selected, but no ruderal tree species are apparent (at least in Europe; Pierce *et al.* 2013) biomes dominated by woody species should exhibit clustering of species around the CS-selected region of the CSR triangle (whereas herbaceous species in Europe exhibit a much wider range of strategies; Pierce *et al.* 2013). Furthermore, strategies can be expected to be mediated by climatic factors such as temperature, potential evapotranspiration and water availability, which are principal determinants of plant survival and vegetation distribution. However, the relationship between plant primary strategies and climate has not previously been investigated, despite the potential importance of plant responses to climatic changes in shaping future vegetation. For the present study, a general prediction can be made that biomes characterized by climatic extremes should include species with a greater degree of functional specialization. For example, in the desert biome plants survive using contrasting life histories that can be summarized as essentially 'ephemeral therophyte' or 'long-lived and durable' (Chesson *et al.* 2004). We can thus predict that the CSR signature of the desert biome will be polarized between extreme R- and S-selected strategies, and that these too are correlated with climatic factors, particularly precipitation seasonality. Montane grasslands and alpine herbaceous vegetation are known to exhibit CSR strategies that range between R- and S-selection, with C-selection relatively rare (Caccianiga *et al.* 2006; Pierce *et al.* 2007a,b), but these studies have investigated specific plant communities and have not enjoyed the opportunity for comparison with the range of strategies evident within the biome as a whole, or indeed with other biomes. Certain biomes, such as tropical moist broadleaf forest, have yet to be interpreted in a plant functional strategy/climate context. Thus, a secondary aim of the present study was to apply the global CSR analysis tool to determine whether it is possible to discern broad patterns of plant functional variability and specialization in response to climatic factors operating in biomes world-wide.

Materials and methods

TRAIT DATA

A total of 116 979 plant functional trait records, composed of 38 835 individual measurements of leaf area (LA; mm^2), 48 468 measurements of SLA (mm^2 mg^{-1}) and 29 676 of LDMC (%), measured from plants growing in nature were obtained from the TRY global trait data base (www.try-db.org; Kattge *et al.* 2011). This included traits from preceding data bases such as the LEDA traitbase (www.leda-traitbase.org; Kleyer *et al.* 2008). The data set included records from all continents except Antarctica, from 16 countries and several biogeographical regions within many of these countries (species native range and typical biome information is summarized in Appendix Table S1, Supporting Information). A total of 3068 species growing in a wide range of biomes, including tropical woody vegetation of various types, were represented by complete sets of LA, LDMC and SLA data. Of these species, a subset of 371 species was available for which sets of 14 whole-plant, leaf, flowering and seed traits were available, including the additional traits leaf nitrogen concentration (LNC), leaf carbon concentration (LCC), leaf dry weight (LDW), canopy height (CH), lateral spread (LS), flowering start (FS), flowering period (FP), seed mass (SM), seed volume (SVo), total mass of seeds (TMS) and seed variance (SVa) (these data are available from the TRY data base and are also published as an appendix to Pierce *et al.* 2014a).

The number of replicate values for each trait of each species was typically between 10 and 15, but varied from a minimum of 3 to a maximum of 349. Nomenclature is reported in Appendix Table S1 and follows the Missouri Botanical Garden Tropicos system (www.tropicos.org). Additional taxonomic and growth habit information was obtained from the Encyclopedia of Life (www.eol.org) and GBIF (www.gbif.org/species/search).

PRODUCTION OF A GLOBAL CSR ANALYSIS TOOL

Global calibration of the CSR tool involved an initial multivariate analysis (PCA) of the key leaf traits (as a method of determining the three-way relationship between traits rather than as an analysis of plant adaptation *per se*), regression of trait values against PCA axes and the use of these regression equations to produce a Microsoft Excel spreadsheet. This spreadsheet aims to allow novel target species to be compared against the multivariate space over which the global data set was ordinated.

First, a centred Pearson PCA was performed using XLSTAT 2012.5.01 software (Addinsoft, New York, NY, USA) and Varimax rotation applied to the first two axes. As a small number of species with disproportionately large leaves are evident in the world flora, with most species exhibiting smaller leaves, trait values were transformed to constrain the most extreme values and to provide distributions as close as possible to normality prior to PCA. In this case, LA data were standardized using the maximum value, followed by square root transformation (Podani 2007). LDMC data were logit transformed (logit transformation is considered a more appropriate method for proportion data with respect to traditional arcsine transformation; Warton & Hui 2011), and SLA data were log transformed.

Transformed trait values were regressed against values of the PCA axis along which the trait exhibited maximum variance (e.g. logSLA against PCA1). The regression equation describing the curve of best fit was then incorporated into a Microsoft Excel spreadsheet that used the equation to compare trait values for any given target species against the global spectrum for that trait. This effectively assigned target species three covarying dimensions: a 'LA dimension' based on PCA2, a 'LDMC dimension' based on positive variability along PCA 1 and a 'SLA dimension' based on negative variation along PCA1. As PCA values may be negative or positive, the minimum (i.e. the most negative) values along PCA axes were then determined for each trait and these were used as a constant, added to all values of each trait in order to translate the trait dimensions into an entirely positive space. The next spreadsheet function determined the maximum values, giving the range of values for each trait. In order to produce ternary coordinates (i.e. three coordinates for a triangular graph), a function was then added to the spreadsheet that summed the three dimensions and divided by 100, allowing determination of the proportional contributions of LA, LDMC and SLA for each species. Thus, the resulting triangular ordination of species represented a 'trade-off triangle' against which target species can be compared.

As no species exhibited zero leaf area or mass, it was not possible for species to be ordinated along the axes themselves nor at the apices of the trade-off triangle. Thus, a spreadsheet function was implemented that essentially expanded, along the three axes, the space occupied by species to fill the entire ternary plot, resulting in full occupation of the triangle and thus positioning of species within the CSR triangle. This was achieved by multiplication of all values by a rescaling constant that allowed the maximum and minimum values to fully occupy the available range. The final spreadsheet (Appendix Table S2: 'StrateFy') is available online as Supporting Information and incorporates all functions to easily allow the CSR analysis of novel plant species from leaf traits.

CORRESPONDENCE BETWEEN VARIATION IN 3 AND 14 FUNCTIONAL TRAITS

To test whether the three key leaf traits (i.e. LA, LDMC and SLA) can provide a reliable multivariate structure for assigning general ecological strategies to plants, we used the subset of species for which 14 vegetative and reproductive trait data were available without any missing data (see Pierce *et al.* 2014a). To this end, a co-inertia analysis (hereafter, COIA) is a general and flexible method that measures the concordance (i.e. co-structure) between two multivariate data sets that share the same objects (in this case, species; Dray, Chessel & Thioulouse 2003). This approach was applied to quantify and test the association between two matrices: (i) three traits per 371 species; and (ii) fourteen traits for the same 371 species. The COIA provides a correlation coefficient ('RV') that measures the strength of the association between matrices. This coefficient is bounded between zero (i.e. no association) and one (i.e. maximum association), with significance (*P*-value) accessed by a Monte Carlo test (with 100 000 permutations). To implement the COIA, a PCA was used for both matrices after data transformation to improve normality. Analyses were carried out using R software (R Development Core Team 2013) with the ADE4 package (Dray & Dufour 2007).

COMPARISON WITH A LOCALLY CALIBRATED METHOD

In addition to the new globally calibrated method, CSR ternary triplets were also calculated using the local tool of Pierce *et al.* (2013; calibrated with six traits for the Flora of Italy) and regression of values obtained using both methods was also performed in order to allow comparison between the locally and globally calibrated techniques.

A TEST USING KNOWN VEGETATION CHANGES ALONG SUCCESSION

In order to test whether the CSR analysis method agreed with expectations of vegetation responses to an environmental gradient, the StrateFy tool was used to calculate CSR strategies for the species characteristic of four phytosociological syntaxa (i.e. plant communities *sensu* Braun-Blanquet 1925) associated with a sequence of vegetation development encompassing a primary succession and related pasture vegetation. Specifically, in the European Alps, mobile screes represent highly disturbed environments where vegetation is composed of annual therophytes (phytosociological syntaxon *Thlasietea rotundifolii* Br.-Bl. *et al.* 1947). With the development of the vegetation and stabilization of scree debris (and where topography and aspect result in long-lying snow cover), snowbed vegetation arises and is characterized by a mixture of nanophanerophytes and hemicryptophytes (*Salicetea herbaceae* Br.-Bl. *et al.* 1947; Tomaselli 1997). This can develop further on acid, nutrient poor soils into a climax vegetation dominated by slow-growing graminoids such as the sedge *Carex curvula* and the grass *Festuca halleri* (phytosociological alliance *Caricion curvulae* Br.-Bl. 1925) (Tomaselli & Rossi 1994). When these unproductive siliceous grasslands experience grazing by large domestic livestock, dominance shifts towards the rhizomatous mat-grass *Nardus stricta* and the vegetation alliance is characterized by greater floristic richness than that evident for *Caricion curvulae* (i.e. syntaxon *Nardion strictae* Br.-Bl. in Br.Bl. & Jenny 1926; Gennai *et al.* 2014). Grazing of alpine pastures increases nutrient turnover rates and selective grazing and the patchy concentration of nutrients following defecation are thought to provide contrasting microsites for a range of life histories, fostering species richness, but with dominant grass species nonetheless exhibiting conservative leaf economics and stress tolerance (Pierce *et al.* 2007a,b). We expected that along this vegetation sequence plant communities would shift from R-selection towards S-selection and ultimately, in the *Nardion* pasture, to an intermediate, relatively C-selected mean strategy with a greater range of strategies apparent.

GLOBAL FOURTH-CORNER AND RLQ ANALYSES OF CSR STRATEGY/ENVIRONMENT RELATIONSHIPS

Globally, the combined fourth-corner and RLQ method of Dray *et al.* (2014) was used to test the relationship between CSR strategies and environmental variation within biomes. Fourteen biomes were defined according to Olson *et al.* (2001) and are listed as part of Appendix Table S1. Information regarding the biome(s) within the native range of each species was obtained from the comparison of the global distribution of biomes with the georeferenced records of each species (from GBIF) occurring inside its native range. The native range of each species was obtained from sources such as GRIN taxonomy for plants (www.ars-grin.gov/cgi-bin/npgs/html/tax_search.pl?language = en), eMonocot (http://emonocot.org) and Catalogue of Life (www.catalogueoflife.org/col/search/all). Additionally, we investigated the CSR strategies evident for life-form categories (tree, shrub, liana, graminoid, forb (i.e. herbaceous dicot), herbaceous vine, annual and biennial herb, perennial herb) and for taxonomic families that were represented by a minimum of 30 species in the data set.

The fourth-corner and RLQ approach involved the simultaneous use of three matrices: (i) a 'community' matrix with sample sites in rows and species in columns; (ii) an environmental matrix with sample sites in rows and environmental variables in columns; and (iii) a functional matrix with traits in rows and species in columns. The fourth-corner approach tests the relationship between each species trait and each environmental variable, while the RLQ analysis tests the co-structure between all species traits with all environmental variables (Dray *et al.* 2014).

The functional matrix was defined by the 3068 species with three traits (i.e. C, S, R percentages). The 14 world biomes (defined by Olson *et al.* 2001) were treated as sampling sites, and the presence (incidence) of the 3068 species in these biomes was equivalent to a community matrix. To generate the environmental matrix, we assessed average environmental characteristics for each biome using bioclimatic variables (temperature seasonality, annual mean temperature, precipitation seasonality and annual precipitation) for the recent half-century (1950–2001) obtained from the WorldClim project (Hijmans *et al.* 2005), in addition to global potential evapo-transpiration (Trabucco & Zomer 2009), at a spatial resolution of 0·0083° (~1 km^2). Temperature and precipitation seasonality was calculated as the standard deviation of monthly values multiplied by 100 and precipitation seasonality as the coefficient of variation of monthly values (Hijmans *et al.* 2005). In order to obtain unbiased averages for each biome, we created 200 000 uniformly random points for the entire globe, covering all terrestrial biomes, using the package gismo for R (R Development Core Team 2013). To conduct the RLQ analysis, a correspondence analysis was used for the community matrix, while a PCA was used for the functional and environmental matrices. For the PCA applied to the functional matrix, species were weighted by their overall relative frequency across biomes (i.e. the number of biomes in which each species occurred), whereas for the PCA applied to the environmental matrix, biomes were weighted by the overall frequency of species observed (Dray & Dufour 2007). Separate fourth-corner and RLQ analyses were conducted for each biome, each analysis involving only species occurring in that biome. Significance was obtained through a Monte Carlo test based on the total co-inertia, using the combined null models 2 (permutation of sampling sites) and 4 (permutation of species) with 50 000 permutations per test (Dray *et al.* 2014). Analyses were carried out using R software (R Development Core Team 2013) with the ade4 package (Dray & Dufour 2007).

Results

'WIDE COVERAGE, FEW TRAITS' VS. 'RESTRICTED COVERAGE, MANY TRAITS'

We found a strong and highly significant concordance between the multivariate space produced by three and 14 traits (RV = 0·597; $P < 0·001$; Fig. 1): that is, there was a relatively small loss of information when only three leaf traits were used instead of 14 traits, and the multivariate plant functional space described by leaf traits alone was representative of whole-plant functional variation (Fig. 1).

A GLOBAL CSR ANALYSIS METHOD

The three-way trade-off between LA, LDMC and SLA for the 3068 species of the main global data set, presented in Fig. 2, confirmed that variation in LA was orthogonal to variation in SLA and LDMC in the world flora. Indeed, SLA and LDMC values ranged in opposite directions between two extremes (negative and positive, respectively) of the first axis of variability (PCA1) and thus an axis of leaf economics (Fig. 2a; for eigenvalues see Fig. 2b). The second axis of variability (PCA2) was delimited by leaf area, with large leaves evident only at intermediate leaf economics (Fig. 2a): species with extremely acquisitive or extremely conservative leaves were consistently small (Fig. 2a), confirming that high values of LA, SLA and LDMC were mutually exclusive in the global data set. In other words, dense, tough leaves were not large; soft, acquisitive leaves were not tough and conservative; only leaves with intermediate economics were large.

Transformed leaf area was highly and positively correlated with PCA2 ($R^2 = 0·998$, $P < 0·0001$) following the polynomial linear equation detailed in Fig. S1a. Transformed LDMC was strongly and positively correlated with PCA1 ($R^2 = 0·794$, $P < 0·0001$) following the equation presented in Fig. S1b. Log SLA was strongly and negatively correlated ($R^2 = 0·782$, $P < 0·0001$) with PCA1 following the equation shown in Fig. S1c. These equations allowed comparison of target plant species with the trade-off between these traits and thus determination of the CSR strategy (see Fig. 3 and the practical tool available as Appendix S2; 'StrateFy').

COMPARISON WITH A LOCALLY CALIBRATED METHOD

When the degree of C-, S- and R-selection calculated by the globally calibrated method were regressed against C, S and R values calculated using the method of Pierce *et al.* (2013), the results were strongly and positively correlated with one another. Specifically, for the degree of C-selection determined by both methods, $R^2 = 0·920$, $F = 9398·1$, $P < 0·0001$, for S-selection $R^2 = 0·891$, $F = 24968·3$, $P < 0·0001$ and for R-selection $R^2 = 0·866$, $F = 19\ 725·1$, $P < 0·0001$ (Fig. S2).

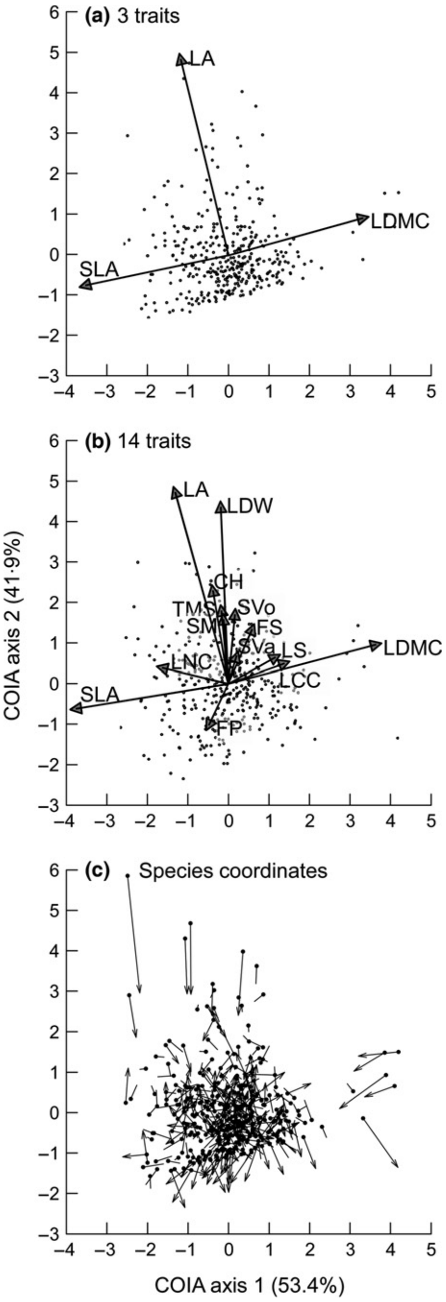


Fig. 1. Projection of two main axes of co-inertia analysis (COIA) for 371 species: variable loadings for data sets including (a) three traits, (b) 14 traits and (c) a joint representation of species scores from the three trait (dots) and 14 trait (arrow tip) data sets. Percentage of variance explained by each axis (eigenvalues) are shown in the axis legend. Traits are CH: canopy height, FP: flowering period, FS: flowering start, LA: leaf area, LCC: leaf carbon concentration, LDMC: leaf dry matter content, LDW: leaf dry weight, LNC: leaf nitrogen concentration, LS: lateral spread, SLA: specific leaf area, SM: seed mass, SVo: apparent seed volume, SVa: seed variance, TMS: total mass of seeds. Data were log transformed to conform to normality and to constrain extreme values.

A TEST USING KNOWN VEGETATION CHANGES ALONG SUCCESSION

The CSR strategies evident for species characteristic of primary succession from scree vegetation to siliceous alpine

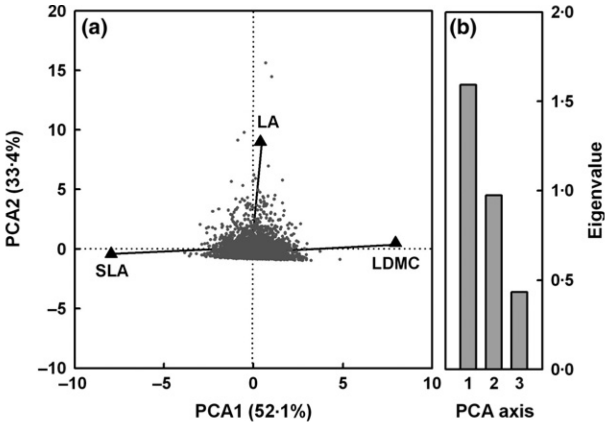


Fig. 2. (a) Biplot showing the relationship between the three traits leaf area (LA), leaf dry matter content (LDMC) and specific leaf area (SLA) for 3068 tracheophyte species from across the world used as a basis for calibrating the CSR classification method (principal components analysis; PCA), and b) eigenvalues for PCA axes. Data were transformed to constrain extreme values (LA was standardized using the maximum value and then square root transformed, SLA was log transformed and LDMC logit transformed).

grassland, terminating with alpine *Nardus* pasture, are evident in Fig. 4. Pioneer vegetation on screes, as expected, was characterized by mainly R-selected species and exhibited an R-selected mean strategy (C:S:R = 12:0:88 %). Species characteristic of vegetation at an intermediate point along the succession exhibited a mean strategy of SR (4:58:37%) and species of the climax vegetation exhibited a high degree of stress tolerance (mean strategy = 6:94:0%; Fig. 4a). Under pasture, siliceous alpine grassland species exhibited a wider range of strategies encompassing C/CR-selected species such as *Gentiana punctata*, S-selected *Nardus stricta* (3:97:0%), R/CR-selected species such as *Campanula barbata* (37:0:63%) and a mean of CR/CSR-selection (40:24:36%; Fig. 4a). The overall trajectory of primary succession in this context is thus characterized by an initial shift from R- to S-selection, with management increasing the range of strategies present and including a higher degree of C-selection relative to the other vegetation types.

CSR STRATEGIES EVIDENT WITHIN BIOMES GLOBALLY

The CSR strategies evident within biomes were calculated using the globally calibrated CSR analysis tool and are shown in Fig. 5 (details of CSR strategies for each species within every biome are listed in Appendix S1). Tropical and subtropical broadleaf forest (both moist and dry forest biomes) exhibited a broad range of strategies but these were highly clustered around CS/CSR-selected median strategies (for both biomes, median C:S:R = 43:42:15%; Fig. 5a,b). Tropical and subtropical coniferous forests also exhibited a median CS/CSR strategy that reflected a slightly greater number of S- and R-selected species at the expense of C-selection (32:46:22%; Fig. 5c). Tropical and subtropical grasslands, savannas and shrublands were highly represented by CS/CSR-selected species (34:51:15%; Fig. 5g). In contrast, biomes such as temperate broadleaf and mixed forests (Fig. 5d) and temperate coniferous forests (Fig. 5e) exhibited a SR/CSR-selected median strategy and a wide range of CSR strategies for individual species, filling the CSR triangle relatively uniformly. This denoted the presence and the even distribution of the full gamut of ecological strategies in these biomes. Deserts also exhibited a range of CSR strategies, with a CSR-selected median (Fig. 5m). Other biomes exhibited variation between relatively restricted strategy variation to wide variation (Fig. 5).

Fourth-corner and RLQ analyses for tropical and subtropical broadleaf forest (both moist and dry forest biomes) (Fig. 6a,b) showed that C- and S-selection were highly correlated with environmental variables: positively with annual mean temperature, annual precipitation and global potential evapo-transpiration, but negatively with temperature seasonality ($P < 0{\cdot}05$, and in some cases $P < 0{\cdot}01$ or $P < 0{\cdot}001$). R-selection exhibited the exact opposite association with environmental variables. In contrast, no significant correlation was found between CSR strategies and environmental variables in temperate broadleaf and coniferous forests (Fig. 6d,e). A wide range of CSR strategies was evident in the desert biome that was significantly correlated with environmental variables: C- and S-selection were positively correlated with annual mean temperature, precipitation seasonality and potential evapo-transpiration, and negatively with temperature seasonality, with R-selection exhibiting contrasting correlations with these factors (Fig. 6l).

CSR STRATEGIES WITHIN GROWTH HABIT CATEGORIES AND FAMILIES

Different growth habit categories exhibited variation in overall and median CSR strategies (Fig. S3). Trees were clustered around a CS median strategy, with no R-selected trees apparent (C:S:R = 43:47:10%; Fig. S3a) and shrubs centred around an S/CSR strategy (20:61:20%; Fig. S3b). Lianas were relatively specialized and clustered around CS/CSR-selection (52:35:14%; Fig. S3c). Graminoids exhibited a strong S-selected component, with variation around an S/CSR median strategy (14:56:29%; Fig. S3d). Forbs (herbaceous dicots) occupied the entire triangle and exhibited a comparatively generalist R/CSR strategy (30:20:51%; Fig. S3e). Annual herbs exhibited an R/CSR median strategy (25:14:61%), with species clustered towards R-selection (Fig. S3g). Perennial herbs had an SR/CSR median strategy (25:35:41%) and occupied the entire triangle (Fig. S3h).

Some plant families were predominantly R-selected (e.g. Brassicaceae, Campanulaceae, Caryophyllaceae, Plantaginaceae; Fig. S4d,e,g,p), and others were dominated by S-selected species (Cyperaceae, Ericaceae, Juncaceae, Salicaceae; Fig. S4h,i,l,w) or were clustered around a relatively

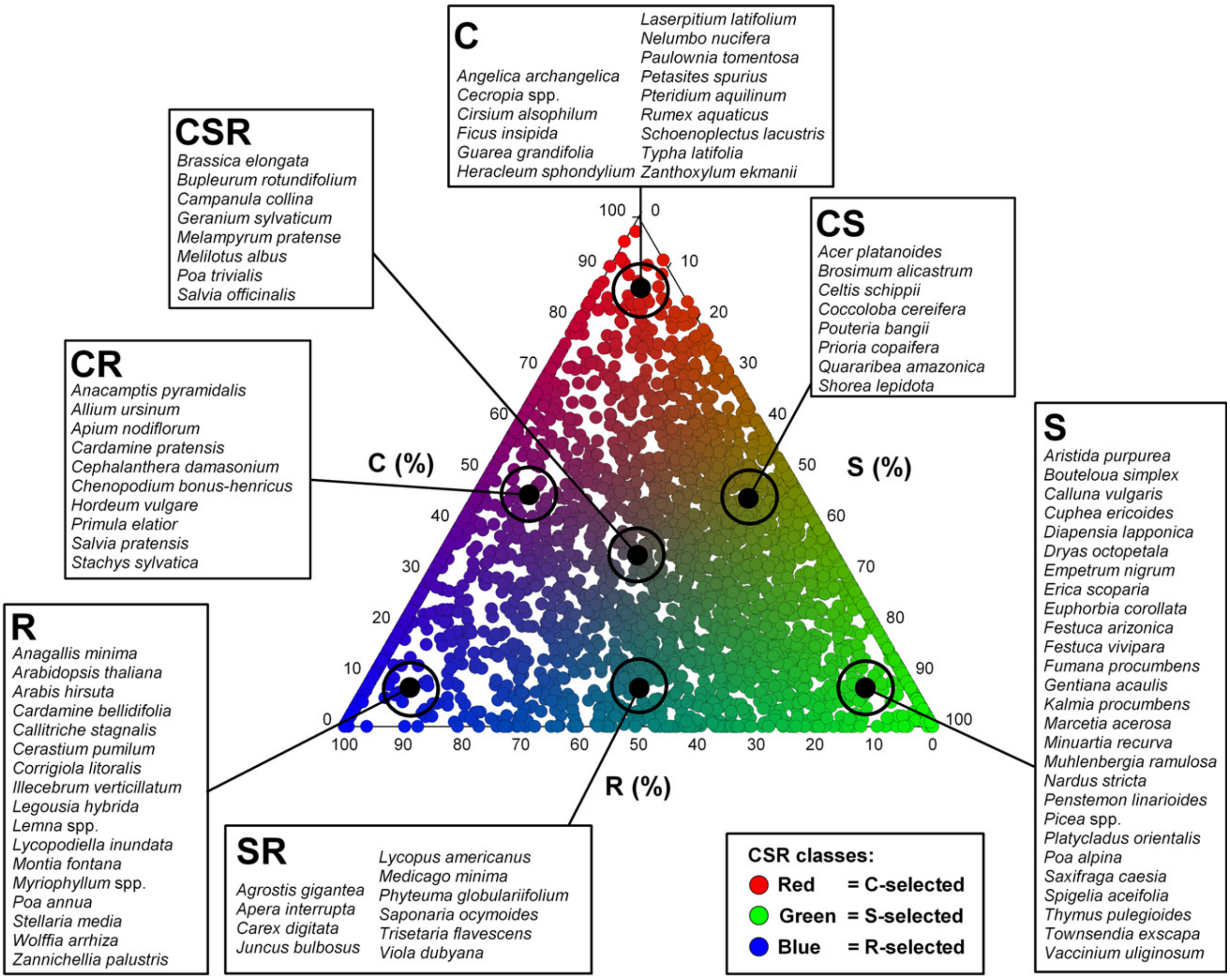


Fig. 3. Relative proportion (%) of C-, S- and R-selection for 3068 tracheophyte species measured from natural habitats across the world, using the globally calibrated CSR analysis tool 'StrateFy'. Species names represent examples of the seven secondary CSR strategy classes (C, CS, CR, CSR, S, SR and R) suggested by Grime (2001).

S-selected point (e.g. Rosaceae; 28:49:2%, S/CSR; Fig. S4u). Poaceae exhibited a median strategy of S/CSR (15:53:33%; Fig. S4q) and varied greatly between strategy extremes. A small number of families exhibited a relatively high degree of C-selection, such as Apiaceae (47:25:28%, C/CSR; Fig. S4a).

Discussion

The globally calibrated CSR analysis method allowed strategies to be determined for a wide range of vascular plant species world-wide from habitats as diverse as tropical broadleaf rain forest, desert shrublands, mangroves and alpine pasture. The use of a small number of leaf traits has the advantage that large numbers of individuals or species comprising vegetation can be rapidly measured and compared. Indeed, studies of strategy variation within and between plant communities are currently applied inconsistently due to methodological constraints and measurement issues, but many of these can now be avoided due to the simplicity of the new method. For example, Schmidtlein, Feilhauer & Bruelheide (2012) mapped CSR strategies across landscapes as a general indicator of changes in plant function across a mosaic of environments, but the traits used, and thus the overall analysis, were limited to herbaceous species and grassland vegetation. The current method will allow functional comparison of a much more inclusive set of vegetation types world-wide and will allow plant function to be considered in the broadest possible context. Despite the simplicity of the method, we have shown it to broadly represent plant functioning and to be consistent with expected patterns of plant function and along primary succession as predicted by traditional phytosociological interpretation of vegetation.

Application of the CSR analysis to biomes world-wide revealed that certain biomes are characterized by relatively functionally restricted floras (i.e. clustered within particular zones of the CSR triangle), such as tropical and subtropical grasslands (median strategy CS/CSR; Fig. 5g). Others, sometimes despite the prevalence of extreme abiotic conditions, host comparatively uniform strategy distributions and wide variation within the CSR triangle. For example,

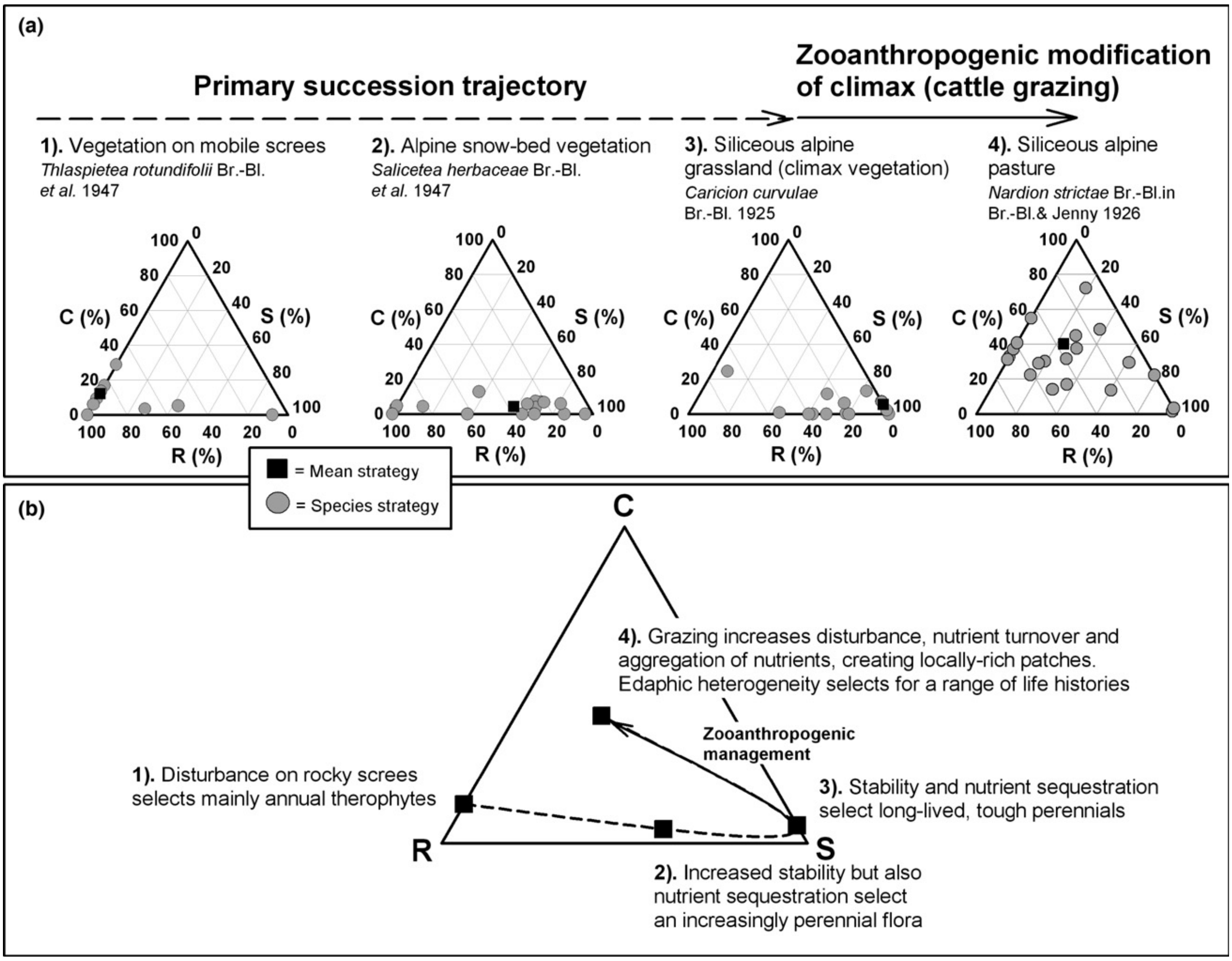
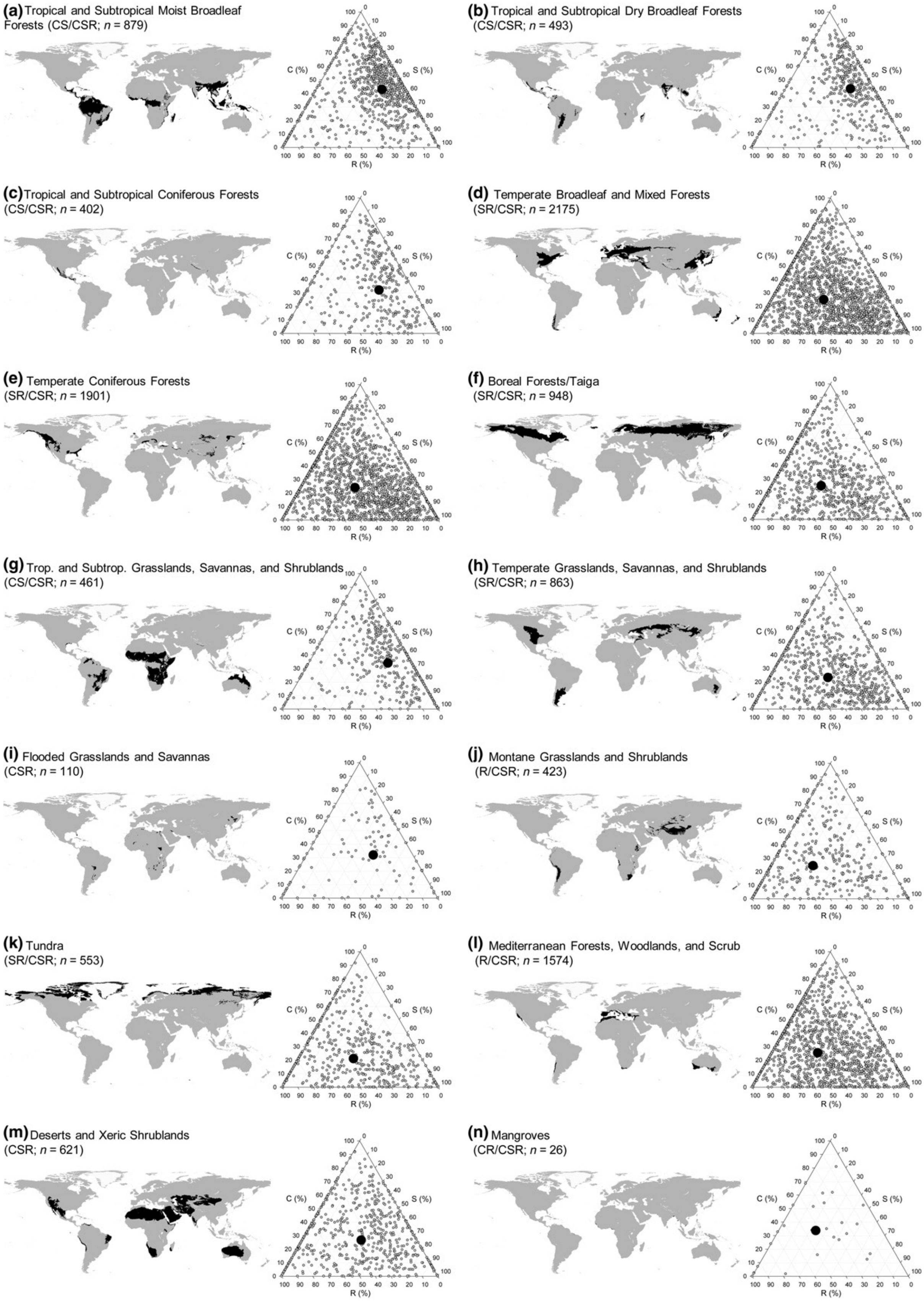


Fig. 4. An example of local application of the globally calibrated CSR analysis tool 'StrateFy' to species characteristic of phytosociological syntaxa undergoing primary succession following a trajectory from highly disturbed alpine scree slopes (*Thlasietea rotundifolii* Br.-Bl. *et al*. 1947) to siliceous grassland climax vegetation (*Caricion curvulae* Br.-Bl. 1925) further modified by cattle grazing to become alpine pasture (*Nardion strictae* Br.-Bl. in Br.Bl. & Jenny 1926). Panel (a) shows separate plant communities recognized by classical phytosociology as phases in the succession sequence, and (b) a summary of the phytosociological 'evolution' of the vegetation represented as a trajectory in CSR space. Species data represent the mean of 10 replicate measurements for characteristic species of each syntaxon measured in the central Italian Alps.

deserts and xeric shrublands (Fig. 5m) include highly contrasting CSR strategies that reflected the presence of both xeromorphic stress tolerators (e.g. *Larrea divaricata*; C:S:R = 1:99:0 %, S) and ruderal annual herbs (e.g. *Claytonia perfoliata*, 21:0:79%, R/CR; Appendix S1), some of which occupy locally humid sites (e.g. R/CR-selected *Mimulus guttatus*). The idea that biological diversity in arid environments depends on highly contrasting perennial and annual life histories, microsite differences and niche differentiation is already well-established (e.g. Chesson *et al*. 2004). The value of CSR analysis is that it provides a quantitative method for comparing plant function between sites and geographic locations where equivalent ecological roles are performed by taxonomically distinct actors, for example *L. divaricata, Cuphea ericoides* (C:S:R = 0:100:0%; S) or *Sebastiania ditassoides* (1:99:0%; S).

As a further example of the wide applicability of the method beyond herbaceous vegetation, a range of CSR strategies was evident in tropical and subtropical forest biomes, but strategies were particularly clustered around the CS region as predicted (Fig. 5). Furthermore, a trade-off was apparent between CS- and R-selection that was correlated with environmental gradients: CS-selection was associated with relatively stable situations (i.e. with less temperature seasonality) that were warmer and wetter, with greater annual precipitation and potential evapo-transpiration. Pioneer species in tropical forests were found to be relatively C-selected, such as Neotropical *Cecropia longipes* (C), *Ficus insipida* (C/CS) and *Urera baccifera* (C/CR; Appendix Table S1). Indeed, although disturbances and ruderal species are present in tropical forests, disturbance is not a prevalent factor in the same way that regular grazing or cutting determines the general character of pastures or meadows. Instabilities such as gap formation in tropical forests are local events that do not shape the forest in its entirety. Gap formation in particular is characterized by a



(a) Tropical and Subtropical Moist Broadleaf Forests (CS/CSR; *n* = 879)

(b) Tropical and Subtropical Dry Broadleaf Forests (CS/CSR; *n* = 493)

(c) Tropical and Subtropical Coniferous Forests (CS/CSR; *n* = 402)

(d) Temperate Broadleaf and Mixed Forests (SR/CSR; *n* = 2175)

(e) Temperate Coniferous Forests (SR/CSR; *n* = 1901)

(f) Boreal Forests/Taiga (SR/CSR; *n* = 948)

(g) Trop. and Subtrop. Grasslands, Savannas, and Shrublands (CS/CSR; *n* = 461)

(h) Temperate Grasslands, Savannas, and Shrublands (SR/CSR; *n* = 863)

(i) Flooded Grasslands and Savannas (CSR; *n* = 110)

(j) Montane Grasslands and Shrublands (R/CSR; *n* = 423)

(k) Tundra (SR/CSR; *n* = 553)

(l) Mediterranean Forests, Woodlands, and Scrub (R/CSR; *n* = 1574)

(m) Deserts and Xeric Shrublands (CSR; *n* = 621)

(n) Mangroves (CR/CSR; *n* = 26)

Fig. 5. Total (grey filled circles) and median (black filled circles) CSR strategies for 14 principal biomes world-wide (as defined by Olson *et al.* 2001). For each biome, median CSR category and sample size (number of species) are shown between parentheses. The distribution of each biome in the world map is denoted by black areas.

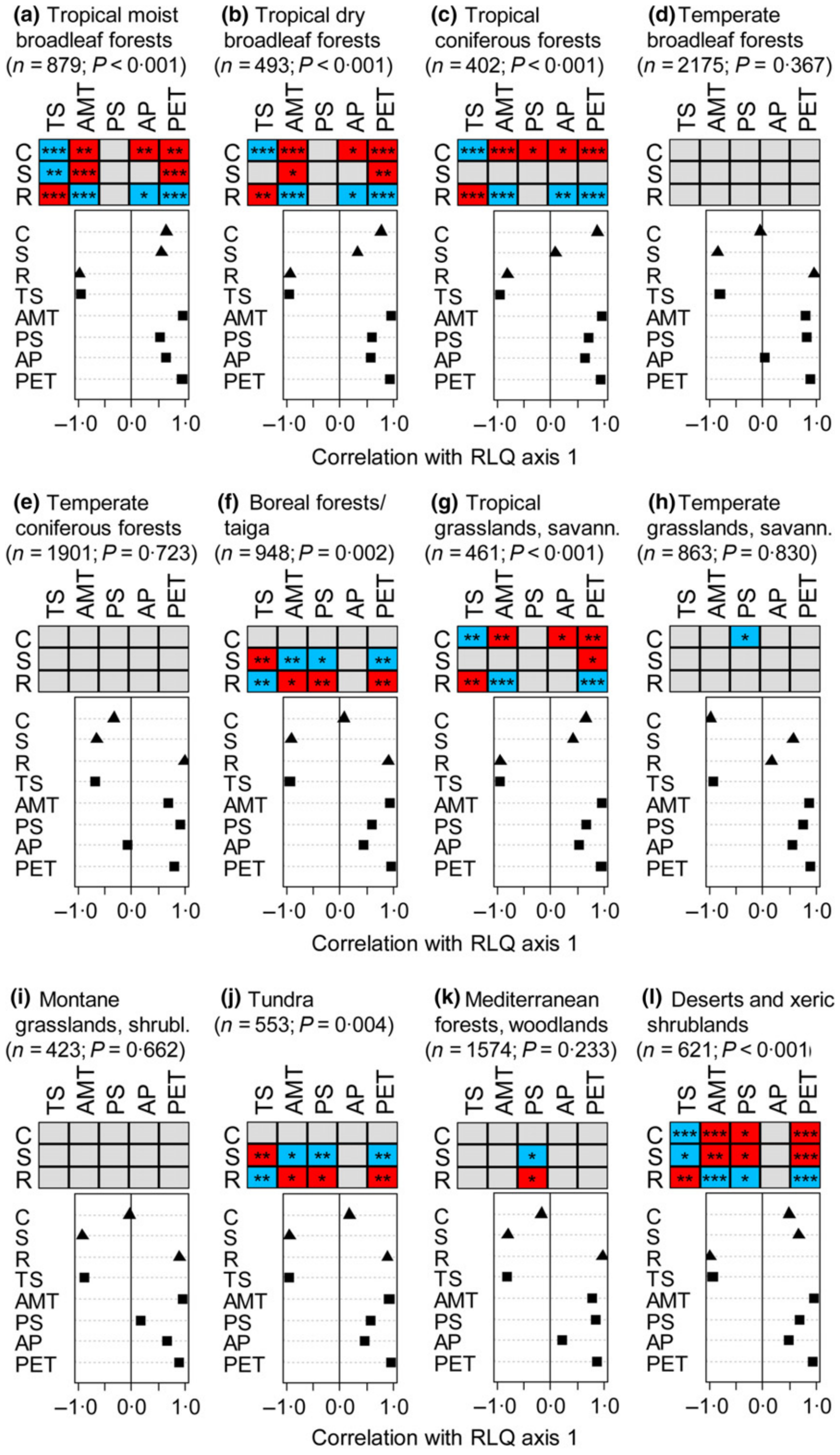


Fig. 6. Global-scale fourth-corner analysis (coloured grids) and RLQ analysis (white dot charts) of the relationship between CSR strategies and environmental variables within biomes: (a) tropical moist broadleaf forests; (b) tropical dry broadleaf forests; (c) tropical coniferous forests; (d) temperate broadleaf and mixed forests; (e) temperate coniferous forests; (f) boreal forests/taiga; (g) tropical grasslands, savannas and shrublands; (h) temperate grasslands, savannas and shrublands; (i) montane grasslands and shrublands; (j) tundra; (k) Mediterranean forests and scrub; (l) deserts/xeric shrublands. TS = temperature seasonality; AMT = annual mean temperature; PS = precipitation seasonality; AP = annual precipitation; PET = global potential evapo-transpiration). Fourth-corner statistic: red = positive, blue = negative, grey = not significant, $*P < 0{\cdot}05$; $**P < 0{\cdot}01$; $***P < 0{\cdot}001$ (*n* = number of species, *P* = significance for the overall association between C-, S- and R-selection and environmental variables).

pulse of light availability, and the ensuing competition apparently favours C-selection with succession proceeding relatively uninterrupted towards a closed tree canopy. Canopy tree species in tropical moist forest were shown to exhibit a stress tolerance component (e.g. *Brosimum alicastrum*, CS; *Platypodium elegans*, CS/CSR; *Prioria copaifera*, CS). This perhaps reflects local sequestration of resources in long-lived tissues in later successional stages (Grime 2001), or increasing adaptation to drought tolerance (Engelbrecht *et al.* 2007; Baltzer *et al.* 2008). R-selected tropical rain forest species were evident and potentially occupy specific microsites at fine scales. The high diversity of tropical forests may also partly be related to specific, single traits operating during the life cycle, such as flowering and fruiting characters and symbioses (Grime & Pierce 2012). The many and varied mechanisms proposed to explain higher diversity at low latitudes (discussed by Gaston 2000) probably apply as much to functional diversity as they do to taxonomic diversity, with geographic area and environmental stability (both seasonal and historical) being amongst the most evident factors affecting the creation of species richness.

Globally, the variation in strategies within biomes is likely to be influenced by the presence of contrasting growth forms. Forbs exhibited extremely broad strategy diversity and a generalist median strategy of R/CSR, while trees ranged from C to S, with a CS median strategy similar to the CS/CSR median strategies evident in tropical forests (Fig. S3). The presence or absence of particular strategies at a given location is also likely to be affected by historical and phylogenetic constraints, with restriction of CSR strategies evident in some families but not others (Fig. S4).

The 'strategy of a species' as presented here is an average calculated from individuals of each species sampled at a particular location. Ecotypic variation throughout the home range of a species and phenotypic plasticity could potentially broaden the range of strategy variation for a given species and is a complicating factor when CSR strategies measured at one site are assumed to be relevant to other situations. Thus, consideration of the CSR strategy of a species across a biome world-wide, as in the present study, should be interpreted with caution and should be seen as a summary or abstract for the species *in lieu* of trait data for all populations throughout the geographic range: this is the best that can be managed with current global data sets. Future detailed study of the functional differences between biomes should ideally involve replicated surveys within a range of habitat types and would be a massive undertaking involving a great deal of international cooperation and funds. Indeed, the biome-level analysis presented here was limited by the lack of available data regarding the relative abundance of species within biomes at the global scale and could not differentiate between prevalent and rare strategies. Thus, median CSR strategies for each biome were not weighted and rare species will have had a disproportionally strong influence on the median strategy. Indeed, median strategies for biomes were generally located towards the centre of the triangle (Fig. 5).

Nonetheless, just as species richness and taxonomic identities are fundamental aspects of plant diversity, 'strategy richness' and the character of the strategies present are important aspects of ecological diversity that can now easily be quantified and compared. In local-scale studies in which relative abundance has been quantified, differing degrees of dominance between CSR strategies are evident. For example, microsite differences and niche partitioning between contrasting CSR strategies have been invoked as a mechanism of coexistence and local biodiversity creation on Brazilian coastal Atlantic forest inselbergs (de Paula *et al*. 2015). Similarly, xeric sand calcareous grasslands in Europe include a mixture of relatively abundant stress-tolerator graminoids and larger numbers of infrequent ruderal or competitive-ruderal herbs, and CSR strategies are thus markedly different between dominant and subordinate plants at the centimetre scale (Pierce *et al*. 2014b). Future application of CSR analysis in further biogeographical and ecological contexts world-wide will allow general conclusions with regard to how the equilibrium between dominant and subordinate species may change in response to environmental perturbation and with regard to the precise relationships between microsite factors and particular plant species.

In conclusion, the CSR analysis tool derived from 116 979 records of leaf size and economics traits measured from 3068 species growing in nature world-wide has allowed a preliminary CSR analysis of major biome classes globally. The C, S and R values were in agreement with phytosociological observations of vegetation responses to an environmental gradient along a primary succession. Thus, the global system is consistent with earlier locally calibrated methods and studies of plant strategies and can provide a functional explanation consistent with descriptive phytosociological methods of interpreting vegetation. A unified framework now exists for ecological strategy classification, using readily determined leaf traits of plants as diverse as temperate ferns, lianas and tropical trees. The global strategy–environment relationships that the method can resolve will form a baseline for predicting which kinds of species can be expected to assemble where in response to environmental perturbation resulting from factors such as climatic or land-use changes.

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Data accessibility

All data are archived and are available from the TRY plant trait data base: www.try-db.org.

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Supporting Information

Additional Supporting Information may be found online in the supporting information tab for this article:

Fig. S1. Regressions between transformed values of a) leaf area (LA), b) leaf dry matter content (LDMC), and c) specific leaf area (SLA) and PCA axis scores for 3068 tracheophyte species from across the world.

Fig. S2. Regressions between the degree of C-, S- and R-selection (panels a, b, and c, respectively) as determined by the globally-calibrated method (*x*-axis) and the CSR analysis method of Pierce *et al*. (2013) calibrated using the Flora of Italy (*y*-axis).

Fig. S3. CSR strategies of growth habit categories for 3068 species from across the world, calculated using the globally-calibrated CSR analysis tool 'StrateFy'.

Fig. S4. CSR strategies for major flowering plant families (i.e. those most highly represented in the database; minimum 30 species), calculated using the globally-calibrated CSR analysis tool 'StrateFy'.

Table S1. Species list including authorities, life forms, biome information and CSR strategies.

Table S2. 'StrateFy', the global vascular plant CSR calculator tool in Microsoft Excel format.

An application of the CSR method to analyze plant communities of high-alpine landforms

Aims. Aim of this study is to test whether the ecological differences (e.g. soil and microclimate) among high-alpine landforms correspond to differences in morpho-functional traits (e.g. leaf parameters and CSR strategies) among their related plant communities.

Methods. Three study areas of the Italian Alps were investigated: Valle Anzasca (Monte Rosa, western Alps), Val d'Ultimo and Valle del Braulio (Ortles-Cevedale, central Alps). The areas embrace a wide range of altitudes (c. 1900–2600 m a.s.l.), substrates (silicate and carbonate rocks) and geographical contexts (from western to central Alps), but in all of them three landform categories characterized by different ecological conditions (Tampucci et al., 2016b, 2016c) and different plant communities (Tampucci et al., 2015, 2016a) can be distinguished: 1) control slopes characterized by relatively mature soils (low coarse-debris fraction, low pH, high organic matter content) and standard ground surface temperatures for the considered elevations, hosting vegetation near to the "climax"; 2) iceless debris-featured landforms (scree slopes or recent moraine) characterized by different soil features but similar ground surface temperature with respect to the control slope, hosting pioneer plant communities; 3) icy debris-featured landforms (active rock glaciers or debris-covered glacier) characterized by similar soil features but lower ground surface temperature with respect to the iceless debris-featured landform, hosting pioneer plant communities particularly cold-adapted. Our hypotesis is that landform categories differ each other in terms of plants mean leaf parameters and mean CSR strategies.

One hundred twenty-nine plant species surveys of $25m^2$ were performed throughout the investigated landforms, estimating the percentage of each plant species cover with a resolution of 5%. The following leaf parameters of each plant species was calculated: leaf area (LA), Leaf dry matter content (LDMC), specific leaf area (SLA) (Pierce et al., 2013). For each vegetation survey, the mean value of each leaf parameter was calculated weighting leaf parameter of each plant species with plant species cover. To infer the difference of mean leaf parameters among landform categories, ANOVA with Tukey's post-hoc test for multiple comparisons was performed. CSR (competitive, stress-tolerant, rueral) strategy (Grime, 1977; Grime and Pierce, 2012) was assessed for each species following the method proposed by Pierce et al. (2013). The mean CSR strategy for each landform category was finally represented through the CSR triangular diagram.

Results. Control slopes significantly differ from debris-featured landforms for higher LA, higher LDMC and lower SLA, while no significant differences occur between iceless and icy debris-featured landforms (Fig. 1, table 1). All the investigated plant communities show a general propensity for the S strategy, but those of control slopes show a remarkable C component (thus tending to an overall SC strategy), while those of debris-featured landforms show a remarkable R component (thus tending to an overall SR strategy) (Fig. 2).

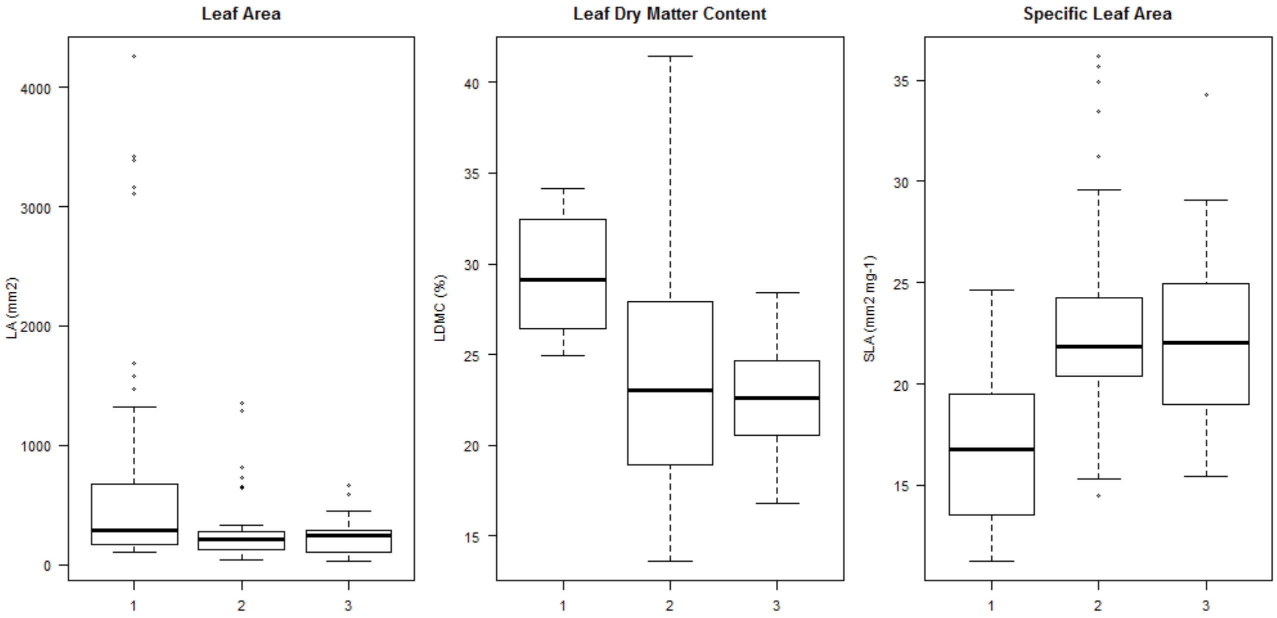

Fig. 1. Boxplot of leaf parameter mean values for each landform category: control slope (1), iceless debris-featured landforms (2), icy debris-featured landforms (3).

Leaf Area			**Leaf Dry Matter Content**			**Specific Leaf Area**		
1 vs 2	**1 vs 3**	**2 vs 3**	**1 vs 2**	**1 vs 3**	**2 vs 3**	**1 vs 2**	**1 vs 3**	**2 vs 3**
3,00E-03*	5,93E-04*	0,90	2,18E-05*	2,18E-05*	0,61	2,18E-05*	2,19E-05*	0,38

Table 1. Multiple comparisons of leaf parameters among landforms by Tukey's post hoc test. Landform categories: control slope (1), iceless debris-featured landforms (2), icy debris-featured landforms (3).

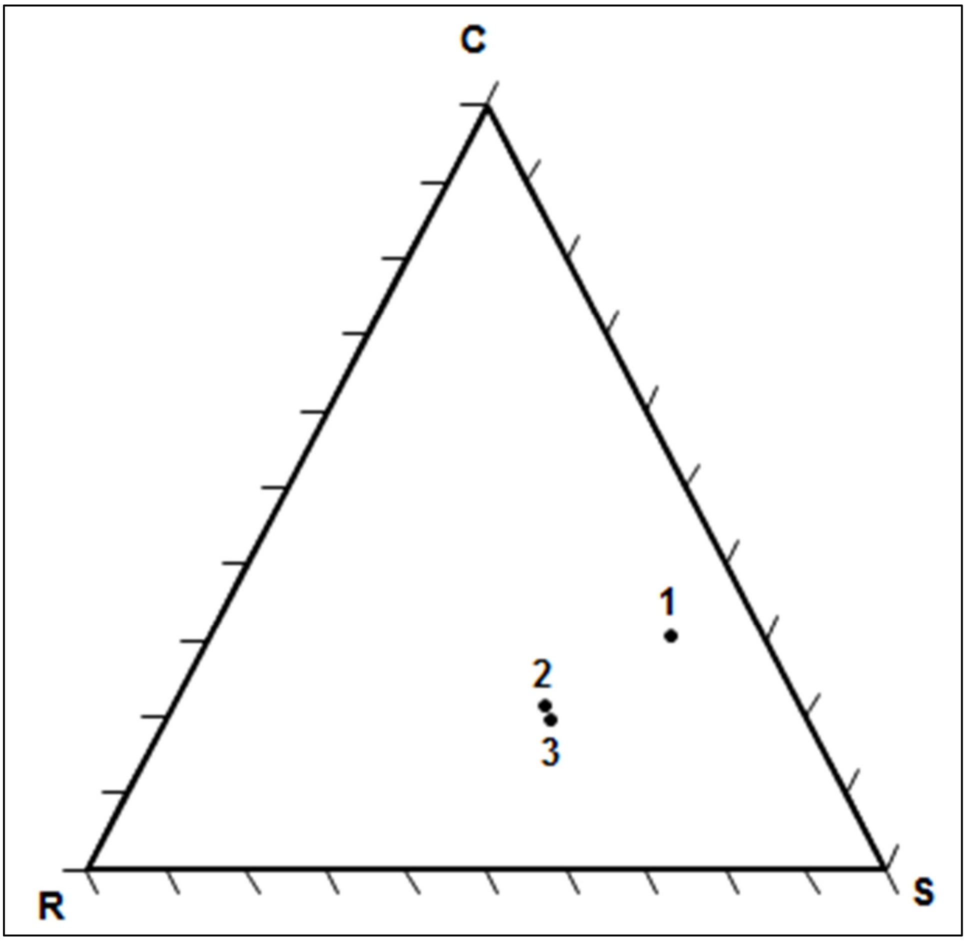

Fig. 2. Triplot representing the mean CSR strategy for each landform category: control slope (1), iceless debris-featured landforms (2), icy debris-featured landforms (3).

Discussion. Our hypothesis that landform categories differ each other in terms of plants mean leaf parameters and mean CSR strategies is supported only concerning the comparison between control slopes and debris-featured landforms as a whole. Such result suggest that in the considered context, plant functional traits are mainly driven by soil factors rather than microclimate ones. The overall weight of the S component is likely due to the harsh conditions imposed by high-alpine climate (e.g. low temperatures and brief vegetative period). The prevalence of the SC strategy on control slopes confirm the maturity of their related plant communities, according to Caccianiga et al. (2006). The prevalence of the SR strategy on debris-featured landforms suggest a relevant role of disturbance likely due to the ground instability.

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Functional diversity and life-history trait patterns of carabid beetles and spiders along a primary succession

Running title: Functional trait patterns along a glacier foreland

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Abstract. Patterns of species richness and species assemblage composition of ground-dwelling arthropods in primary successions along glacier forelands are traditionally described using a taxonomic approach. However, as applied in this research and summarized in this paper, a functional approach would ensure a better characterization of the environment highlighting the functional role of the key-organisms along the succession. This approach allows us to investigate patterns of functional diversity and life-history traits of ground beetles and spiders along a primary succession on a debris-covered glacier and its forefield. We sampled ground beetles and spiders in different successional stages, representing five stages of deglaciation. We investigated life-history traits and patterns of functional traits diversity with special focus on traits turnover. Our results showed that the studied alpine debris-covered glacier hosts ground beetle and spider assemblages mainly characterized by the following traits: walking colonisers, ground hunters and small sized species. These traits are typical of species living in cold, wet and gravelly habitats. Functional trait diversity increased along the succession, and life history traits follow the “addition and persistence model” since most traits are not mutually exclusive along the succession, thus there is no turnover, but addition of new traits and variation in their proportion within each species assemblage along the succession. Ground beetles distribution along the primary succession seems to be driven by foraging strategies while the spiders distribution is triggered by both dispersal ability and foraging strategies. This is the first study to measure different components of functional diversity of ground-dwelling arthropods in response to glacier retreat. The proposed functional approach improves our knowledge on the adaptive strategies of ground-dwelling arthropods in colonising glaciers surface and recently deglaciated terrains; landforms that are quickly changing due to the current global warming.

Key-words: Araneae, Carabidae, debris covered glacier, dispersal, glacier foreland, turnover

Introduction

Two of the main visible effects of climate warming on alpine areas are glacier retreat and increasing supraglacial debris on glacier surfaces (e.g. Citterio *et al.,* 2007; Paul *et al.,* 2007). Several studies describe the structural changes (species richness trends and species turnover/persistence) in ground-dwelling arthropod assemblages along the primary succession on recently deglaciated areas (i.e. glacier forelands) (see Hagvar 2012). Spatial distribution of ground-dwelling arthropods is predominantly determined by site age (time since deglaciation), with additional influence from local fine-scale environment conditions, like soil grain size, vegetation cover and soil organic matter. These environmental factors are usually function of the time since deglaciation (see. Kaufmann 2001, Tampucci *et al.,* 2015). More recently, attention has been moved from the glacier forelands to the surface of debris-covered glaciers, since it has been highlighted that debris covered glaciers are suitable habitats for micro- meso- and macro-fauna and plant life (Caccianiga *et al.,* 2011; Gobbi *et al.,* 2011; Azzoni *et al.,* 2015). Debris-covered glaciers are formed by frequent slipping and casting of deposits creating large quantities of stony material which covers the glacier surface, in particular on the ablation area (Citterio *et al.,* 2007), and they significantly increased during the last decade. Arthropod distribution on debris covered glaciers is mainly determined by rock grain size, debris thickness, glacier movements/instability, and microclimate conditions (Gobbi *et al.,* 2011). Traditionally, a taxonomic approach was used to describe ground-dwelling arthropod assemblages along primary successions (e.g. Kaufmann 2001, Gobbi *et al.,* 2006, Vater, 2012), in contrast to the functional trait approach to understanding ecosystem complexity and dynamics (Diaz & Cabido, 2001; Losapio *et al.,* 2015). A possible explanation regards the lack of knowledge about species traits of many taxa and whether these traits are sensitive to environmental changes occurring in harsh environments. Ground beetles (Coleoptera: Carabidae) and spiders (Arachnida: Araneae) can be considered as one of the most important meso- and macro-fauna living on recently deglaciated terrains in terms of species richness and abundance (Hagvar 2012). Carabid beetles and spider life-history traits along environmental gradients are quite well known in terms of species traits type (e.g. Schirmel *et al.,* 2012) and response traits (*sensu* Díaz *et al.,* (2013) i.e. traits that impact an individual's capacity to colonise and persist in a habitat). On the other hand, there are no studies involving both spider and ground beetle life-history traits that describe, via a functional approach, the ground-dwelling arthropod functional diversity and life-history traits turnover along a primary succession on glacier forelands and on the glacier surfaces. In the present study, we described carabid beetle and spider functional diversity patterns on an alpine debris-covered glacier and along its glacier foreland. In particular, we hypothesize that (i) the functional diversity of carabid beetles and spiders increases with time since deglaciation and that (ii) time since deglaciation triggers the turnover of life-history traits. To test these hypotheses we use well-established response traits as well as new functional traits never used previously in studies of primary successions.

Material and Methods

Study area

The study was carried out on the glacier foreland of Vedretta d'Amola glacier (Adamello-Presanella Group, Central-eastern Italian Alps, 46°13'12"-10°41'02) (Fig. 1), a debris-covered glacier of about 82.1 hectares (area recorded in summer 2012), covered for 2/3 by stony debris with variable depth, from a few centimeters to about one meter.

The glacier foreland is about 1.23 km long, covers an altitudinal range of about 150 meters, and is characterized by a large moraine system dating back to the Little Ice Age (LIA, c. AD 1850). Field observations and various sources including maps, reports, aerial photographs, iconography, and records of length change collected over the last 100 years allowed to reconstruct the glacier tongue position during the LIA, in 1925, in 1994, and in 2003 (Fig. 1).

The snow-free period usually lasts from late June to September. Annual mean ground temperature on the glacier foreland, recorded during the period 15 July 2011 – 14 July 2012, was 3.1 °C, while mean relative air humidity was 94.3% (datalogger located at about 15 cm depth in the stony debris at plot 10, see Fig.1). The mean annual temperature on the supraglacial debris was 0.5 °C (datalogger located at 10 cm depth in the supraglacial debris at site 2, see Fig. 1).

On the supraglacial debris (mean elevation: 2642 m asl) the pioneer plant community (total plant cover <10%) is dominated by *Cerastium uniflorum*, *C. pedunculatum*, *Saxifraga oppositifolia*. On the glacier foreland (mean elevation: 2520 m asl) the plant community (plant cover ranging from 5% to 70% along the foreland) is dominated by *Poa alpina*, *P. laxa*, *Saxifraga bryoides*, *Geum reptans*, *Luzula alpino-pilosa*. Outside the glacier foreland (mean elevation: 2426 m asl), Late Glacial sites are occupied by *Carex curvula*-dominated communities with >80% ground cover.

Sampling design

We selected eleven sampling plots located along a linear transect starting on the glacier surface and ending on Late-glacial substrata outside the LIA moraines (Fig.1). We assigned to each plot a class of deglaciation: Class 0 (not yet deglaciated – glacier surface; plots 1, 2, 3, 4), Class 1 (areas deglaciated in the period 1994-2003; plots 5, 6), Class 2 (1925-1994; plots 7, 8), Class 3 (1850-1925; plots 9, 10), and Class 4 (Late Glacial Period; plot 11) (Fig. 1). Plots were selected on the base of the following three criteria: (i) areas not subjected to physical disturbance, (ii) detection probability of the considered species (e.g. on the glacier surface – class 0 – we located four plots due to the low species detection probability (see Gobbi *et al.,* 2016).

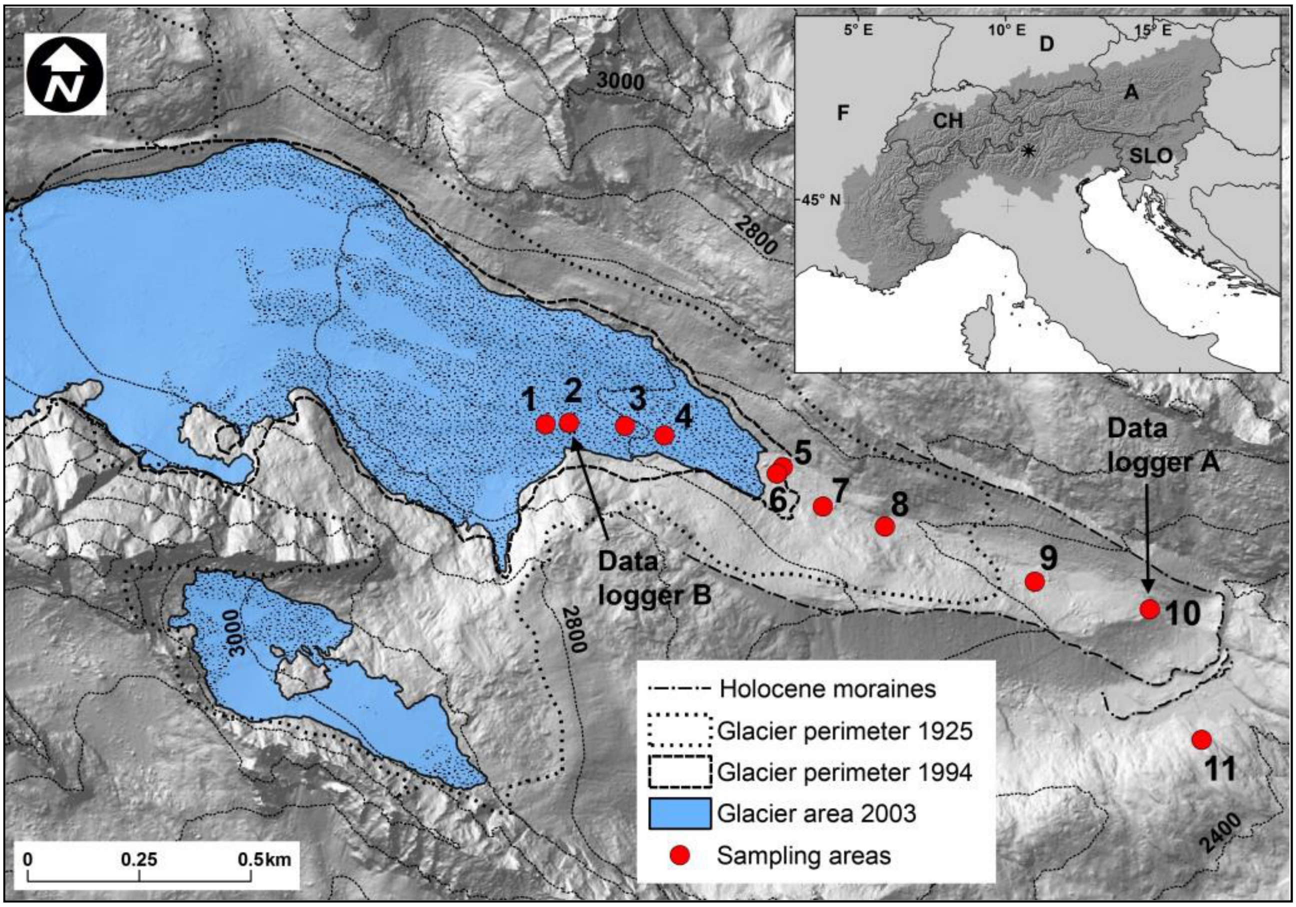

Figure 1. Geographic location of the sampling plots in relation to the chronosequence of glacier retreat. Plots 1, 2, 3, 4 = Class 0 (not yet deglaciated – glacier surface); plots 5, 6, = Class 1 (areas freed by the glacier in the period 1994-2003); plots 7, 8 = Class 2 (1925-1994); plots 9, 10 = Class 3 (1850-1925); and plot 11 = Class 4 (Late Glacial Period).

Sampling method

Carabid beetles and spiders were sampled by means of pitfall traps (Eymann *et al.,* 2010). In each plot three traps were located about 10 m apart, which led to a total of 33 pitfall traps. Traps consisted of plastic vessels (7 cm of diameter and 10 cm of height) baited with a mixture of wine-vinegar and salt. The traps were active over the entire snow free seasons, from early July to late September 2011-2012. Plots 2, 4, 5, 8 and 10 were studied in year 2011, whereas plots 1, 3, 6, 7, 9 and 11 were studied in 2012. Samples were taken at 25-day intervals. Nomenclature refers to the checklist of the European Carabid beetles Fauna (Vigna Taglianti, 2004) and to The World Spider Catalogue (WSCA, 2016)

Environmental variables

We recorded abiotic (percentage of gravel, soil pH, and soil organic matter) and biotic (plant species richness and vegetation cover) variables within a buffer of 1 m around each trap.

A substrate sample of 1–2 kg was taken at every plot for particle size distribution. Two hundred grams of substrate were sampled at each pitfall trap for organic matter content analysis (Walkley–Black method: Walkley & Black, 1934) and pH measurement. All the soil samples were taken at the surface. We recorded plant cover using a 50 cm diameter metal circle placed at the four opposite sides of the pitfall trap. Vascular plants, bryophytes, and ground lichens occurring within the plot were recorded; the overall vegetation cover and that of every species were visually estimated with a resolution of 5%. The mean values from the four 50 cm samplings was calculated to obtain a single value associated with each trap. For each plot, environmental variables recorded around the three pitfall traps were averaged.

Functional traits

Carabids. We considered the following well-established response traits of primary succession (Gobbi *et al.,* 2010; Schirmel *et al.,* 2012): dispersal ability (flying dispersers = winged species; ground dispersers = wingless species); diet (omnivorous, carnivorous), and mean body length (millimeters) of the pool of species in each plot. We analyzed for the first time along primary succession the following traits: larval hunting strategy (surface runner, surface walker, soil pore explorer) and adult hunting strategy (zoospermophagous, olphactory-tactil predator, visual predator). Data about species traits were obtained on the base of specialized literature (Hůrka 1996; Brandmayr *et al.,* 2005; Homburg *et al.,* 2014) (Table 1).

Spiders. We considered the following response traits: adult dispersal ability (flying dispersers = ballooners; ground dispersers = walkers); hunting strategies (ground hunters, sheet web weavers, other hunters) and mean body length (millimeters) of the pool of species in each plot. Traits were gathered on the base of Spiders of Europe (Nentwig *et al.,* 2016) and specific information on ballooning was derived, whenever possible from literature (Bell *et al.,* 2005; Blandenier, 2009). We assigned functional traits according to Cardoso *et al.,* (2011). In this respect, the mixed guild “other hunters” — small sheet web weavers and stalkers — includes in our case, Linyphiidae belonging to the subfamily Erigoninae (Salticidae are represented by one single species, and two individuals) (Table 1).

For each plot, we calculated the proportion of each trait within the community.

Data analysis

Environmental variables. Due to the high number of environmental variables recorded on the field we performed a preliminary correlation analysis in order to minimize multicollinearity-related problems on the estimate of the regression model parameters (Legendre & Legendre 2012). Time since deglaciation, vegetation cover, plant species richness, soil gravel percentage, pH and organic matter resulted highly correlated (Spearman's rho > 0.9 in all cases except one – time since deglaciation vs pH - where it is > 0.7; Table S1). Thus, time since deglaciation was considered the sole explanatory variable in further regression analysis. This was concluded because time since deglaciation is the only variable that may influence the others, with a positive influence on plant species richness, percentage of vegetation cover, organic matter content and a negative influence on pH and gravel percentage. Furthermore, time since deglaciation was described as the main variable influencing carabid and spider primary succession along glacier forelands (see Hagvar, 2012).

Functional Diversity. To quantify the functional diversity of carabid and spider assemblages along the succession, we computed four functional diversity indices, both for carabids and spiders: functional richness, functional evenness, functional dispersion, Rao's quadratic entropy. These functional diversity indices are indicators of community assembly processes (Mason *et al.,* 2012). Functional richness (FRic) is the number of functionally singular species, measured as a number of unique trait value combinations (Villegèr *et al.,* 2008). Functional evenness (FEve) describes both the evenness of abundance distribution and the distances between species in the functional trait space, weighted by species relative abundance (Villegèr *et al.,* 2008). This index was not calculated for sites with less than three functionally singular species. Functional dispersion (FDis) estimates the dispersion of the species in the multidimensional trait space, calculated as the weighted mean distance of individual species in the traits space to the weighted centroid of all species, accounting for species relative abundance (Laliberté & Legendre 2010). Rao's quadratic entropy (RaoQ) expresses the mean distance between two randomly selected individuals, it is affected by species diversity, univariate trait distribution and the covariance between traits (Botta-Dukát, 2005). RaoQ quantifies both the distribution of functional units in functional space and the volume occupied in the functional space, thus it incorporates the previous functional diversity components linked to community assembly (Mason *et al.,* 2012). In plots 1 and 2 of the class 0 no carabids were collected; thus, these two sites were excluded when calculating the indices to the carabid community. We computed functional diversity using FD R package version 1.0-12 (Laliberté *et al.,* 2014).

Species traits distribution. We analysed carabid and spider traits turnover or 'persistence' along the succession according to the descriptive analysis proposed by Vater (2012) and Vater & Matthews (2013, 2015). Specifically, we analysed three community parameters for each class of deglaciation: (1) total functional traits (number of functional traits at plot level), (2) functional traits first appearances (number of functional traits appearing for the first time along the succession, including first-and-last appearances), (3) functional traits last appearances (number of functional traits appearing for the last time along the succession, including first-and-last appearances).

Statistical analysis. Given that parametric tests could not be properly employed because some assumptions were not met (e.g. homoscedasticity was violated and some response variables were not normally distributed), we used Generalized Linear Regression Models (GLMs) in order to detect possible differences in functional diversity indices and life-history trait composition among successional stages. Specifically, GLMs were fitted including functional diversity indices and species traits as response variables and the class of deglaciation as explanatory variable. Results were reported in terms of: (1) p-values, adjusted using the Bonferroni correction, and (2) multiple comparison between means for all the possible pairs of class of deglaciation (Wald test). In the case of presence of mutually exclusive trait (e.g. dispersal ability: ballooners vs no-ballooners) the GLM was performed considering only one trait (e.g. ballooners). Functional diversity indices were described by Gaussian distribution except for carabids FDis and RaoQ that are better described by a Gamma distribution. The proportion of each species trait in each plot was arcsin(sqrt(x)) transformed to achieve a satisfactory approximation of the Gaussian distribution.

The proportion of adult carabid hunting strategies with each class of deglaciation were not tested by the GLM since all the species except two (*Amara erratica* and *Notiophilus biguttatus*) are olphactory-tactil predators, in the same way that adult feeding guilds were not tested since all species except one (*Amara erratica*) are carnivorous (see. Tab. 1). The proportion of carabid species with spermophagous larvae was not tested by the GLM since all specie except one are carnivorous, thus we tested only the proportion of spermophagous individuals in each site. The spider hunting guild "other hunter" proportion was not tested by the GLM because belonging only to three species, and eight individuals.

Results

Functional diversity

Carabids (see. Fig 2 and Tables S2). FRich, FEve, FDis increased significantly along the age gradient as described by the four the classes of deglaciation (FRich: Wald test = 78.6; p<0.0001; FEve: Wald test = 495.0; p<0.0001; FDis: Wald test = 11.27; p<0.01). RaoQ differed significantly (Wald test = 42.13; p<0.0001), however without a clear trend.

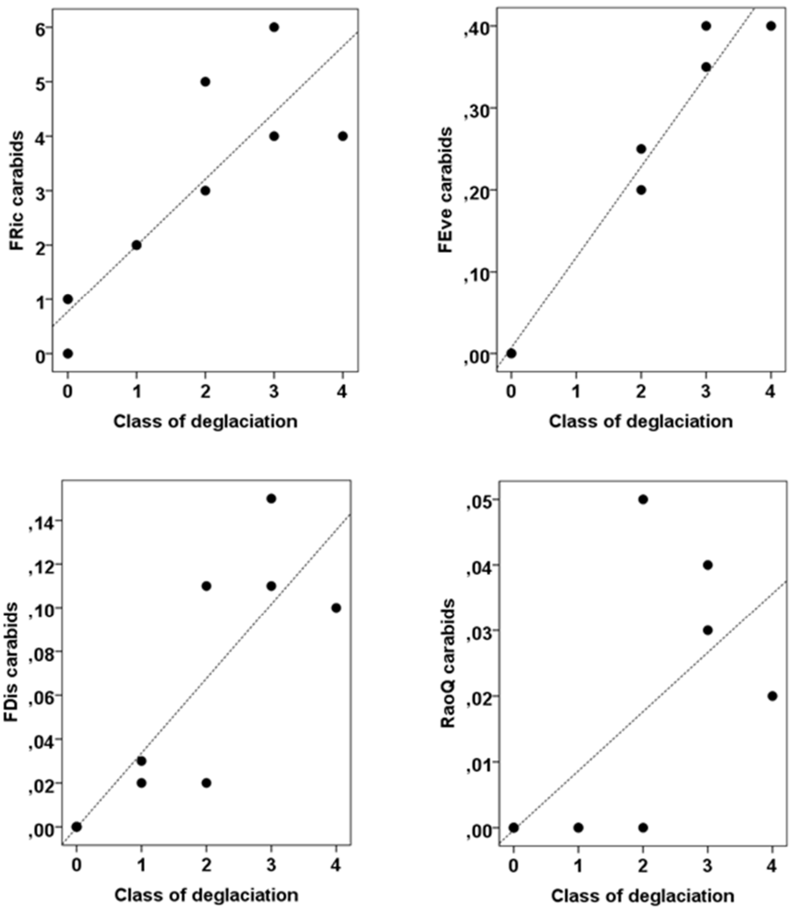

Figure 2. Functional diversity indices of carabid beetles among the classes of deglaciation. Differences were tested using GLM. Only variables significantly different among stages are shown. The dashed line represents the overall regression line.

Spiders (see. Fig 3 and Tables S3). FRich changed significantly between classes of deglaciation (Wald test = 36.27; p<0.0001). Classes 0 and 1 showed significantly lower FRich values with respect to the classes 2-4. FEve changed significantly across the study sites (Wald test = 22.51; p=0.0001).Class 0 and Class 4 showed significantly lower and higher FEve with respect to all other classes of deglaciation. FDis and RaoQ did not differ between classes of deglaciation.

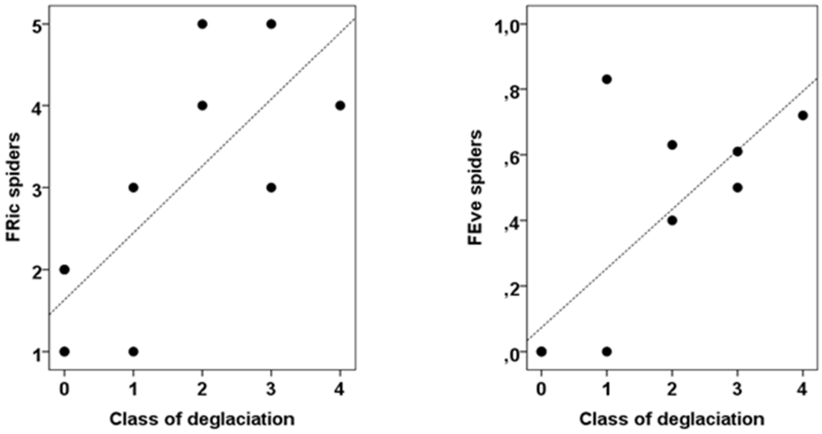

Figure 3. Functional diversity indices of spiders among the classes of deglaciation. Differences were tested using GLM. Only variables significantly different among stages are shown. The dashed line represents the overall regression line.

Life history traits

Carabids (see. Fig 4 and Tables S2). The proportion of species and individuals with surface walking larvae changed significantly between classes od deglaciation (surface walkingr species: Wald test = 329.87; p< 0.0001; surface walking individuals: Wald test = 84.36; p<0.0001). Specifically, surface walking larvae appeared in Class 2 and increased significantly until Class 4. The proportion of species and individuals with surface running larvae did not differ significantly. The proportion of soil pore exploring species and individuals changed significantly with classes of deglaciation (species: Wald test = 20.45; p<0.0001; individuals: Wald test = 116.53; p<0.0001), but their presence is limited to classes 2 and 3. The spermophagous (Wald test = 10.67; p=0.031); only appeared in Class 2.

The proportion of wingless species and individuals did not change significantly with the classes of deglaciation. The mean body length however, increased significantly (Wald test = 16.35; p<0.003).

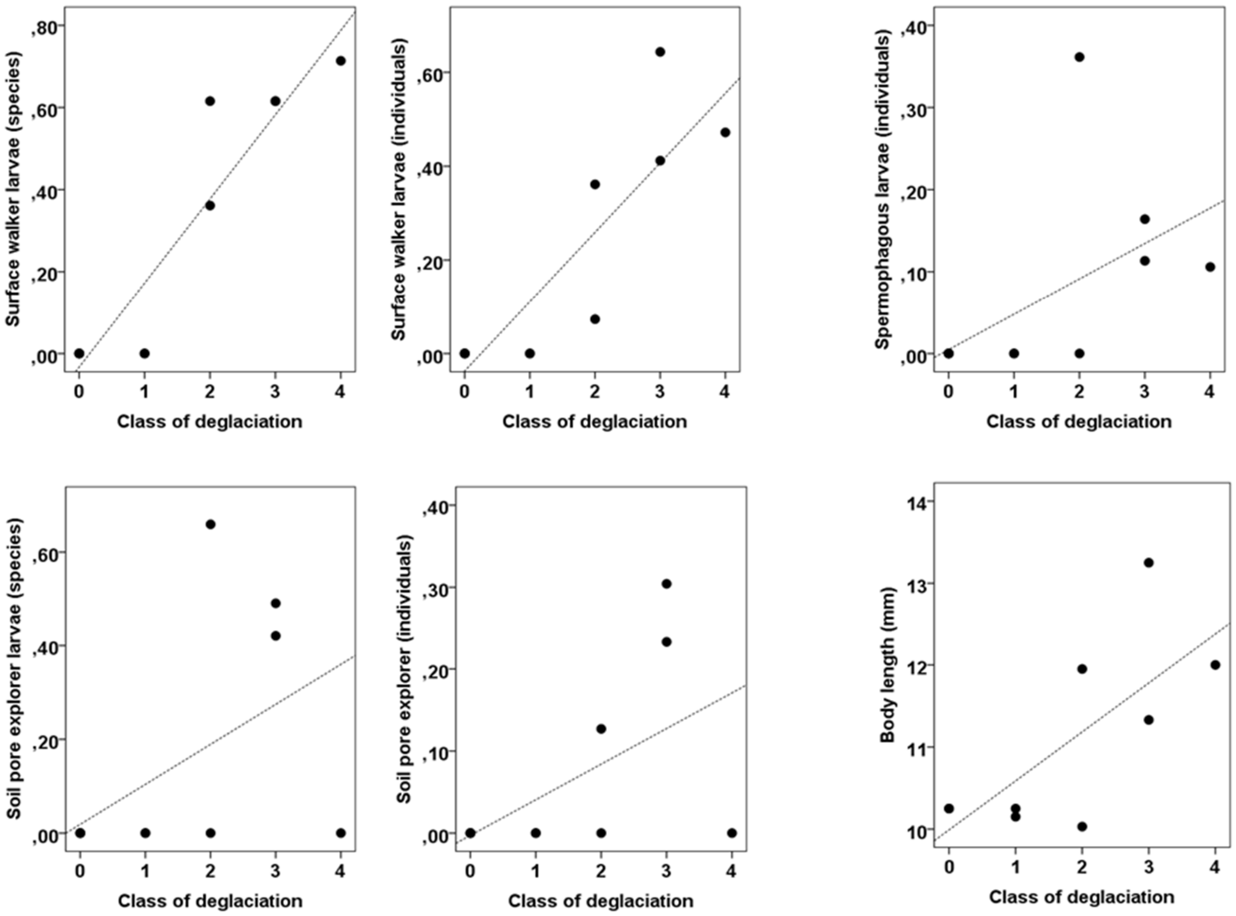

Figure 4. Proportion (arcsin(sqrt(x)) transformed) of species and individuals of life-history trait categories of carabid beetles, and mean body size along the glacier foreland. Differences were tested using GLM. Only variables significantly different among stages are shown.

Spiders (see. Fig 5 and Tables S3). The proportion of ground hunter species changed significantly with increasing age as reflected across Classes 0-4 (Wald test = 14.86; p=0.005). Class 0 showed significantly higher values with respect the other classes; Class 1 showed lower values respect to the Classes 2-4. The proportion of ground hunting individuals did not show any pattern of change.

Again, sheet web weaver species showed no clear pattern whereas, the proportion of sheet web weaver individuals changed significantly (Wald test = 23.55; p<0.0001) with site age. Specifically, the highest values were reached in Class 0 and the lowest values in Class 1. This was then followed by an increase.

The proportion of high dispersal species (ballooners) and individuals decreased significantly with site age (species: Wald test = 15.6; p=0.004; individuals: Wald test = 36.29; p=0.0001). The highest proportion of high dispersal species was found in the Class 0 and 1.

The mean body length increased significantly (Wald test = 21; p<0.0001) with the site age gradient .

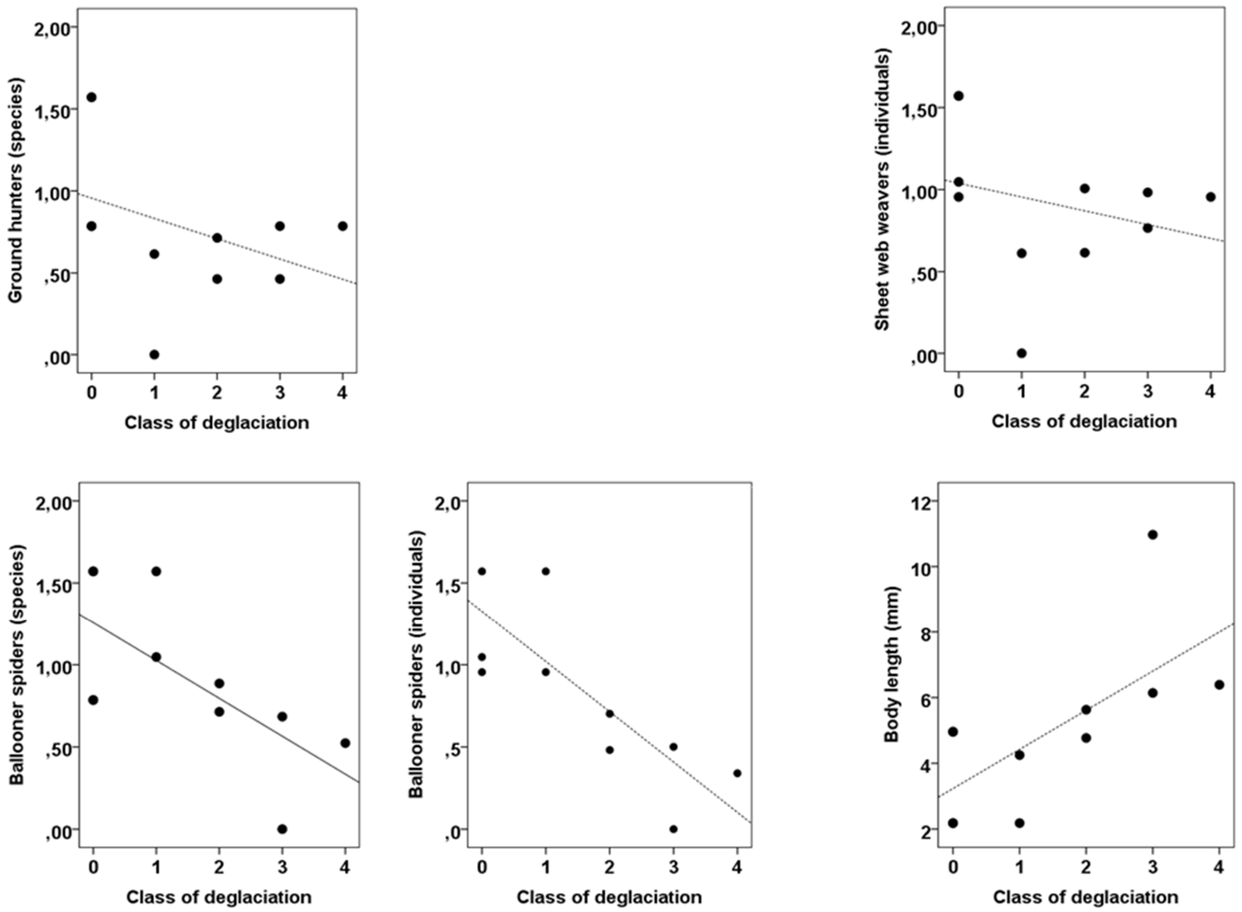

Figure 5. Proportion (arcsin(sqrt(x)) transformed) of species and individuals of life-history trait categories of spiders, and mean body size along the glacier foreland. Differences were tested using GLM. Only variables significantly different among stages are shown. Only variables significantly different among stages are shown.

Species traits distribution

Carabids. The total number of functional traits increased among classes of deglaciation until the Class 3, then slightly decrease in class 4. Functional traits first appearances tend to decrease with site age with the exception of Class 2. No last appearances occurred until Class 3, where a single functional trait disappeared (Fig.6A).

Spiders. The total number of functional traits followed a concave pattern, with the lower values in Class 0 and 4 and the higher values in Class 1, 2 and 3. Functional trait first appearances regularly decreased along the deglaciation gradient as reflected from Class0-4, while the only one last appearance occurred in Class 3 (Fig. 6B).

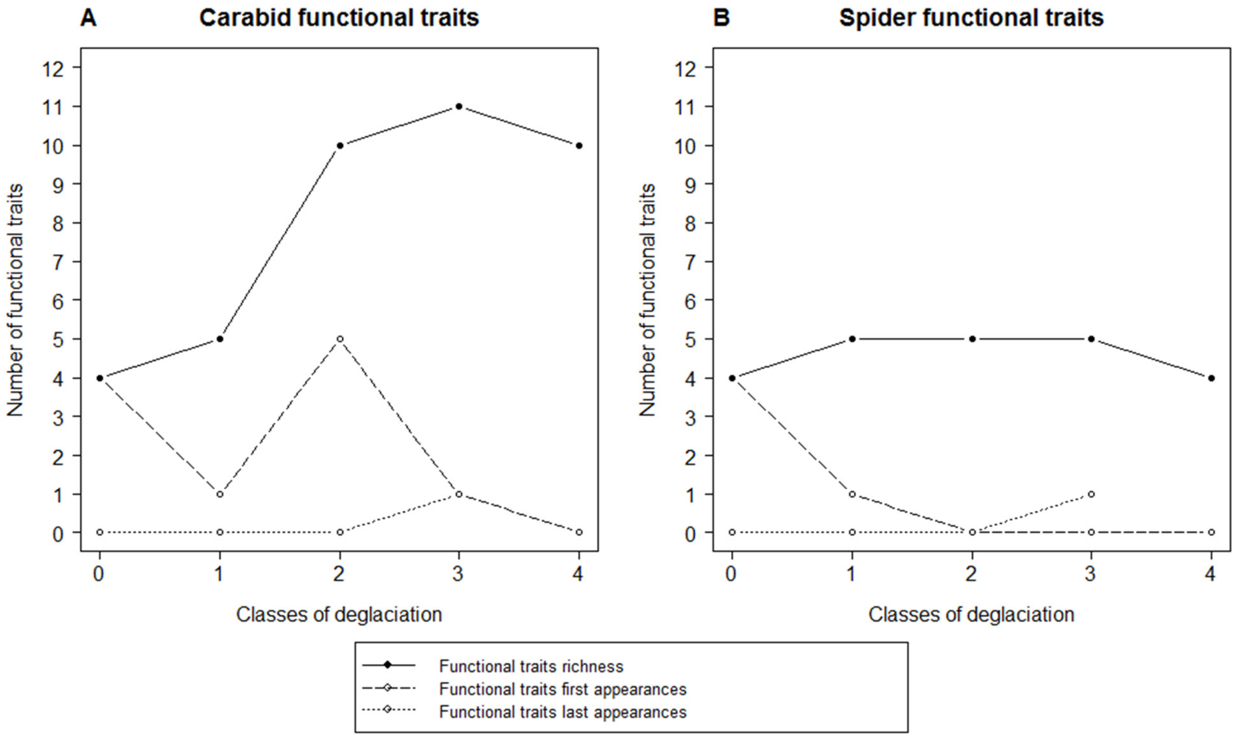

Figure 6. Functional trait richness and functional trait first and last appearances among the classes of deglaciation; (A) carabids, (B) spiders.

Table 1. List of the sampled carabids and spiders and their life-history traits.

Carabid beetles	**Dispersal ability**	**Adult hunting strategies**	**Larval hunting strategies**	**Diet**
Amara erratica	winged	zoospermophagous	spermophagous	Omnivorous
Carabus adamellicola	wingless	olphactory-tactil predator	surface walkers	Carnivorous
Carabus depressus	wingless	olphactory-tactil predator	surface walkers	Carnivorous
Cychrus attenuatus	wingless	olphactory-tactil predator	surface walkers	Carnivorous
Nebria germari	wingless	olphactory-tactil predator	surface runner	Carnivorous
Nebria jockischii	winged	olphactory-tactil predator	surface runner	Carnivorous
Notiophilus biguttatus	wingless	visual predator	surface runner	Carnivorous
Oreonebria angustata	wingless	olphactory-tactil predator	surface runner	Carnivorous
Oreonebria castanea	wingless	olphactory-tactil predator	surface runner	Carnivorous
Platynus teriolensis	wingless	olphactory-tactil predator	surface walkers	Carnivorous
Princidium bipunctatum	winged	olphactory-tactil predator	soil pore explorer	Carnivorous
Pterostichus multipunctatus	wingless	olphactory-tactil predator	soil pore explorer	Carnivorous
Trechus tristiculus	wingless	olphactory-tactil predator	soil pore explorer	Carnivorous
Spiders	**Dispersal ability**	**Hunting strategies**		
Acantholycosa pedestris	ground disperser	ground hunter		
Arctosa alpigena	ground disperser	ground hunter		
Coelotes pickardi tirolensis	ground disperser	sheet web weaver		
Diplocephalus helleri	ballooner	other hunter		
Drassodex heeri	ground disperser	ground hunter		
Erigone dentipalpis	ballooner	other hunter		
Meioneta rurestris	ballooner	sheet web weaver		
Mughiphantes handschini	ballooner	sheet web weaver		
Oreonetides glacialis	ballooner	sheet web weaver		
Pardosa nigra	ground disperser	ground hunter		
Pardosa oreophila	ground disperser	ground hunter		
Sitticus longipes	ground disperser	other hunter		
Tenuiphantes monachus	ballooner	sheet web weaver		

Discussion

Species and their life-history traits on the debris-covered glacier

Debris-covered glaciers with their tongue descending below the treeline can host arthropod life on their surface (Gobbi *et al.,* 2011). Our study demonstrated that a debris-covered glacier with its tongue located above the treeline, is also capable of hosting arthropods. Specifically, we collected three different ground-dwelling arthropod species on the glacier: the carabid beetle *Nebria germari*, the wolf spider *Pardosa nigra* and the lyniphiid spider *Meioneta rurestris*. Both *N. germari* and *P. nigra* are walking colonisers with low dispersal ability, as the former is wingless and the latter is not ballooner, at least at the adult stage. Both species are ground hunters; specifically, *N. germari* is an olphactory-tactil predator with nocturnal foraging habits, while *P. nigra* is a visual predator with diurnal foraging habits. Therefore, the niche competition is reduced for these two species as they feed on similar prey, mainly collembolan and other insects (Raso *et al.,* 2014) transported as aeroplankton (Hagvar, 2012). Given the collection of juvenile instars on the glacier, it seems likely that both species complete their life cycle on the ice.

The spider *Meioneta rurestris* is a widespread spider in Europe and its presence on the glacier is likely to be a result of its ability to quickly colonise pioneer habitats (Meijer, 1977). For this species however, we have no evidence of its ability to reproduce on the glacier, although we may assume this.

Functional diversity

Functional diversity patterns along the primary succession revealed community assembly processes in accordance with Mason *et al.,* (2012, 2013) and Mouchet *et al.,* (2010). For both carabid and spider assemblages, increasing FRic along the succession indicates an increasing influence of niche complementarity on species occurrence and community structure (Mason *et al.,* 2013). FEve is maintained along the succession for both carabid and spider assemblages. The observed trends reflect those observed in a study carried out on the same area, which showed an increase in flower-visiting insect functional diversity along the plant primary succession (Losapio *et al.,* 2015). The observed patterns in functional diversity indices provide evidence that environmental factors, such as vegetation cover and soil features, limit the presence of certain life-history traits. The magnitude of this habitat filtering process (*sensu* HilleRisLambers *et al.,* 2012: environmental factors limiting the occurrence of species without certain traits) decreased along the succession, thus yielding more functionally diversified communities.

RaoQ trends of carabid communities indicate functional divergence in assemblages (i.e. became more dissimilar) during the first part of the succession, while in late-succession stages, species assemblages converge (i.e. became more similar) in their life-history traits. This pattern suggests that mechanisms of community assembly and species coexistence change along the succession, and the importance of differentiation in life-history traits depends on the successional stage. In particular, niche differentiation and complementarity appear to increase in relation to ecosystem maturity and complexity along the glacier foreland. On the other hand, habitat selection and competition, causing functional traits redundancy and convergence, may be more influential in the more homogeneous sites of the late succession, where species with similar traits are more likely to coexist (Mason *et al.,* 2012).

Species traits distribution

Traits distribution analysis revealed that on the glacier (Class 0) and during the first stage of deglaciation (Class 1) the early successional carabid assemblages were characterized by species with the following features: surface running larvae, mainly wingless species, olphactory-tactil predators, and small size.

Surface running larvae are probably linked to the gravelly soils of the early successional stages, as they are effective at capturing preys in these refuge-rich sites. Accordingly to this hypothesis, species with soil exploring larvae (i.e. small larvae living into the soil (Brandmayr *et al.,* 2005)) appeared in the mid- and late-successional stages, where the habitat maturity should sustain several species of prey that live in the soil and have a low ability to escape (e.g. earthworms, flies larvae).

After 20 years since glacier retreat (Class 1) until the late successional stages (Class 3-4) all larval hunting strategies (surface walkers, surface runners, soil pore explorers, spermophagous), adult diet types (carnivorous, omnivorous) andwing statuses (wingless and winged) were represented and persisted along the glacier foreland. Therefore, in contrast to our expectations, the proportion of wingless and carnivorous species did not increase along the succession. This result contrasts the pattern found in other glacier forelands where wingless species results are linked to stable and mature environments (Gobbi *et al.,* 2006; Gobbi *et al.,* 2010). The result is influenced by the abundance of the wingless and carnivorous *Nebria germari* on the glacier and in the first stage of deglaciation (Class 1).

Most of the species sampled are olphactory-tactil hunters. This hunting strategy is considered to be the most primitive hunting strategy, performed by unspecialized nocturnal predators with small eyes (Brandmayr *et al.,* 2005; Fountain-Jones *et al.,* 2015). Since the olphactory-tactil hunting strategy is related to nocturnal predation (Brandmayr *et al.,* 2005), we can hypothesize that this strategy has been positively selected to partially avoid niche competition with spiders. Visual predators appeared only in late successional stages (Classes 3-4). Visual hunting is typical of diurnal predators (e.g. *Notiophilus* spp.) with large eyes (Brandmayr *et al.,* 2005; Fountain-Jones *et al.,* 2015). Most carabids specialized in feeding on springtails occurring in late successional stages, where high vegetation cover favors high springtail abundance (Schirmel *et al.,* 2012).

Carabid body size increased along the primary succession, confirming that body length of ground predator species is higher in less disturbed habitats, such as late successional stages (Ribera *et al.,* 2001;

Gobbi *et al.,* 2010; Schirmel *et al.,* 2012). In these stages, habitat maturity and stability allow longer larval development, whilst the higher trophic availability allows greater foraging rates (Blake *et al.,* 1994).

The analysis of spider trait distribution revealed that most of the hunting strategies are represented along the primary succession. Ground hunters increased after the early successional stages (Site 1), probably due to the increase of niche availability (Losapio *et al.,* 2015). The same pattern emerged when considering the abundance of sheet web weaver spiders. However, sheet web weavers spiders living on the vegetation could bias this trend. We point out that there might be a bias due to some sheet web weavers spiders living on the vegetation, being less likely to be collected into the pitfall traps. The proportion of ballooners is higher on the glacier and in early successional stages, then decreased along the succession, as they are first colonisers. As a consequence, the dispersal strategy (ballooners vs ground dispersers) influenced spider distribution. Ballooning may be initiated by both environmental and physiological factors, and in general overcrowding and food shortage can stimulate aerial dispersal (Duffey, 1998). Coulson *et al.,* (2003) also observed ballooning spiders during summer along a glacier foreland (July, August), suggesting that in alpine areas, ballooning takes place during the entire snow free period.

Spider body length increased along the primary succession. Since bigger species are generally not ballooners, this trend can be explained by the correlation between body size and dispersal ability. In addition, our results are consistent with mechanisms invoking metabolic rate and desiccation resistance to predict an increase of body size from cool and moist habitats, such as the glacier surface and early successional stages, to warmer and dryer habitats, as late successional stages (Entling *et al.,* 2010).

In contrast to our expectations, we did not observed a true turnover of carabid and spider functional traits, along the primary succession. Indeed, most of the traits were added and persisted, according to the “addition and persistence model” (Vater 2012; Vater & Matthews 2013, 2015). Our results bring to advance the hypothesis that, in our study system, carabid distribution is mainly driven by trophic factors, since only traits linked to hunting strategies varied along the succession. On the other hand, spider distribution is mainly driven by both a trophic and dispersal meaning.

Conclusions

Our results highlighted that carabid and spider primary successions along a glacier foreland can be described not only by considering species diversity and turnover, as traditionally performed, but also via the functional diversity and traits distribution approach, as already applied to plant assemblages (e.g. Caccianiga *et al.,* 2006; Erschbamer & Mayer, 2012). However, unlike plant assemblages (Erschbamer & Mayer, 2012), in our study system carabid and spider species assemblages cannot be discriminated from their life-history trait types, as they mainly follow the “addition and persistence model” and not the “replacement change model” (Vater & Matthews, 2012). On the other hand, the proportion of each trait within each species assemblage clearly changes in relation to the successional gradient; the species assemblages can thus be discriminated on the base of the proportion of each trait. The use of life-history traits proved a useful tool to describe in more detail, the ecological and behavioral features of the ground-dwelling arthropods involved in a primary succession triggered by glacier retreat.

To our knowledge, this is the first study to measure different components of functional diversity of ground-dwelling arthropods in response to glacier retreat and in harsh high altitude environments. Using the trait-based approach and including functional diversity components, we provide a valuable contribution describing the adaptive strategies of carabids and spiders that colonise glaciers surfaces and recently deglaciated terrains; landforms that are rapidly changing in response to the current global warming.

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Plants and arthropods of periglacial and glacial landforms: towards a synthesis at Alpine scale

Aims. Data collected in all the study areas of the PhD project (Chapter 1, Fig. 1) were merged in a database in order to perform a first synthesis at Alpine scale on periglacial and glacial landforms as habitat for plant and arthropod species. In this preliminary analysis we aim to: 1) describe plant and arthropod assemblages of the investigated areas and landforms; 2) compare the distributional patterns of plant and arthropod assemblages throughout areas and landforms; 3) provide a synthetic biogeographical and ecological outline of each plant and arthropod species.

Methods. Data were collected following the methods explained in the chapters 2.3, 2.5 and 3.1. Species occurrence for each sampling point were summarized at the level of plots, thus a matrix of 112 plots and 373 species (250 plants, 40 carabid beetles and 83 spiders) was analyzed. To describe and compare plant and arthropod assemblages of the investigated areas and landforms, plots were compared by a cluster analysis on the presence/absence species matrix, using the UPGMA method with Jaccard similarity index. To provide a synthetic biogeographical and ecological outline of each plant and arthropod species, species relative frequencies for each area and each landform were calculated and gathered in five frequency classes with a resolution of 20%.

Three main areas were discerned: A) Pennine Alps as western inner mountain range (Valle Anzasca and Valle del Lys); B) Rhaetian Alps as central inner mountain range (Val d'Amola; Val d'Ultimo and Valle del Braulio); C) Orobian Alps as central peripheral mountain range (Val Seriana, Val Brembana and Val Gerola). Three landform categories corresponding to different ecological conditions were discerned: 1) control slopes (iceless stable slopes supposed to have the potentiality for the full development of soil and plant and arthropod communities); 2) iceless debris-featured landforms (scree slopes, glacier forelands and recent moraines); 3) icy debris-featured landforms (active rock glaciers and debris-covered glaciers).

Plots codes were organized as follows. The first acronym indicates the area: Amo = Amola (Val d'Amola), Ult = Lago Lungo (Val Ultimo), Bra = Vedrettino (Valle del Braulio), Ole = Col d'Olen (Valle del Lys), Bel = Belvedere (Valle Anzasca), Tro = Trobio (Val Seriana), Tbg = Tre Signori (Val Brembana, Province of Bergamo), Tso = Tre Signori (Val Gerola, Province of Sondrio), Mor = Valmorta (Val Seriana). The second acronym indicates the landform: CS = control-slope, SS = scree-slope, IM = iceless-moraine, F1 = glacier foreland <100y, F2 = glacier foreland >100y, RG = active rock-glacier; DG = debris covered-glacier. The subsequent digit indicates the plot number.

Results

The dendrogram of plant species (Fig. 1) separated first of all the basophilous plant assemblages of Valle del Braulio (cluster1; most frequent species: *Arabis pumila, Poa minor, Saxifraga caesia, Achillea atrata, Saxifraga aphylla, Ranunculus alpestris*) and the subalpine ones of Valle Anzasca (cluster 2; most frequent species: *Avenella flexuosa, Dryopteris dilatata, Luzula sieberi, Hieracium murorum, Calamagrostis villosa, Veratrum lobelianum*). A third large cluster gathered plots belonging to different areas and landforms (cluster 3; most frequent species: *Poa alpina, Linaria alpina, Silene acauluis, Sedum alpestre, Veronica alpina, Poa laxa*). However, two further clusters are clearly recognizable within the latter: the first one gather mainly control slopes and iceless debris-featured landforms (cluster 3a; most frequent species: *Cardamine resedifolia, Agrosis rupestris, Luzula alpino-pilosa, Leucanthemopsis alpina, Euphrasia minima, Poa alpina*), while the second gather iceless and icy debris-featured landforms (cluster 3b; most frequent species: *Androsace alpina, Artemisia genipi, Ranunculus glacialis, Geum reptans, Oxyria digyna, Saxifraga bryoides*).

The dendrogram of arthropod species (Fig. 2) showed a main dichotomy discerning the plots of Orobian Alps (cluster 1; most frequent species: the carabid beetles *Pterostichus lombardus, Carabus castanopterus, Oreonebria lombarda* and *Amara alpestris*; the spiders *Acantholycosa pedestris* and *Mughiphantes pulcher*) from those of the inner ones, independently from the landforms. The cluster of inner Alps showed no clear further partitions, but a series of sub-clusters mainly based on the area. Sub-clusters gathering plots of the Western inner Alps were mainly characterized by the carabid beetles *Carabus concolor* and *Pterostichus cribratus* and the spiders *Coelotes pickardi pastor, Robertus truncorum, Pardosa saturatior* and *Oedothorax agrestis*. Sub-clusters gathering plots of the central inner Alps were mainly characterized by the carabid beetles *Carabus adamellicola, Carabus sylvestris, Amara erratica* and *Cychrus attenuates* and the spiders *Xysticus lanio* and *Pardosa giebeli*.

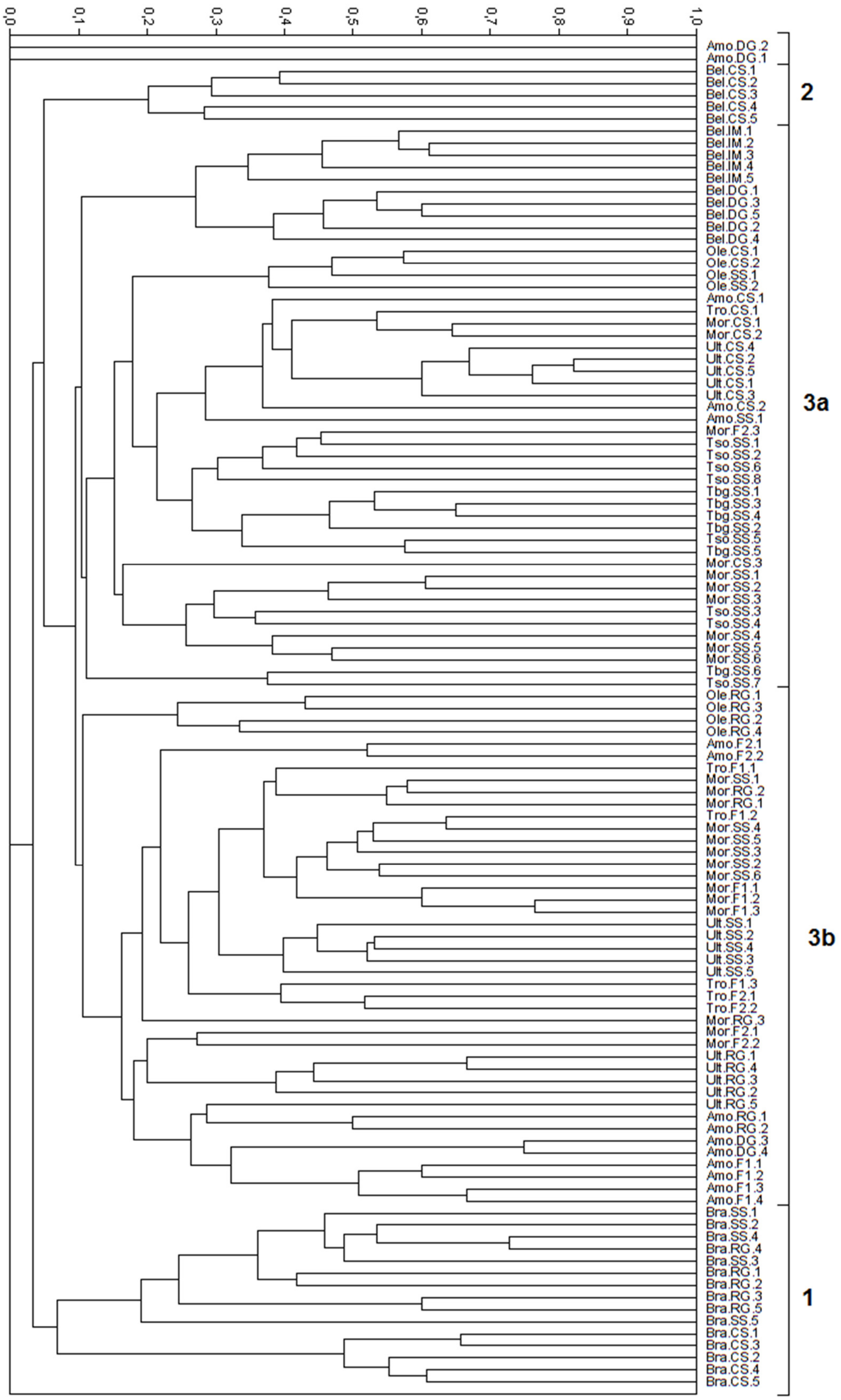

Fig. 1. Dendrogram resulting from the cluster analysis of plots on the basis of plant species.

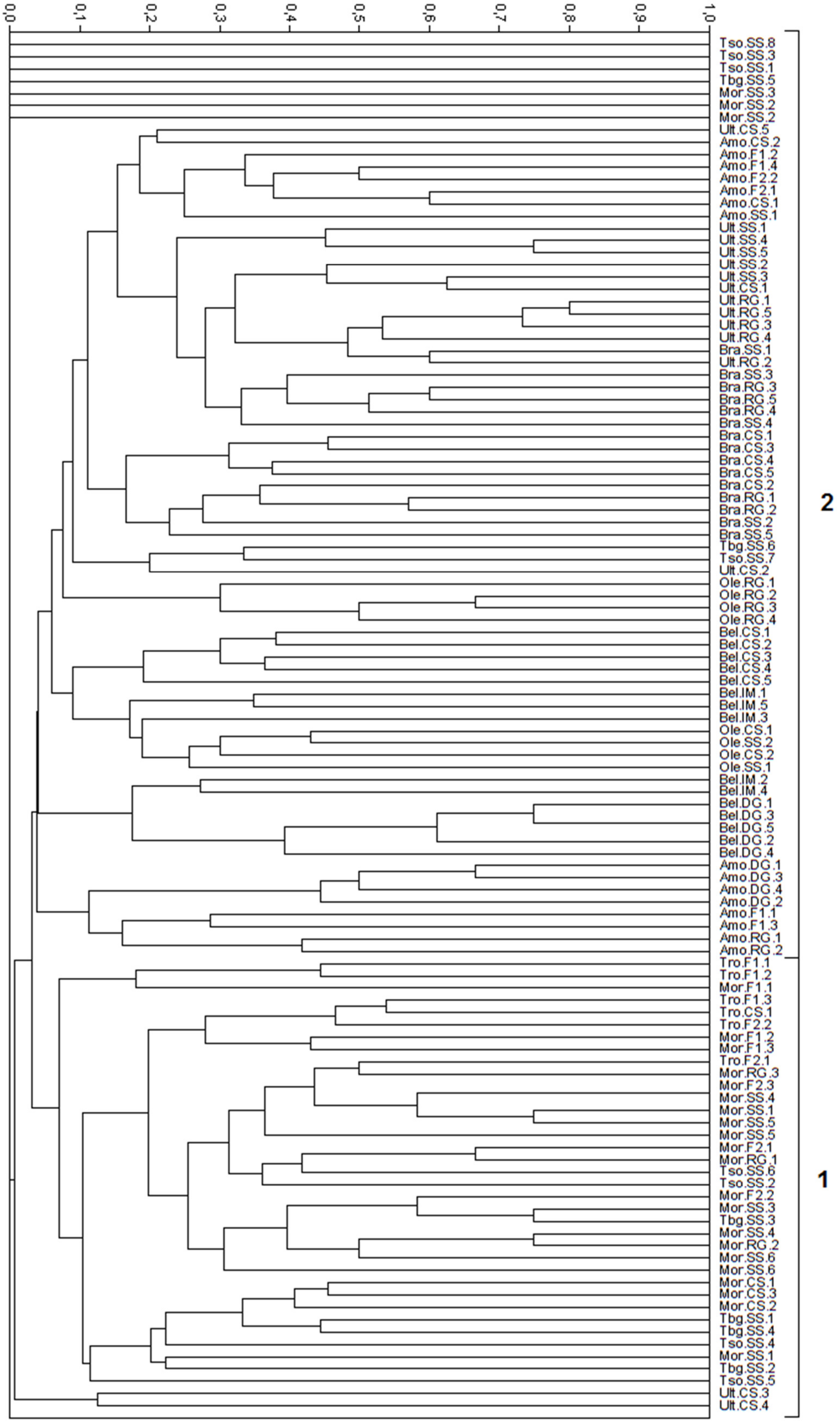

Fig. 2. Dendrogram resulting from the cluster analysis of plots on the basis of arthropod species.

Discussion

Plant and arthropod assemblages on periglacial and glacial landforms were preliminary described and compared. The synoptic tables of species frequencies throughout areas and landforms (tables 1 and 2) provide a synthetic information about the biogeographical and ecological outlines of each species.

Our preliminary analysis based on the presence/absence species matrix suggest that plants and arthropods may follow quite different distributional pattern: while plant assemblages seems to be mainly driven by landforms in spite of the area, arthropod assemblages could be higher affected by the biogeographical context. Most of the arthropod assemblages clustering seems to be based on the presence/absence of carabid beetles rather than spiders, thus carabid beetles could result as more reliable biogeographical markers than spiders, probably as a consequence of a lower dispersal abilities.

However, multivariate analyses based on species abundance is needed to shade light on periglacial and glacial landforms as habitat and warm-stage refugia for cold-adapted species. Further, to perform a synthesis work at Alpine scale, a functional approach is advisable in order to overtake the taxonomical differences due to biogeography. The functional classification should be performed at least on the basis of species thermal requirements (to distinguish cold-adapted species) and dispersal abilities (to distinguish high- from low-dispersal species). Moreover, analyses focused on subsets of target taxa is advisable in order to reduce the number of variables (species) with respect to the observations (plots).

Table 1. Synoptic table of plant species frequencies throughout the investigated areas and landforms. Areas were indicated as follows: A) Pennine Alps (Valle Anzasca and Valle del Lys); B) Rhaetian Alps (Val d'Amola; Val d'Ultimo and Valle del Braulio); C) Orobian Alps (Val Seriana and Val Brembana). Landforms were indicated as follows: 1) control slope (iceless stable slope, supposed to have the potentiality for the full development of soil and plant and arthropod communities); 2) iceless debris-featured landforms (scree slopes, glacier forelands and recent moraines); 3) icy debris-featured landforms (active rock glaciers and debris-covered glaciers). Species frequencies were indicated as follows: I = 1-20%; II = 21-40%; III = 41-60%; IV = 61-80%; V = 81-100%.

Species	Area			Landform		
	A	B	C	1	2	3
Achillea atrata		I		II	I	I
Achillea macrophylla	I			I		
Achillea moschata	II				I	
Achillea nana	I		I	I	I	
Adenostyles alliariae	I			I		
Adenostyles leucophylla		I	I		I	I
Agrostis alpina		I	I	II	I	
Agrostis rupestris	III	II	III	III	III	II
Agrostis schraderiana	I	I	I	I	I	
Agrostis stolonifera	IV			I	I	I
Alchemilla alpina	I		I	I	I	
Alchemilla pentaphyllea	I			I		
Alchemilla vulgaris	I	I	I	II	I	
Alnus viridis	I			I	I	
Androsace alpina	I	I	II		II	I
Antennaria carpatica			I	I	I	
Antennaria dioica			I		I	
Anthoxanthum alpinum	II	I	I	III	I	I
Anthyllis vulneraria		I	I	II	I	
Arabis alpina	I	II	II		II	I
Arabis caerulea		I	I	I	I	I
Arabis pumila		II		I	I	I
Arenaria biflora	I	I	I	I	I	I
Armeria alpina	I			I	I	
Arnica montana	I			I		
Artemisia genipi		I	I		I	I
Asplenium viride		I	I	II	I	
Aster bellidiastrum		I	I	II	I	
Astrantia minor	I		I	II	I	
Athyrium distentifolium	II		I	I	I	
Avenella flexuosa	II		I	II	I	
Bartsia alpina	I	II	I	III	I	
Betula pendula	I					I
Biscutella laevigata			I		I	
Botrychium lunaria			I		I	

Bupleurum stellatum			I	I		
Caeloglossum viridis		I			I	
Calamagrostis villosa	II			I	I	
Calluna vulgaris		I		I		
Campanula barbata	I		I	I		
Campanula cochleariifolia		I	I	II	I	I
Campanula excisa	I			I		I
Campanula rotundifolia			I	I	I	
Campanula scheuchzeri	II	I	I	III	I	I
Cardamine resedifolia	IV	I	IV	II	III	II
Carduus carlinaefolius			I		I	
Carex curvula	I	I	I	III	I	I
Carex firma		I		II		
Carex foetida	I			I	I	
Carex ornithopoda		I		II		
Carex parviflora	I	I		I	I	
Carex rupestris		I		I		I
Carex sempervirens	I	I	II	II	I	
Centaurea nervosa	I			I		
Cerastium arvense	II		I	I	I	
Cerastium cerastoides			I		I	
Cerastium latifolium		I	I		I	
Cerastium pedunculatum	II	I	I		I	II
Cerastium uniflorum		III	II		II	II
Chaerophyllum hirsutum	I			I		
Cicerbita alpina	I			I		
Cirsium spinosissimum	I	I	II	I	I	I
Coeloglossum viride			I		I	
Corallorhiza trifida	I			I		
Corydalis lutea			I		I	
Crepis kerneri		I		I		
Cryptogramma crispa	I	I	II		II	
Cystopteris fragilis	II	I	I	I	II	I
Dactylorhiza maculata	I			I		
Daphne striata		I	I	I		
Diphasiastrum alpinum		I		I		
Doronicum clusii		I			I	II
Doronicum grandiflorum	I		III	I	II	
Draba aizoides		I	I	I	I	
Dryas octopetala		I		II		
Dryopteris dilatata	I			I		
Dryopteris filix-mas	I			I		
Dryopteris villarii			I		I	
Elyna myosuroides		I		I		
Empetrum hermaphroditum		I		I		
Epilobium alsinifolium	I					I
Epilobium anagallidifolium	I		I	I	I	
Epilobium fleischeri	I				I	
Epilobium nutans	I				I	
Erigeron uniflorus		I	I	II	I	I
Euphrasia minima	III	II	I	IV	I	I
Festuca arundinacea	I			I		

Festuca halleri	II	I	I	I	I	I
Festuca nigrescens	I	I	I	I	I	
Festuca quadriflora		I	I		I	
Festuca varia	III		II	II	II	I
Festuca violacea	I			I	I	
Galium anisophyllon	I		I	I	I	
Gentiana bavarica	I	I		I		I
Gentiana engadinensis		I		I		
Gentiana germanica			I	I		
Gentiana kochiana		I	I	II		
Gentiana punctata		I		I	I	
Gentiana purpurea	I		I	II	I	
Gentiana ramosa	I			I		
Gentiana verna		I	I	I	I	I
Gentianella germanica		I		I		
Geranium sylvaticum	I			I		
Geum montanum	II	I		II	I	
Geum reptans		I	III		III	I
Globularia cordifolia		I		I		
Gnaphalium hoppeanum		I		I		I
Gnaphalium supinum	II	I	II	II	II	I
Gypsophila repens			I		I	
Helianthemum alpestre		I		I		
Helictotrichon versicolor	I	I	I	III	I	
Hieracium bifidum		I		I		
Hieracium glanduliferum		I	I	II	I	
Hieracium intybaceum			I		I	
Hieracium morisianum	I			I		
Hieracium murorum	I			I		
Hieracium pilosella		I			I	
Hieracium staticifolium	I				I	
Hieracium villosum		I		I		
Homogyne alpina	I	II	II	IV	I	I
Huperzia selago	I	I	I	II	I	
Juncus jacquinii	I			I	I	
Juncus trifidus	III	I	I	II	I	I
Juniperus nana	I	I	I	II		
Larix decidua	II	I		I	I	I
Leontodon helveticus	I	II	III	IV	II	I
Leontopodium alpinum			I	I		
Leucanthemopsis alpina	III	III	III	III	III	II
Ligusticum mutellina	I	I	I	III	I	
Linaria alpina	II	I	III		II	II
Lloydia serotina		I	I		I	I
Loiseleuria procumbens		I	I	II		
Lotus alpinus	II	I	I	II	I	I
Luzula alpino-pilosa	II	III	III	III	III	II
Luzula lutea	II	I	I	I	I	I
Luzula sieberi	I			I		
Luzula spicata	I	I	I	I	I	
Maianthemum bifolium	I			I		
Melampyrum sylvaticum	I			I		

Milium effusum	I			I		
Minuartia rupestris			I		I	
Minuartia sedoides	I		I	I	I	
Minuartia verna		I		II		
Moehringia ciliata		I		I	I	I
Myosotis alpestris	II	I	I	II	I	I
Nardus stricta	I	I		II		
Oreochloa disticha		I	I	I	I	
Oxalis acetosella	I			I		
Oxyria digyna	I	II	III		III	II
Papaver aurantiacum		I	I		I	I
Pedicularis kerneri	I	I	I	II	I	
Pedicularis tuberosa	I		I	I	I	
Pedicularis verticillata			I		I	
Peucedanum ostruthium	I		I	I	I	
Phleum rhaeticum	I			I	I	
Phyteuma betonicifolium	I			I	I	
Phyteuma hedraianthifolium			I	I	I	
Phyteuma hemisphaericum	I	I	I	IV	I	I
Phyteuma orbiculare			I		I	
Pinguicula alpina		I		I		
Pinguicula leptoceras		I	I	I		
Pinus mugo		I		I		I
Plygonum viviparum	I			I		
Poa alpina	II	II	IV	IV	IV	I
Poa glauca			I		I	
Poa laxa	III	II	I	I	II	III
Poa minor		II		I	I	I
Poa nemoralis	I			I		
Polygonum viviparum		II	I	IV	I	
Polypodium vulgare	I			I		
Polystichum lonchitis	I		I	I	I	
Potentilla aurea	I	I	I	III		
Potentilla brauneana		I		I		
Potentilla nitida			I	I	I	
Prenanthes purpurea	I			I		
Primula daonensis		I	I	II	I	
Primula glutinosa		I		II		
Primula hirsuta	I		I	I	I	
Primula latifolia			II	I	I	
Pritzelago alpina	I	II	II	I	II	I
Pseudorchis albida	I		I	I	I	
Pulsatilla alpina		I	I	I	I	
Pulsatilla vernalis			I	I		
Pyrola minor	I	I		I		
Ranunculus alpestris		I		II		I
Ranunculus glacialis	I	I	II	I	II	I
Ranunculus montanus	I	I	I	I	I	
Rhinanthus alpinus	I				I	
Rhodiola rosea			I		I	
Rhododendron ferrugineum	II	II	I	IV	I	I
Rubus idaeus	I			I		

Rumex alpestris	I			I		
Rumex scutatus	II				I	I
Sagina saginoides	II	I	I		I	I
Salix appendiculata	III			I	I	I
Salix helvetica	II	I		I	I	I
Salix herbacea	I	II	I	IV	I	I
Salix reticulata		I		I		
Salix retusa		I	I	I	I	
Salix serpillifolia		II		II	I	I
Saussurea discolor			I	I		
Saxifraga aizoides		I	I		I	
Saxifraga androsacea		I	I		I	
Saxifraga aphylla		I			I	I
Saxifraga aspera	I				I	I
Saxifraga biflora	I					I
Saxifraga bryoides	II	III	III	I	III	III
Saxifraga caesia		I		II	I	I
Saxifraga exarata	II	I	I	I	I	I
Saxifraga hostii		I		I		
Saxifraga oppositifolia	I	II	II		II	II
Saxifraga paniculata		I	II		I	I
Saxifraga seguieri	I	I	I		I	
Saxifraga stellaris	I		I		I	I
Sedum alpestre	II	I	III	II	III	I
Sedum atratum		I	I	II	I	
Selaginella selaginoides		I	I	II		
Sempervivum montanum	II	I	I	II	I	I
Senecio doronicum			I	I	I	
Senecio halleri	I			I	I	
Senecio incanus		I	I	I	I	I
Sesleria caerulea		I		I		
Sibbaldia procumbens	I	I	I	I	I	
Silene acaulis	III	II	III	III	III	I
Silene quadridentata			I		I	
Silene rupestris	II				I	I
Silene vulgaris	II			I	I	
Soldanella alpicola		II	I	II	I	I
Soldanella alpina	I	I	I	II		I
Solidago virgaurea	I		II	I	I	
Sorbus aucuparia	I			I		
Stellaria nemorum	I			I		
Streptopus amplexifolius	I			I		
Taraxacum sp	I	I	I	II	I	I
Thesium alpinum	I			I		
Thlaspi rotundifolium	II		I	I	I	I
Thymus sp		I	I	I	I	
Trifolium alpinum	I			I		
Trifolium pallescens	II		I	I	I	
Trifolium pratense	II			I	I	
Tussilago farfara			I		I	
Vaccinium gaultherioides	I	I	I	IV	I	
Vaccinium myrtillus	II	I	I	II	I	

Vaccinium vitis-idaea			I	I		
Valeriana saxatilis		I		I		
Veratrum lobelianum	I			I		
Veronica alpina	I	II	III	II	III	I
Veronica aphylla		I		I		
Viola biflora	I	I	I	I	I	
Viola comollia			I		I	I

Table 2. Synoptic table of arthropod species frequencies throughout the investigated areas and landforms. Areas were indicated as follows: A) Pennine Alps (Valle Anzasca and Valle del Lys); B) Rhaetian Alps (Val d'Amola; Val d'Ultimo and Valle del Braulio); C) Orobian Alps (Val Seriana and Val Brembana). Landforms were indicated as follows: 1) control slope (iceless stable slope, supposed to have the potentiality for the full development of soil and plant and arthropod communities); 2) iceless debris-featured landforms (scree slopes, glacier forelands and recent moraines); 3) icy debris-featured landforms (active rock glaciers and debris-covered glaciers). Species frequencies were indicated as follows: I = 1-20%; II = 21-40%; III = 41-60%; IV = 61-80%; V = 81-100%.

Species	Area			Landform		
	A	B	C	1	2	3
Abax arerae			I		I	
Acantholycosa pedestris		I	II	I	I	I
Agyneta gulosa			I	I		
Agyneta rurestris			I		I	
Amara alpestris			I	I	I	
Amara erratica	I	I		I	I	I
Amara pratermissa		I		I		
Amara quenseli	I	I		I	I	I
Anguliphantes monticola	I	II		I	I	I
Arctosa alpigena lamperti		I		I		
Bembidion glaciale	I					I
Bembidion rhaeticum			I	I		
Bembidon bipunctatum nivale		I		I		
Bolyphantes alticeps	I			I		
Calathus micropterus	I			I		
Carabus adamellicola		I		I	I	
Carabus castanopterus			III	I	II	I
Carabus concolor	II			I	I	
Carabus depressus	I	I		I	I	
Carabus problematicus		I		I		
Carabus sylvestris		I		I		
Caracladus avicula	I				I	
Centromerus pabulator	I	I		II		
Centromerus subalpinus	I	I		I		
Ceratinella brevis			I	I		
Cicindela gallica	I				I	
Clubiona alpicola		I				I
Coelotes pickardi pastor	II			II	I	
Coelotes pickardi tirolensis		III	III	III	II	II
Coelotes rudolfi	II			I	I	
Cryphoeca nivalis		I			I	
Cybaeus intermedius	I			I		
Cychrus attenuatus		I		I	I	
Cychrus cordicollis	I			I	I	
Cymindis vaporariorum		I		II		I

Dicranopalpus gasteinensis	II				I	I
Diplocephalus helleri	II	I	I	I	II	I
Drassodes lapidosus	I				I	
Drassodex drescoi	I				I	
Drassodex heeri		I	I	II	I	I
Entelecara media		I	I	I	I	I
Erigone cfr. arctica		I		I		
Erigone dentipalpis		I	I		I	
Gnaphosa badia	I			I		
Gnaphosa petrobia		I	I	I	I	
Haplodrassus aenus	I			I		
Haplodrassus signifer	I	I		I		
Harpalus atratus		I		I		
Iberina montana			I		I	
Incestophantes frigidus	I			I		
Leistus nitidus	I			I		
Lepthyphantes hamatus	I					I
Lepthyphantes nodifer	I			I		I
Mecynargus brocchus			I		I	
Mecynargus paetulus		I		I		
Meioneta rurestris		I		I		I
Mermessus trilobatus		I			I	
Micaria aenea	I			I		
Micrargus apertus	I			I		
Mitopus morio	I			I		
Mughiphantes armatus		I				I
Mughiphantes handschini	I	I	I	I	I	I
Mughiphantes mughi	I			I		
Mughiphantes pulcher			I		I	I
Mughiphantes variabilis		I		I	I	I
Nebria germari		II		I	I	I
Nebria jockischi		I			I	
Notiophilus biguttatus		I		I	I	I
Oedothorax agrestis	II				I	I
Oreonebria castanea	III	III	I	II	II	II
Oreonebria lombarda			I	I	I	I
Oreonebria soror soror		I			I	I
Oreonebria soror tresignore			I		I	
Oreoneta montigena		I	I	I	I	I
Oreonetides glacialis		I			I	I
Oreonetides vaginatus		I		I	I	
Ozyptila trux		I		I		
Pallidophantes pallidus	I		I	I		
Pardosa blanda	I		I	II	I	
Pardosa ferruginea	I			I		
Pardosa giebeli		I		II		
Pardosa mixta	I			I		
Pardosa nigra	III	III		II	II	III
Pardosa oreophila		I	I	I	I	
Pardosa saturatior	II				I	I
Pelecopsis parallela		I		I		
Pelpecopsis radicicola	I	I		I		

Platynus depressus	I				I	
Platynus teriolensis		I	I	I	I	
Porrhomma myops		I		I		
Princidium bipunctatum		I		I	I	
Pterostichus cribratus	II			I	I	
Pterostichus lombardus			III	I	II	I
Pterostichus multipunctatus	II	I	II	II	II	I
Pterostichus spinolae	I			I		
Pterostichus unctulatus	I			I		
Robertus arundineti	II			I	I	
Robertus truncorum	II			II	I	I
Rugathodes bellicosus	I			I	I	I
Rugathodes instabilis		I			I	
Sitticus longipes		I	I	I	I	I
Tenuiphantes jacksoni	II			I	I	
Tenuiphantes jacksonoides		I		I	I	
Tenuiphantes monachus		I			I	
Tenuiphantes tenuis	I				I	
Theridion petraeum	I				I	
Trechus brembanus			I		I	
Trechus insubricus			I		I	
Trechus tristiculus		I			I	I
Trichotichnus laevicollis	I	I		I		I
Troglohyphantes lucifuga	I	I		I	I	
Troglohyphantes sciakyi		I	I		I	I
Walckenaeria antica			I		I	
Walckenaeria capito	I	I	I	I	I	
Walckenaeria cuspidata	I			I		
Walckenaeria obtusa	I			I		
Walckenaeria vigilax		I	I	I	I	
Xysticus audax	I				I	
Xysticus desidiosus	I	I	I	II		
Xysticus lanio		II		II	I	I
Xysticus ulmi	I			I		
Zelotes devotus			I	I	I	
Zelotes subterraneus	I			I	I	

Conclusions and perspectives

This PhD project implemented the knowledge about the ecology of active rock glaciers and debris-covered glaciers on inner mountain ranges, and of glacier forelands and recent moraines on peripheral mountain ranges. We focused in particular on that ecological features which likely play a key role in affecting the potentiality of such landforms as warm-stage refugia for cold-adapted species. Concerning active rock glaciers and debris-covered glaciers on inner mountain ranges, we focused on their ability to support cold-adapted species in adverse climate context due to the microclimate features provided by the underlying ice. Concerning glacier forelands and recent moraines on peripheral mountain ranges, we focused on their ability to long-lasting support pioneer cold-adapted species in spite of their replacement with mid- and late-successional ones. In both the cases, a crucial role of macroclimate is apparent.

Active rock glaciers and debris-covered glaciers does not differ from the surrounding debris-featured iceless landforms for soil parameters, but for a cold microclimate likely due to the underlying ice. The microclimate can explain the ability of such landforms to host characteristic cold-adapted plant and arthropod species. This common feature is the main topic which allows to consider both active rock glaciers and debris-covered glaciers as potential warm-stage refugia, but some important difference occurs between the two landforms. Active rock glaciers show relatively low thermal differences with the surrounding landforms and are unable to cross the altitudinal zonation of mountain ecosystems, thus can only enhance the occurrence of cold-adapted species within their normal altitudinal distribution. By contrast, the high thermal difference with the surrounding landforms and the ability to cross the altitudinal zonation of mountain ecosystems allows debris-covered glaciers to stand out for the presence of cold-adapted species even below their normal altitudinal distribution.

Such picture concerns the Alps with their related macroclimate, but cannot be generalized to all the mountain systems of the world. First of all, the geographical distribution of landforms depends on macroclimate. Scree slopes, rock glaciers, debris-covered glaciers and debris-free glaciers make up a geomorphic continuum depending on the relative contribution of debris and snow at topoclimatic scale (Humlum, 1998, 2000), which in turn is linked to the macroclimate spectrum from cold-dry continental to cold-wet oceanic regions (Haeberli, 1985; Barsch, 1996; Scotti et al., 2013, 2014). Moreover, the macroclimate drives the altitudinal arrangement of landforms (Scotti et al., 2013, 2014), affecting their intrinsic ability to host cold-adapted species in adverse climate contexts. Cold-wet oceanic climates relegate active rock glaciers to high elevation (e.g. rock glaciers of Orobian Alps, Scotti et al., 2013), but allow glaciers to reach low elevation in strength of high accumulation rates able to compensate the ice losses (e.g. glaciers of Patagonia, Warren and Aniya, 1999). By contrast, cold-dry continental climates limit the ability of glaciers to extend themselves on a wide altitudinal range, but allow active rock glaciers to descend below the climatic treeline (e.g. active rock glaciers of Sierra Nevada, Millar et al., 2013). Summarizing, we can hypothesize that active rock glaciers and debris-covered glaciers perform a similar ecological role in opposite macroclimate conditions.

Besides driving the distribution of active rock glaciers and debris-covered glaciers as potential warm-stage refugia, the macroclimate can also limit the effects of climate change themselves on high mountain landscapes and ecosystems. Mountain ranges characterized by oceanic climate could prevent the extinction risk for pioneer cold-adapted species along a chronosequence of glacier retreat, due to the long-lasting persistence of glaciers at relatively low altitudes (as a consequence of high winter precipitations) and the slow colonization of glacial landforms (as a consequence of long lasting snow-cover and long-lasting temperatures around zero). Comparing our studies with previous ones (e.g. Schönswetter et al., 2005; Lohse et al., 2011; Latella et al., 2012; Martini et al., 2012), peripheral mountain ranges in particular outlines as oceanic areas of crucial biogeographical importance during both the opposite climate extremes: in cold-climatic stages they can provide refugia for a lot of species, as a consequence of the relatively low ice-sheet expansion; in warm-climatic stages they may provide refugia for cold-adapted species in particular, as a consequence of their climatic, thus glaciological and ecological peculiarities.

Therefore, a first perspective rising up from our study is an ecological investigation at global scale to analyze how macroclimate affects: 1) the arrangement of active rock glaciers and debris-covered glaciers as habitat with respect to the climatic treeline; 2) the ecological differences of active rock glaciers and debris-covered glaciers with the surrounding iceless landforms; 3) the temporal patterns of colonization of glacier forelands and recent moraines.

We mainly tested whether the investigated landforms have the ecological requirements to be considered as potential warm-stage refugia for cold-adapted species; however, the most certain way to infer the actual biogeographical role of such landforms is to know if they acted as refugia in past warm-climate stages (e.g. the Holocene Climate Optimum). The present geographical distribution of species on mountain ranges is supposed to be differently linked to the past location of refugia depending on their own dispersal ability: while low-dispersal species may be still spatially linked to refugia, high-dispersal ones likely expanded to all the suitable areas once the suitable climate returns, thus concealing the past location of refugia. However, contraction and expansion to and from refugia leave genetic signatures of high diversity in refugia and low diversity in expansion areas (Hewitt, 2004; Keppel et al., 2012).

Therefore, a second perspective rising up from our study is a phylogeographical analysis aimed to test whether species genetic diversity follow the distributional pattern of warm- rather than cold-stage refugia. Our biogeographical analyses on Orobian Alps as model system of peripheral mountain ranges may provide a first basis to carry on such line of research.

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PIANTE VASCOLARI: SPERMATOFITE

Androsace brevis (Hegetschw.) Ces.

F. MANGILI, D. TAMPUCCI, M. CACCIANIGA

Nomenclatura:
Nome scientfico: *Androsace brevis* (Hegetschw.) Ces.
Sinonimi: *Aretia brevis* Hegetschw.; *Androsace charpentieri* (Heer) Rchb.f.; *Androsace alpina* (L.) Lam. var. *charpentieri* Heer
Famiglia: *Primulaceae*
Nome comune: Androsace orobia

Descrizione. Pianta perenne erbacea, che forma cuscini densi ed appiattiti o cespi radi. Foglie di 3–5 mm, oblanceolate, arrotondate all'apice, provviste sui margini e sulla pagina inferiore di peli stellati con 2–3 diramazioni della lunghezza di 0,05–0,1 mm Peduncoli fiorali 2–3 volte più lunghi delle foglie. I fiori hanno calice di 3,5–4,5 mm, corolla del diametro di 5–8 mm, di colore rosa, purpurea al centro e lobi leggermente smarginati all'apice. (PIGNATTI, 1982). Il frutto è una capsula sub-sferica solitaria, di 4–5 mm di diametro, contente 4 (3) semi, di cui uno è frequentemente più piccolo degli altri.

Biologia. Camefita pulvinante, con fioritura da fine maggio a metà giugno. Fioriture eccezionali sono state osservate dagli Autori in agosto ed in settembre da PROVASI (1922). La formazione del frutto inizia in giugno e termina con il rilascio dei semi in settembre. La biologia riproduttiva di questa specie, ad oggi, non è stata sufficientemente investigata: non si conoscono né gli impollinatori né le modalità di dispersione e non si hanno informazioni circa l'effettiva vitalità e capacità germinativa dei semi. Osservazioni condotte dagli autori sul M. Ponteranica nel 2013 hanno permesso di evidenziare un bassissimo rapporto tra numero di fiori prodotti e numero di frutti giunti a maturazione.

Ecologia. Specie acidofila, caratteristica di crinali oltre i 2000 m di quota delle Alpi Orobie occidentali e della porzione delle Alpi Lepontine, a cavallo tra il Lago di Lugano e il Lago di Como. Si rinviene esclusivamente su substrati permiani di natura terrigena. Dal punto di vista bioclimatico si trova in ambito temperato, regione mesaxerica, sottoregione ipomesaxerica, tipo C (TOMASELLI *et al.*, 1973). Secondo AESCHIMANN (2004) la specie è ascrivibile all'alleanza *Androsacion vandellii* Br.-Bl. *in* Br.-Bl. *et* Jenny 1926. Non esistono, comunque, studi specifici per permettere una definizione più precisa delle cenosi di crescita dal punto di vista fitosociologico.

Distribuzione in Italia.
Regione biogeografica: le stazioni di *A. brevis* rientrano nella regione biogeografica eurosiberiana, Provincia alpina, settore Alpi Centrali (RIVAS-MARTINEZ *et al.*, 2004). Secondo BLASI, FRONDONI (2011), l'areale della specie è circoscritto all'interno dei settori ecogeografici 12A (*Prealpine Range Section*) e 12B (*Orobie Alps Section*).
Regioni amministrative: l'areale della specie è circoscritto alla regione Lombardia, province di Bergamo, Como, Lecco e Sondrio.
Numero di stazioni: in provincia di Bergamo la specie è presente in modo discontinuo lungo la cresta spartiacque con la provincia di Sondrio. Le stazioni, distanti tra loro più di 500 m, sono situate sul monte Fioraro (limite orientale nelle Alpi Orobie), aree sommitali del M. Ponteranica, Denti della Vecchia, Pizzo dei Tre Signori (MARTINI *et al.*, 2012). Non più confermata la stazione riportata da FENAROLI (1956) sul M. Torena, (alta Val Seriana), verosimilmente a causa di confusione della specie con *Androsace alpina* (L.) Lam., ampiamente diffusa nell'area (MARTINI *et al.,* 2012).
Provincia di Sondrio: la specie segue il crinale orobico di confine con la provincia di Bergamo dal M. Fioraro verso occidente, con grosse lacune distributive. La distribuzione è quindi speculare a quella del versante bergamasco. Interamente in territorio sondriese sono le popolazioni presenti sul Pizzo Olano e sul Pizzo Stavello (FERRANTI, 2012). Particolare interesse merita una stazione disgiunta situata sulla cresta SSE del Pizzo di Prata, Val Codera, sulle Alpi Retiche (MAGNI, 2013). Non è stata recentemente confermata la presenza al Passo del Muretto (Val Malenco), riportato in SCHÖNSWETTER *et al.* (2003), dove è invece presente *A. alpina* (L.) Lam. (Giancarlo Donadelli *in verbis*). A tal proposito, nel prossimo futuro andrebbero confermate anche le altre stazioni retiche citate in SCHÖNSWETTER *et al.* (2003) presso

il Rifugio Gianetti ed il Passo dell'Oro (Val Masino), di cui gli autori non riportano i risultati dell'analisi genetica; in quest'ultima località è certamente presente *A. alpina* (L.) Lam., come testimonia il campione d'erbario conservato presso il Museo Civico di Storia Naturale di Morbegno, raccolto da G. Perego, determinato da S. Sgorbati. Occorre inoltre segnalare che la presenza riportata in FORNACIARI (1958) al passo di Gavia non è stata confermata dalle più recenti ricerche (MARTINI *et al.*, 2012), che confermano invece in tutta l'area del passo Gavia la presenza di *A. alpina* (L.) Lam.

Provincia di Lecco: sono presenti tre nuclei principali, sulle aree sommitali della Cima di Camisolo, del M. Rotondo, su quelle del M. Legnone. La popolazioni della cima di Camisolo sono contigue a quelle del Pizzo dei Tre Signori sul confine con il bergamasco, mentre le altre due aree sono separate da una lunga cresta culminante nel Pizzo Alto, in cui la specie non è presente (PROVASI, 1922).

Provincia di Como: sono presenti due nuclei principali disgiunti, il primo gravitante attorno al Pizzo di Gino alla testata della Val Cavargna: M. Garzirola, Cima Verta, M. Stabiello, Cima Pianchette, il secondo, posto ad una notevole distanza, è situato sulla cresta tra Sasso Canale e Sasso Campedello (ARTARIA, 1893). Oltre a queste aree è presente alla testata della Valle di San Jorio (all'omonimo passo).

Tipo corologico e areale globale. Secondo AESCHIMANN *et al.* (2004) la specie è da considerarsi un endemismo alpino – orientale, comprendendo il suo areale una piccola porzione delle alpi Orobie, Retiche occidentali e Lepontine orientali. Il suo areale globale si estende marginalmente anche in Svizzera, sul M. Camoghè (KÄSERMANN, MOSER, 1999), mentre la presenza generica nel cantone dei Grigioni riportata in AESCHIMANN (2004) non è stata più confermata (SCHÖNSWETTER *et al,* 2003), e non è presente neppure sulla cartografia floristica svizzera (INFO FLORA, 2014).

Minacce. Secondo lo schema di classificazione IUCN (2012) la specie è sottoposta alle seguenti minacce:

2.3.1: *Nomadic grazing.* Il sovrappascolo può condurre le popolazioni a locali contrazioni, in particolare il pascolamento caprino, per l'abitudine di stabulare in aree di vetta favorevoli alla specie, calpestando i pulvini o alterando con le deiezioni il processo pedogenetico (Cima Pianchette, M. Ponteranica, M. Stavello); inoltre l'eccessivo apporto di nutrienti favorisce l'ingresso di specie nitrofile non legate alle cenosi di cresta, quali *Urtica dioica* L. e *Blitum bonus-henricus* (L.) C.A.Mey.

6.1: *Recreational activities.* Molte stazioni di crescita sono situate in prossimità o addirittura all'interno di sentieri molto frequentati (Monte Rotondo, Monte Fioraro, Monte Ponteranica, Monte Garzirola), dove il calpestio può danneggiare anche gravemente i pulvini.

8.2: *Problematic native species/diseases*. Le recenti variazioni climatiche (VESCOVI *et al.*, 2007) hanno consentito la colonizzazione di alcune stazioni di specie di taglia maggiore come *Festuca luedii* (Markgr.-Dann.) Foggi, Gr.Rossi, Parolo et Wallosek, in grado di ricoprire i pulvini di *A. brevis* portandoli a morte per mancanza di radiazione solare.

11.1: *Habitat shifting and alteration.* Nei riguardi del cambiamento climatico *A. brevis* sembra essere estremamente vulnerabile, poiché le popolazioni si trovano in posizione di vetta o di crinale e sono, quindi, impossibilitate ad un'ulteriore risalita in quota; le catene su cui la specie cresce hanno inoltre un'altitudine piuttosto modesta, limitando ulteriormente gli spazi vitali potenziali e rendendo le popolazioni particolarmente sensibili ad incrementi di temperatura.

12.1: *Other threats.* La capacità riproduttiva della specie non è ancora nota. Osservazioni condotte dagli autori sul M. Ponteranica nel 2013 hanno permesso di evidenziare che la specie presenta un bassissimo rapporto tra numero di fiori prodotti e numero di frutti giunti a maturazione.

Criteri IUCN applicati.

In base ai dati disponibili è stato applicato il criterio B.

Criterio B

Sottocriteri

B1 – Areale (EOO): 907 km^2;

B2 – Superficie occupata (AOO): 92 km^2, calcolato mediante griglia di 2×2 km (GARGANO, 2011).

Opzioni

a) Numero di "location": considerate come minacce prevalenti *nomadic grazing*, *habitat shifting e alteration,* e *problematic native species/diseases,* possono essere individuate 3 *locations* sulle Alpi Lepontine (dove la specie è presente ad altimetrie più basse rispetto alle Alpi Orobie) corrispondenti alle aree più accessibili e alle creste di bassa quota (M. Garzirola, crinale Cima Pianchette – Pizzo di Gino e Cima di Cugn), 5 *locations* sul crinale Orobico spartiacque; sul M. Fioraro, dove la popolazione è ridottissima a causa della colonizzazione delle creste da parte di specie competitrici; sul M. Stavello, dove le popolazioni sono danneggiate dall'eccessiva stabulazione del bestiame; sul M. Ponteranica, M. Rotondo e M. Legnone; un'ulteriore *location* coincide con la stazione disgiunta del Pizzo di Prata, dove la popolazione è fortemente danneggiata dal pascolamento di selvatici (camosci).

b) (iii) Declino della qualità/estensione dell'habitat: alcune stazioni non sono state riconfermate, come quelle per il Passo di Gavia, il Passo del Muretto (Val Malenco) e del M. Torena (alta Val Seriana). Sulla base delle recenti conoscenze e della revisione degli erbari storici (MARTINI *et al.*, 2012) è verosimile che la specie non sia in realtà mai stata presente in questi siti. Per quanto riguarda la qualità dell'habitat, è da considerarsi fortemente degradato a causa della minaccia 2.3.1 nei siti di M. Garzirola e Cima Pianchette (Alpi Lepontine), nelle stazioni di M. Fioraro e M. Stavello (Alpi Orobie) e nella stazione disgiunta del Pizzo Prata (Alpi Retiche).

Categoria di rischio.
Criterio B – EOO inferiore a 5000 km^2, AOO inferiore a 500 km^2. Numero di *location* inferiore a 10 e scomparsa di alcune stazioni storiche. Categoria di rischio: *Vulnerable*, VU B1ab(iii).

Interazioni con la popolazione globale. Le 2 stazioni accertate per la Svizzera sono le uniche esterne all'areale lombardo, che risulta quindi essere suddiviso in due grossi nuclei posti a notevole distanza uno dall'altro, divisi dal Lago di Como, e da due stazioni disgiunte (M. Sasso Canale e Pizzo di Prata). Le popolazioni elvetiche del M. Camoghè sono direttamente connesse con quelle del gruppo del Pizzo Gino. Essendo quindi praticamente nulle le relazioni con l'areale globale, di fatto limitatissimo al di fuori di quello lombardo, non si ritiene di applicare il declassamento della categoria assegnata.

***Status* alla scala "regionale":** *Vulnerable*, VU B1ab(iii)
- *status* alla scala globale: *Not Evaluated* (NE);
- precedente attribuzione a livello nazionale: *Not Evaluated* (NE).

Strategie/Azioni di conservazione e normativa.
In Lombardia *A. brevis* è protetta in modo rigoroso (categoria C1) dalla legge regionale n.°10 del 31 marzo 2008, unitamente a tutte le altre specie del genere *Androsace* (Regione Lombardia*,* 2010*)*. In Svizzera la specie è sottoposta a protezione totale nel cantone Ticino (legge del 01 luglio 1975), ed è inclusa nella *Lista Rossa delle specie minacciate in Svizzera* (Moser *et al.,* 2002). L'areale italiano di *A. brevis* ricade solo parzialmente in aree protette: le popolazioni orobiche rientrano nel Parco delle Orobie Bergamasche, in particolare nel SIC IT2060001 (Valtorta e Valmoresca), ma non vi è indicazione della specie nell'Atlante dei SIC della Provincia di Bergamo (Perracino, 2010), anche se vi ricadono le popolazioni del M. Ponteranica. In provincia di Sondrio alcune stazioni sono incluse nel Parco delle Orobie Valtellinesi, in particolare nei SIC IT2040026 (Val Lesina), IT2040028 (Val del Bitto e di Albaredo), IT2040027 (Valle del Bitto e di Gerola), anche se in quest'ultimo SIC non è indicata la sua presenza nell'Atlante dei SIC della Provincia di Sondrio sebbene le popolazioni del M. Rotondo e del Pizzo Stavello ricadano in queste aree protetta (Scherini, Parolo, 2010).
Non sono incluse in alcuna area protetta tutte le popolazioni in territorio italiano poste ad occidente del lago di Como e la stazione disgiunta dalla Val Codera. Semi di questa specie sono attualmente conservati presso la *Lombardy Seed Bank*. È attualmente in fase di studio la capacità germinativa dei semi presso il Centro Flora Autoctona, i cui risultati, nell'ambito di un dottorato di ricerca dell'Università degli Studi di Milano (riguardante anche l'autoecologia della specie ed i rapporti con le specie congeneri), saranno pubblicati al termine della sperimentazione.
In merito alla conservazione, sarebbe opportuno inserire le popolazioni alto lariane (M. Garzirola, Pizzo di Gino, Passo di San Jorio) in aree protette. Nelle aree già sottoposte a protezione, sarebbe opportuno controllare e limitare il pascolamento da parte dei capi ovini e caprini in area di cresta.

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Viola comollia Massara

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Nomenclatura:

Nome scientfico: *Viola comollia* Massara
Famiglia: *Violaceae*
Nome comune: Viola di Comolli

Descrizione. Pianta perenne erbacea di 5-10 cm. Fusti striscianti fogliosi all'apice, stipole inferiori ridotte a piccole squame e superiori simili a foglie, talora con due lacinie alla base; foglie verde scuro con lamina ovale intera minore del picciolo. Sepali pelosi sul margine delle appendici; corolla di 2-2,5 cm, superiormente violacea-lillacina con ampia chiazza centrale aranciata, inferiormente giallastra; sperone ottuso di 2(4) mm, lungo circa la metà della corolla (PIGNATTI, 1982).

Biologia. Emicriptofita scaposa con fioritura compresa tra giugno e agosto (PIGNATTI, 1982; AESCHIMANN *et al.*, 2004). Secondo LANDOLT *et al.* (2010) la biologia riproduttiva è caratterizzata da dispersione autocora e mirmecocora, nonché da moltiplicazione vegetativa mediante stoloni.

Ecologia. Specie glareicola d'alta quota, colonizza ghiaioni gravitativi, morene oloceniche e piane proglaciali su substrati cristallini, dal piano alpino (raramente subalpino) al piano nivale. Spesso si rinviene anche in ambienti perialveali e perilacustri, su depositi ghiaiosi a buona disponibilità idrica. La specie è adattata a substrati scistosi silicatici, seppure non sempre strettamente acidi. Particolarmente diffusa sugli argilloscisti della Formazione di Collio, talvolta compare anche su ortogneiss, conglomerati e porfidi riolitici. Entità strettamente ipsofila e microterma, predilige esposizioni settentrionali e quote comprese tra 2000 e 3000 m. Solo raramente, e in condizioni ecologiche particolari, scende a quote inferiori: ad esempio a 1800 m sulla piana alluvionale del bacino artificiale del Barbellino (BG) (ritenuta fluitata in BONA *et al.*, 2013) e a 1690 m sulla piana dello Scimur (SO) (PIROLA, CREDARO, 1977; ANDREIS *et al.*, 1996b), dove presumibilmente sfrutta il microclima legato al vicino Ghiacciaio del Marovin. Segnalazioni a quote inferiori sono da ritenere errate o comunque in attesa di conferma (PIROLA, 1965). Dal punto di vista fitosociologico, la specie è stata proposta come possibile discriminante geografica orobica nell'ambito dell'ordine *Androsacetalia alpinae* Br.-Bl. 1926 (PIROLA, 1965; BANTI, 1989). Essa è generalmente riconducibile all'alleanza *Androsacion alpinae* Br.-Bl 1926 (AESCHIMANN *et al.,* 2004), ma per l'interpretazione sintassonomica a livello di associazione probabilmente sono necessarie ulteriori indagini. Nei lavori di PIROLA (1965) e FUCHS-ECKERT (1986) *Viola comollia* è inquadrata nell'associazione *Oxyrietum digynae* Br.-Bl. 1926, mentre nello studio sulla vegetazione nivale delle Alpi Orobie di PIROLA, CREDARO (1977) figura come caratteristica dell'associazione *Epilobietum fleischeri* Hochst.

Distribuzione in Italia.

Regione biogeografica: stenoendemica circoscritta alla Sezione Alpi Orobie, Provincia Alpina Meridionale, Divisione Temperata secondo BLASI, FRONDONI, (2011); ovvero al Settore Alpi Centrali, Provincia Alpina, Regione Euro-Siberiana secondo RIVAS-MARTINEZ *et al.* (2004).

Regioni amministrative: l'areale è limitato alla Lombardia e ricade nelle Province di Bergamo, Sondrio e Lecco.

Numero di stazioni: in letteratura si contano una trentina di segnalazioni certe a partire dal 1834 (MASSARA, 1834; PIROLA, 1965; FUCHS-ECKERT, 1986; ANDREIS *et. al.*, 1996a, 1996b; MARTINI *et al.*, 2012; BONA *et al.*, 2013). Le stazioni sono concentrate prevalentemente nel settore centro-orientale del crinale orobico, sia sul versante bergamasco (Val Brembana orientale, Val Seriana e Val di Scalve) che su quello valtellinese (dalla Val d'Arigna alla Val Belviso). Facendo riferimento alla Suddivisione Orografica Internazionale Unificata del Sistema Alpino (SOIUSA), l'areale di *V. comollia* rientra completamente nella Sottosezione delle Alpi Orobie (II/C-29.I), con gravitazione nel Supergruppo delle Alpi Orobie Orientali (A). Il nucleo principale copre tutto il Gruppo del Coca (A.2), quindi i Sottogruppi del Barbellino (A.2.a), di Scais-Redorta (A.2.b) e del Pizzo del Diavolo (A.2.c). La specie penetra solo marginalmente nei gruppi limitrofi: a est si spinge nel

Gruppo del Telènek (A.1) solo fino al Monte Demignone e al Monte Venerocolo; a sud non supera le pendici del Monte Grabiasca nel Sottogruppo del Poris-Cabianca (A.3.a) e a ovest entra nel Supergruppo delle Alpi Orobie Occidentali (B) con una stazione sul Monte Masoni. Procedendo ancora verso ovest, la specie ricompare solo all'estremità occidentale della catena orobica con una sottopopolazione isolata sul versante meridionale del Monte Legnone. La stazione copre una superficie di circa 200 m^2 (BANTI, 1989) e dista circa 33 km dal punto più vicino dell'areale principale (Monte Masoni), distanza che supera l'estensione est-ovest dell'areale principale stesso (circa 26 km dal Monte Masoni al Monte Venerocolo). Si ritiene pertanto che il caso del Monte Legnone possa costituire a tutti gli effetti una disgiunzione dell'areale. In sintesi, l'areale regionale (e globale) di *V. comollia* è delimitato a nord dal Pizzo di Rodes e dal Monte Torena, a sud dal Monte Grabiasca e dal Pizzo Tornello, a est dal Monte Venerocolo e a ovest dal Monte Masoni, con disgiunzione puntiforme sul Monte Legnone. Andrebbero comunque confermate alcune segnalazioni storiche, antecedenti il 1968, tra le quali Alpi di Rodes, Corno Stella e Passo del Forcellino (PIROLA, 1965; MARTINI *et al.*, 2012). La specie è stata erroneamente segnalata sulla Cima di Menna, sulla Presolana e sulle Grigne, dove i substrati carbonatici lasciano intuire una probabile confusione con *Viola dubyana* (PIGNATTI, 1982; FUCHS-ECKERT, 1986; MARTINI *et al.*, 2012). Altra segnalazione, mai confermata e ritenuta certamente errata, è quella in Val Davaglione, sul versante retico della Valtellina (FUCHS-ECKERT, 1986).

Tipo corologico e areale globale. Come endemismo delle Alpi Orobie, la distribuzione della specie è limitata al territorio italiano.

Minacce. Facendo riferimento allo schema di classificazione IUCN (2012), la specie può essere considerata vulnerabile alle seguenti minacce:
Minaccia 5.2.1: *Gathering terrestrial plants. Intentional Use (species being assessed is the target).* Possibile raccolta per collezionismo nei pressi di sentieri e infrastrutture turistiche.
Minaccia 11.1: *Climate change and severe weather. Habitat shifting and alteration.* Il ritiro dei ghiacciai e la risalita dei piani altitudinali a causa del riscaldamento climatico, fenomeni particolarmente accentuati sulle Alpi Orobie, possono portare a una progressiva riduzione e frammentazione degli habitat preferenziali della specie.

Criteri IUCN applicati.

Criterio B

Sottocriteri

B1 – Areale (EOO): 160 km^2.
B2 – Superficie Occupata (AOO): 104 km^2. Calcolata mediante griglia 2 × 2 km (GARGANO, 2011).

Opzioni

a) Numero di "location": presenza accertata in 5 *locations* potenzialmente vulnerabili alle minacce 5.2.1 e 11.1 (Gruppo del Legnone, Gruppo del Masoni, Sottogruppi del Pizzo del Diavolo e del Poris, Sottogruppi del Barbellino e di Scais-Redorta, Gruppo del Telènek).
b) (iii) Declino della qualità/estensione dell'habitat: possibile riduzione e frammentazione degli habitat preferenziali a causa del riscaldamento climatico.

Categoria di rischio.
Criterio B – EOO inferiore a 5000 km^2, AOO inferiore a 500 km^2 e numero di *locations* non superiore a 5, porterebbero ad attribuire la specie ad una categoria di rischio; le minacce, però, sono da considerarsi solo potenziali e nessuna di esse fino ad ora ha comportato un effettiva riduzione del numero di individui o dell'habitat. Categoria di rischio: *Near Threatened*, (NT).

Interazioni con la popolazione globale. La popolazione regionale corrisponde alla popolazione globale.

***Status* alla scala "regionale/globale":** *Near Threatened*, (NT);
- precedente attribuzione a livello nazionale: *Not Evaluated* (CONTI *et al.*, 1992; ROSSI *et al.*, 2013; ROSSI *et al.*, 2014).

Strategie/Azioni di conservazione e normativa.
Viola comollia appartiene alla Categoria C1 "Specie di flora spontanea protette in modo rigoroso" ai sensi della L.R. n. 10/2008 "Disposizioni per la tutela e la conservazione della piccola fauna, della flora e della vegetazione spontanea" della Regione Lombardia. Fatta eccezione per la stazione del Monte Legnone, l'intera popolazione della specie è compresa nel Parco Regionale Orobie Bergamasche e nel Parco Regionale Orobie Valtellinesi, intersecando i seguenti siti Natura 2000: ZPS Parco Regionale Orobie Bergamasche (IT2060401), ZPS Parco Regionale Orobie Valtellinesi (IT2040401), ZPS Belviso Barbellino (IT2060506), SIC Alta Val Brembana - Laghi Gemelli (IT2060003), SIC Alta Val di Scalve (IT2060004), SIC Val Venina (IT2040033), SIC Val d'Arigna e Ghiacciaio di Pizzo Coca (IT2040034), SIC Val Bondone - Val Caronella (IT2040035), SIC Val Belviso (IT2040036). L'intero areale di *V. comollia* è incluso negli Elementi di Primo Livello della Rete Ecologica Regionale della Lombardia.
È da segnalare che alcune delle stazioni più periferiche e isolate di *V. comollia* sono anche tra le meno tutelate: la sottopopolazione del Monte Masoni e alcune di quelle comprese tra il Monte Demignone e il Monte Venerocolo rientrano nei Parchi Regionali, ma non nella Rete Natura 2000, mentre la sottopopolazione del Monte Legnone è esclusa da qualsiasi area protetta o sito Natura 2000. Si ritiene inoltre opportuno aggiungere la specie all'elenco floristico del Piano di Gestione del SIC Val Belviso (IT2040036).
Note. *V. comollia* è una specie endemica della Alpi Orobie scoperta e descritta da Filippo Massara nel

1834. Molto simile a *V. cenisia* L., fu temporaneamente considerata una varietà di quest'ultima assieme ad altre entità morfologicamente ed ecologicamente affini endemiche di altre regioni: *V. valderia* All. per le Alpi Marittime, *V. magellanensis* Porta *et* Rigo per l'Appennino abruzzese e *V. cenisia* s. str. (var. *typica* Fiori) per le Alpi Graie, Cozie e Marittime (Pirola, 1965).

Gli autori stanno indagando su possibili cause storiche ed ecologiche dell'attuale distribuzione di *Viola comollia*, in collaborazione con il Gruppo Flora Alpina Bergamasca e il Gruppo Floristico Massara di Morbegno. Si prevedono anche approfondimenti sulla biologia generale della specie e analisi morfofunzionali volte a calcolarne la strategia ecologica secondo la Teoria CSR (Pierce *et al.*, 2013).

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Rinvenimento di una nuova stazione di *Botrychium multifidum* (*Ophioglossaceae*) in Lombardia

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ABSTRACT - *Finding of a new stand of* Botrychium multifidum *(*Ophioglossaceae*) in Lombardy* - This work reports a new stand of *Botrychium multifidum* in Italy, localized in a rich stand of *Sanguisorba dodecandra* in the Scais Valley (Orobian Alps, Italy). An ecological and phytosociological description of the new population, and information about this *policy species* in Italy in the light of the new finding, are given.

Key words: Alpine flora*, Botrychium multifidum*, *Ophioglossaceae, policy species*, Valtellina

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INTRODUZIONE

Botrychium multifidum (S.G. Gmelin) Rupr. è una pteridofita appartenente alla famiglia delle *Ophioglossaceae,* ordine *Ophioglossales* (ANDERSON, 2005).

Si tratta di un elemento corologico circumboreale, diffuso nelle regioni temperato–fredde dell'emisfero nord, con alcune stazioni disgiunte su Alpi, Carpazi, Massiccio Centrale Francese e Himalaya (WAGNER, 1993; JONSELL, 2000; ANDERBERG, 2003), per cui PIGNATTI (1982) considera la specie anche come elemento artico–alpino. Sull'arco alpino AESCHIMANN *et al.* (2004) la indicano genericamente per l'Alta Savoia in Francia, nelle provincie di Torino, Verbania, Sondrio, Brescia, Trento, Bolzano e Belluno in Italia, in Carinzia, Stiria, Tirolo settentrionale, Tirolo orientale e Austria inferiore in Austria, in Schwaben in Germania e nella porzione alpina della Slovenia. Nella banca dati informatica sulla cartografia svizzera (www.infoflora.ch) la specie è indicata presente con due stazioni nei pressi di Davos, nel cantone Grigioni.

In Italia è rara; storicamente FIORI (1943) parla di *B. matricariae*, indicandolo come sinonimo di *B. multifidum* (FIORI, 1943) e segnalandolo in diverse località per il Trentino, l'Alto Adige, la Lombardia (riviste nel più recente lavoro di BONA *et al.*, 2005) ed il Piemonte, dove lo indica per la Val d'Ossola, presso la cascata del Rio Fultuder e presso l'Alpe la Piana: di queste stazioni non si ha certezza della presenza attuale (MARCHETTI, 2004). PIGNATTI (1982) la indica presente genericamente in Piemonte, Lombardia, Trentino Alto–Adige e Toscana. Dati più precisi sulla distribuzione in Italia nord–orientale sono disponibili in BONA *et al.* (2005), che escludono la presenza in Veneto, indicata genericamente in AESCHIMANN *et al.* (2004). In Alto Adige–Sudtirol è certamente presente in Val di Vallaga, nella limitrofa Val di Puntleid (HORN *et al.*, 2005) e in Val Arunda (WILHALM, *in litt.*), mentre è considerata incerta la presenza in Val Senales indicata in FIORI (1943) e ripresa da una segnalazione anonima del 1877 in DALLA TORRE, SARNTHEIN (1906). Per il Trentino la presenza di questa specie è stata confermata solo di recente con una stazione presso Masi di Cavalese (BERTOLLI, PROSSER, 2014), mentre non sono confermati da ritrovamenti recenti i seguenti dati storici: Val di Forzio (LOSS, 1868), Malgazza di Sotto (PFAFF, 1933), Paneveggio (Matz in Herb Gelmi, s.d., TR), Caoria (BALL, 1868), Passo Rolle, Alpe Malgazza e Regana presso Rio Vanoi (FIORI, 1943). In Lombardia la specie è nota esclusivamente per una popolazione di pochi esemplari in Val Brandet (BS), dove la stazione di crescita è seriamente minacciata a causa dell'erosione della sponda da parte del torrente Brandet (BONA *et al.*, 2005). In provincia di Sondrio è indicata la presenza da BONALBERTI *et al.* (1995),

che riprende le segnalazioni storiche di Christ (1900), Levier (1900), Furrer, Longa (1915) Fiori (1943), Fornaciari (1952), Becherer (1968) e Fenaroli (1971) per S. Carlo, Val Fontana, Pian dei Cavalli e Bormio in Alta Valtellina; in queste località non è più stata osservata negli ultimi 30 anni (Bona *et al.*, 2005). Per le restanti regioni, oltre alle segnalazioni di Fiori (1943), i dati più aggiornati disponibili sono le informazioni fornite da Salsi in Marchetti (2003), secondo il quale la specie è presente in Val Formazza (VB) e sul Monte Maiore presso l'Abetone (Ferrarini, 1986), oltre che in un vaccinieto sopra Fanano (MO), tra il monte Lagoni e il monte Libro Aperto (Herb. Salsi, Herb. Marchetti).
Alla luce dei più recenti lavori (Marchetti, 2004; Bona *et al.*, 2005) la specie risulta quindi presente con certezza esclusivamente in Alto Adige (4 stazioni), in Lombardia (2 stazioni, inclusa quella descritta nella presente nota), in Trentino (1 stazione), in Piemonte (1 stazione) e in Emilia-Romagna (2 stazioni).

Descrizione della specie

Presenta 1-2-(3) fronde sterili, inserite alla base della pianta, spesso orizzontali o appressate al suolo, lungamente picciolate, di forma triangolare, da bipinnate a tripinnate–pinnatifide, 15-65 x 18-80 mm, verde scuro lucente. Il paio inferiore di pinne è più largo degli altri. Le pinnule, di forma da obovata a triangolare, presentano un breve gambo. La fronda fertile, con un picciolo di 15-100(150) mm è nettamente più lunga della fronda sterile; presenta forma triangolare, bi-tripinnata, 20-90 x 20-60 mm, di colore rossastro. Le spore maturano dalla tarda estate fino all'autunno (Jonsell, 2000). La specie è estremamente longeva e sembra possa superare i 100 anni di età (Anderson, 2005).
B. multifidum è specie di praterie e pascoli montani e subalpini, di schiarite di vaccinieti e brughiere, su suolo acido, da 950 m a 1.900 m di altitudine (Soster, 2001). Secondo Aeschimann *et al.* (2004), sulle Alpi l'alleanza di riferimento è il *Nardion strictae* Br.-Bl. La specie predilige suoli moderatamente sabbiosi e sembra necessitare di un certo grado di disturbo, talora anche elevato (Jonsell, 2000; Anderson, 2005). Secondo Aeschimann *et al.* (2004) è un elemento corologico Nord-Americano eurosiberiamo (circumboreale), mentre la forma biologica è geofita.

Protezione

B. multifidum è specie protetta in modo rigoroso dalla Regione Lombardia secondo l'Allegato C1 della Legge Regionale 31 Marzo 2008 n. 10 ed è inclusa nell'Allegato 1 (specie di flora rigorosamente protette) della Convenzione di Berna. Per quest'ultimo motivo è stata inclusa nelle *policy species* della Lista Rossa della Flora Italiana (Rossi *et al.*, 2013), dove è classificata *Endangered* (EN), secondo il criterio IUCN B2, sottocriteri ab(*i*, *ii*, *iv*, *v*) (Gargano, 2008).

Descrizione della stazione

Nel Settembre 2011 in un rilievo eseguito in Val di Scais (SO) è stata individuata una stazione di *B. multifidum.* L'identificazione è stata eseguita mediante le chiavi analitiche di Aeschimann, Burdet, 2008. E' stato anche prelevato un campione di spore dalla fronda fertile.
La Val di Scais (SO) è situata sul versante settentrionale delle Alpi Orobie orientali, nel gruppo di Coca (Fig. 1), codice SOIUSA 29.I.A2 (Marazzi, 2005). E' percorsa dal torrente Caronno, che confluisce nel torrente Venina (proveniente dalla parallela Val Venina) poco a monte dell'abitato di Vedello (1.032 m s.l.m.), dove le due valli si uniscono in un'unica valle tributaria in destra orografica della Valtellina. Nella sua porzione più meridionale, la Val di Scais presenta ancora fenomeni di glacialismo attivo con i ghiacciai di Porola e Scais (Bonardi *et al.*, 2012), situazione non comune per le Alpi Orobie.

Fig. 1
Localizzazione della nuova stazione di *Botrychium multifidum.*
Localization of the new station of *Botrychium multifidum*.

La porzione settentrionale, tra l'abitato di Vedello e lo sbocco nella Valtellina, nella quale è ubicata la stazione in esame, è caratterizzata da affioramenti di paragneiss e micascisti della formazione degli Scisti di Edolo. A monte della diga del Lago di Scais (1.450 m) domina la formazione degli Gneiss di Morbegno; la porzione meridionale posta ad altimetria più elevata, oltre i 2.300 m di quota, è formata dalla litofacies arenacea della Formazione di Collio, che costituisce anche le vette che coronano la vedretta di Scais: Punta di Scais (3.038 m), Pizzo di Redorta (3.038 m), Pizzo Brunone (2.724 m) (Servizio Geologico d'Italia, 2011). Il fondovalle è caratterizzato lungo il corso del torrente da estesi depositi di ghiaie e diamicton massivi a clasti spigolosi, mentre i versanti sono occupati da estesi conoidi di deiezione.
Il clima della Valtellina è per la maggior parte di tipo continentale, con temperature minime nel mese di gennaio e massime a luglio e piovosità variabili da circa 700 a oltre 2.000 mm/anno. La Val di Scais, con una piovosità media annua di 1.715 mm/anno (Ceriani, Carelli, 2000) presenta condizioni climatiche di tipo più oceanico rispetto al fondovalle, pure

poco distante, a causa della sua vicinanza con il crinale orobico di confine. Per quanto riguarda la regione biogeografica, la stazione di *B. multifidum* rientra in quella eurosiberiana, Provincia alpina, settore Alpi Centrali (Rivas-Martinez *et al.,* 2004). Secondo Blasi, Frondoni (2011), la stazione è posta all'interno del settore eco-geografico 12B (*Orobie Alps Section*).

La stazione di *B. multifidum* è situata su un ampio conoide consolidato in sinistra idrografica della vallata, poco a nord dell'abitato di Agneda a 1.250 m di quota a margine della strada sterrata che porta alla diga del Lago di Scais (Fig. 2).

Fig. 2

Aspetto della stazione di ritrovamento di *Botrychium multifidum*, 17/10/2011, Val di Scais. Foto di Federico Mangili.

Finding site of *Botrychium multifidum*, 17/10/2011, Scais Valley. Photo by Federico Mangili.

Per un migliore inquadramento della vegetazione, in corrispondenza della stazione di crescita è stato effettuato un rilievo fitosociologico, riportato in Tab. 1.

La copertura vegetale è distante dalla potenzialità forestale della zona, che ricade nella serie prealpina occidentale del faggio e dell'abete rosso (*Oxalido acetoselli-Fagetum sigmetum*, Verde *et al*., 2010). L'area è infatti interessata da un moderato disturbo gravitativo e ad opera delle acque dilavanti, a cui si aggiunge con ogni probabilità l'azione antropica passata.

Descrizione della popolazione

La popolazione rinvenuta consiste in un unico individuo in buono stato vegetativo, che all'epoca del ritrovamento (17 Settembre) presentava la fronda fertile completamente sviluppata con gli sporangi giunti a maturazione. Ricerche accurate nelle vicinanze non hanno consentito di ritrovare altri individui. L'effettiva consistenza della popolazione è tuttavia da definire, in quanto la specie presenta gametofiti sotterranei e anche allo stadio di sporofito è in grado di vivere quiescente nel sottosuolo per uno o più anni (Anderson, 2005). Nel genere *Botrychium* una popolazione normalmente consiste di numerosi gametofiti sotterranei e la presenza di un singolo sporofito può comunque essere indice di una popolazione vitale (Anderson, 2005).

Tabella 1

Rilievo nella stazione di ritrovamento di Botrychium multifidum.

Phytosociological survey in Botrychium multifidum *finding site.*

Esposizione	95°
Inclinazione	20°
Quota (m s.l.m.)	1250
Superficie (m²)	10
Copertura	90%
Sanguisorba dodecandra Moretti	4
Agrostis schraderiana Bech.	2
Anthoxanthum alpinum Love & Love	1
Athyrium filix-femina (L.) Roth.	1
Brachypodium sylvaticum (Huds.) P. Beauv.	1
Chaerophyllum hirsutum L.	1
Dryopteris filix-mas (L.) Schott.	1
Fragaria vesca L.	1
Nardus stricta L.	1
Rubus idaeus L.	1
Berberis vulgaris L.	+
Dactylis glomerata L.	+
Geranium sylvaticum L.	+
Hieracium pilosella L.	+
Laburnum alpinum (Mill.) Bercht. & J. Presl.	+
Phleum pratense L.	+
Pimpinella saxifraga L.	+
Rumex alpestris Jacq.	+
Silene dioica (L.) Clairv.	+
Thalictrum aquilegifolium L.	+
Urtica dioica L.	+
Vincetoxicum hirudinaria Medik.	+
Viola riviniana Rchb.	+
Botrychium multifidum (S.G. Gmelin) Rupr.	r

Conclusioni

Il ritrovamento di *Botrychium multifidum,* entità inclusa nelle *policy species* italiane (Rossi *et al,* 2013*)* è di rilevante interesse, in quanto specie rara in tutto il suo areale e protetta da leggi regionali e internazionali; in altri Paesi (Stati Uniti) è sottoposta a specifici programmi di conservazione (Anderson, 2005). La stazione di Val di Scais porta a due i siti confermati di crescita della specie in Lombardia, che ricordiamo essere ridottissimi sull'intero territorio nazionale.

Dal punto di vista conservazionistico il sito di crescita è incluso nel Parco delle Orobie Valtellinesi, ma desta comunque preoccupazione il ridottissimo numero di esemplari presenti e la vicinanza con la strada sterrata carrabile per la diga di Scais. Si sottolinea inoltre, come ulteriore motivo d'importanza conservazionistica, la notevole presenza di

Sanguisorba dodecandra Moretti, stenoendemica inclusa nella Lista Rossa Italiana e classificata NT (*Near Threatened*) secondo la *Red List* IUCN (Gentili *et al.,* 2010).

In futuro sono necessari ulteriori sopralluoghi, sia per verificare l'eventuale presenza di *Botrychium multifidum* in altri luoghi della valle, dove non mancano gli habitat adatti ad ospitare la specie, sia per verificare il *trend* della popolazione; il particolare ciclo vitale della specie rende infatti necessaria un osservazione prolungata su più anni per valutare l'effettiva consistenza e dinamica della popolazione (Anderson, 2005). Questo vale anche per la verifica delle stazioni storicamente segnalate sul territorio italiano e per la ricerca di nuove stazioni.

La scoperta di questa nuova stazione non fa che confermare l'elevato valore qualitativo del considerevole patrimonio floristico delle Alpi Orobie, unico nell'arco alpino (Martini *et al.,* 2012).

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RIASSUNTO - Questo lavoro segnala il ritrovamento di un nuova stazione di *Botrychium multifidum* localizzata in una ricca stazione di *Sanguisorba dodecandra* in Val di Scais (Alpi Orobie, Italia). I risultati riepilogano le informazioni sulla presenza di questa *policy species* in Italia alla luce di questo nuovo ritrovamento e le caratteristiche stazionali, ecologiche e floristiche del sito di ritrovamento.

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ALCUNE OSSERVAZIONI SULL'ECOLOGIA DI *SAXIFRAGA PRESOLANENSIS* ENG. (SAXIFRAGACEAE) SU SUBSTRATI NON CARBONATICI

Federico MANGILI[1], Duccio TAMPUCCI[1], Marco CACCIANIGA[1]

Parole chiave - Flora Alpina*, Saxifragaceae, Saxifraga presolanensis, policy species,* endemismo, Direttiva Habitat.

Riassunto - Questo lavoro segnala il ritrovamento di una nuova stazione di *Saxifraga presolanensis* su substrato non carbonatico in Val Sanguigno (Alpi Orobie). Si tratta del quarto ritrovamento al di fuori degli affioramenti carbonatici prealpini delle alpi bergamasche, di cui la specie era ritenuta esclusiva. I risultati riepilogano le informazioni sulla distribuzione di questa *policy species*, con particolare riferimento alle stazioni su substrati non carbonatici e sulle loro implicazioni biogeografiche e geobotaniche.

Key words - Alpine flora, *Saxifragaceae, Saxifraga presolanensis, policy specie*s, endemic, Habitat Directive.

Abstract - Some observations on ecology of Saxifraga presolanensis Eng. (Saxifragaceae) on non carbonatics rocks. – This work report a new stand of stenoendemic species *Saxifraga presolanensis*, in Sanguigno valley (Orobian Alps), on non-carbonatic substrate . This is the fourth finding outside the carbonatic outcrops of bergamask pre-alps, where this species was held exclusively. An ecological description, and some consideration of biogeographical and geobotanic implications about this *policy species*, are given.

INTRODUZIONE

Saxifraga presolanensis Eng. è una specie stenoendemica esclusiva delle alpi e prealpi bergamasche *sensu* Marazzi (2005), dove è esclusiva dei substrati carbonatici (Arietti & Fenaroli, 1960). Nel corso del censimento floristico della Val Sanguigno (Alpi Orobie, provincia di Bergamo), realizzato dal gruppo FAB (Flora Alpina Bergamasca) nell'ambito del progetto Bi. O. S. (coordinato dal Parco delle Orobie Bergamasche e cofinanziato dalla Fondazione Cariplo), nel luglio 2012 è stata rilevata una nuova stazione di *S. presolanensis* su substrato afferente alla formazione del Verrucano Lombardo. Il litotipo è caratterizzato da stratificazioni arenacee e conglomeratiche grossolane (Jadoul & Forcella, 2000), la cui analisi mineralogica indica la presenza di feldspati-plagioclasi (0-5%) e vulcaniti, costituiti per il 10-30% da porfidi quarziferi, keratofiri e porfiriti (Assereto & Casati, 1966). Tali minerali sono solo moderatamente calcici e in ogni caso ben più poveri di carbonati di calcio rispetto alla formazione del calcare di Esino, caratterizzato dal 90-95% di $CaCO_3$ e dal 5-10% di $MgCO_3$ (Casati & Gnaccolini, 1967), sul quale è insediata la grandissima maggioranza delle stazioni note di *S. presolanensis* (Federici, 1998; Martini *at al*., 2012). Il ritrovamento, assieme a pochissimi altri già noti (v. paragrafo successivo) riveste quindi un notevole interesse ecologico e biogeografico.

DESCRIZIONE DELLA SPECIE ED AREALE

Camefita pulvinante, presenta cuscinetti del diametro di 6-12 cm. Il fusto è lignificato, con rami rivestiti da un denso involucro di foglie appressate che formano un cuscinetto emisferico, a volte allungato. Le foglie sono oblanceolate-lineari, spatolate, larghe 2-5 mm, lunghe fino a 20 mm, vischiose per la presenza di numerosi lunghi peli ghiandolari. Le foglie degli anni precedenti, grigio-argentee, sono persistenti. Ogni pulvino produce diverse infiorescenze lasse, ramificate, portanti da 2 a 4 fiori con piccoli sepali ovali e petali giallo-verdastri lunghi il doppio dei sepali, tri-dentati all'apice; il frutto è una capsula subsferica (Pignatti, 1982).

Secondo Arietti & Fenaroli (1960) e Pignatti (1982), l'habitat di questa specie è costituito da grotte, anfratti, nicchie di pareti strapiombanti non esposte all'irraggiamento solare e in "ombra d'acqua", ossia al riparo dalle precipitazioni dirette. La specie predilige stazioni esposte a nord alla base di alte pareti che scaricano valanghe, su rocce afferenti a formazioni calcaree mesozoiche. Alla base di queste pareti si accumulano frequentemente placche di neve persistente fino ad agosto-settembre, che contribuiscono a mantenere un ambiente particolarmente freddo e umido (Ferlinghetti & Bassanelli, 2011). Secondo Aeschimann *et al*. (2004) è specie strettamente calcofila del piano alpino e subalpino, la cui alleanza di riferimento è il *Cystopteridion fragilis* J.L.Rich.

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L'areale di *S. presolanensis* (Fig. 1), secondo il sistema SOIUSA, è interamente incluso nelle Prealpi lombarde centrali, sz. 29 (Marazzi, 2005), a cui si fa riferimento per la localizzazione delle stazioni. Scoperta da Engler nel 1894 (Engler & Irmscher, 1919) sul Pizzo della Presolana (codice SOIUSA 29.2.C7), la specie non è più stata osservata per quasi 60 anni, fino alla "riscoperta" nel 1966 sul gruppo del Pizzo Arera (codice SOIUSA 29.1.B5) (Merxmuller & Wiedmann, 1957). Successivamente l'areale è stato esteso al gruppo del Pizzo Camino-Concarena (codice SOIUSA 29.2.C11) con diverse stazioni a cavallo tra le province di Bergamo e Brescia (Arietti & Fenaroli, 1960) e nell'unico settore calcareo del gruppo del Monte Masoni (codice SOIUSA 29.1.B4) (Pitschmann & Reisigl, 1959, 1965), ovvero il Monte Cavallo - Monte Pegherolo. Fondamentale l'apporto dei gruppi FAB (Flora Alpina Bergamasca) e ABB (Associazione Botanica Bresciana), che a partire dalla seconda metà degli anni ottanta hanno individuato numerosissime nuove stazioni all'interno dei gruppi montuosi citati, portando a una significativa revisione dell'areale (Crescini *et al.*, 1985; Bona, 1996; Tagliaferri, 1987; Gelmi, 1989; Federici, 1998). L'areale di questa specie è quindi delimitato a settentrione dalla stazione al Pilone di Monte Fiore (Federici, 1998), a meridione dal passo di Valmora ARIETTI & FENAROLI, 1960), a occidente dal Monte Cavallo (PITSCHMANN & REISIGL, 1959) e ad oriente dalla cresta occidentale del Passo di Garzeto (BONA, 1996): da notare che questa stazione, pur posta nel gruppo del Camino – Concarena si discosta notevolmente dalle altre stazioni note in questo gruppo montuoso, andando a costituire un'estrema propaggine orientale, sempre comunque su rocce calcaree. Ai fini di questo lavoro risultano di particolare interesse le segnalazioni sul versante sud-ovest del monte Corte, in sinistra idrografica alla testata della Val Canale (codice SOIUSA 29.1.B3) e quelle situate sul versante ovest del Pilone di Monte Fiore e sulla cima del Pizzo

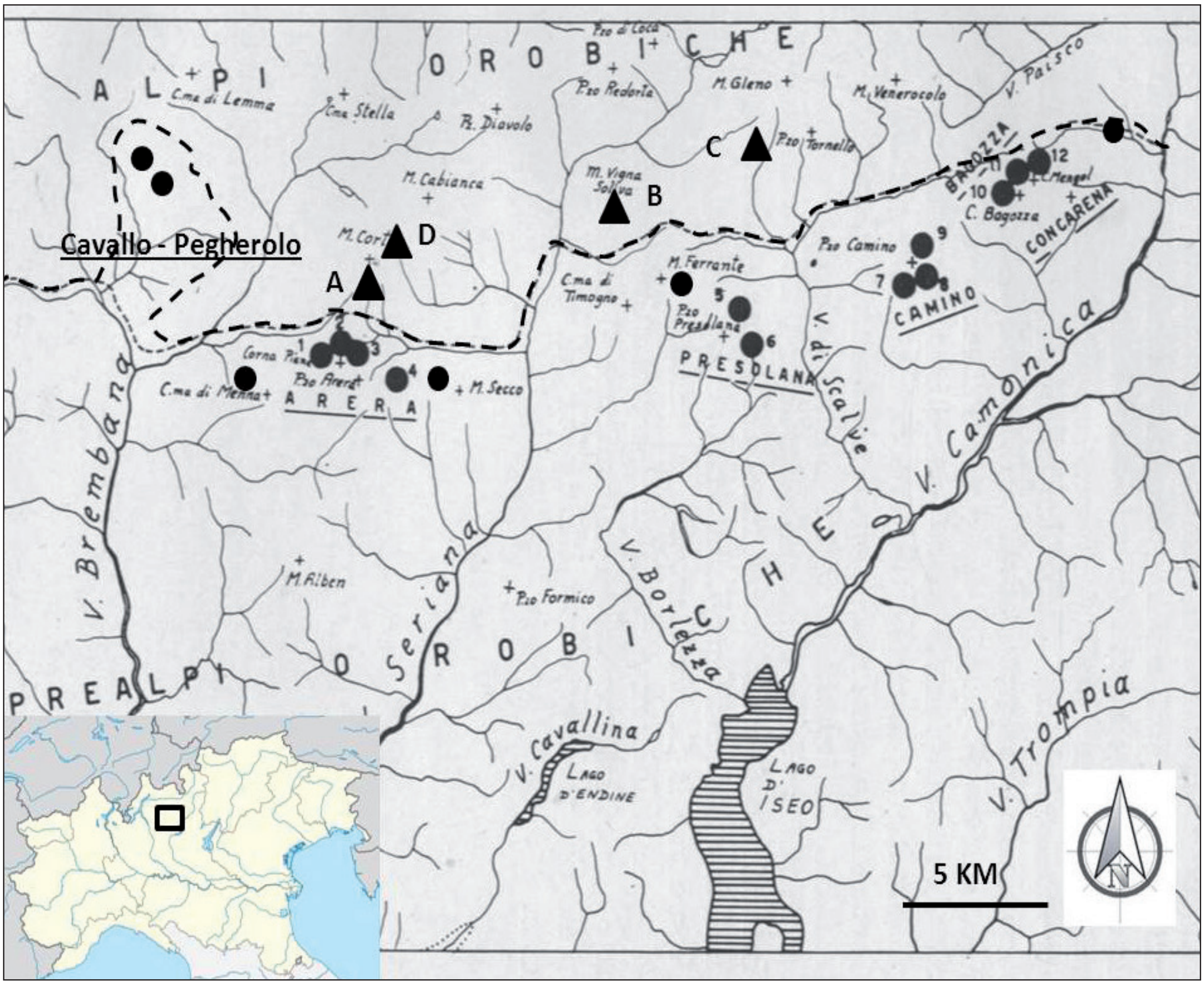

Fig. 1 - Areale di *S. presolanensis*. La linea tratteggiata separa gli affioramenti calcareo-dolomitici mesozoici dai substrati silicei. I cerchi rappresentano le stazioni note su substrato carbonatico, i triangoli quelle su substrati silicei. A: Monte Corte, versante sud-orientale (Federici, 1998); B: Pizzo della Corna (Martini *et al.*, 2012); C: Pilone di Monte Fiore (Martini *et. al.*, 2012); D: Val Sanguigno, nuova stazione. Ridisegnato da Arietti & Fenaroli (1960).

Fig. 2 - Monte Corte, Val Sanguigno (BG), versante nord, zona di ritrovamento della nuova stazione di *S. presolanensis*. 20/07/2012, foto di Federico Mangili

della Corna (codice SOIUSA 29.1.A2), alla testata della Valle Seriana (Federici, 1998; Martini *et al.,* 2012), su Verrucano Lombardo le prime due e sulla formazione del Servino l'ultima, poste rispettivamente a 5 km e 7 km di distanza dai più vicini affioramenti di calcare di Esino e stazioni di *S. presolanensis*.

Protezione

S. presolanensis è inclusa all'allegato IV della Direttiva Habitat 92/43 della Comunità Europea; è inoltre specie protetta in modo rigoroso dalla Regione Lombardia, secondo l'allegato C1 della Legge Regionale 31 Marzo 2008. Nella *red list* IUCN è valutata EN, *endangered* (Mangili & Rinaldi, 2013). È inoltre inclusa nelle *policy species* della Lista Rossa della flora italiana, dove è classificata NT, *near threatened* (Rossi *et al.*, 2013). La stazione rientra nel Parco Regionale delle Orobie Bergamasche e nell'omonima Zona di Protezione Speciale (IT2060401).

DESCRIZIONE DELLA NUOVA STAZIONE

La Val Sanguigno è una valle tributaria destra del fiume Serio appartenente al Gruppo del Poris (A.3 in Marazzi, 2005). Il substrato è costituito dalle successioni sedimentarie permiane afferenti al Verrucano Lombardo e alla Formazione di Collio (Jadoul, 2012). Il clima è di tipo oceanico, caratterizzato da precipitazioni abbondanti e costanti (1600-1800 mm/a in Ceriani & Carelli, 2000), con massimi tendenzialmente equinoziali (Grillini *et al.*, 2011). In termini bioclimatici, l'area si colloca presso le propaggini meridionali della Regione Forestale Mesalpica (Del Favero, 2002), nel campo di pertinenza delle foreste montane di *Fagus sylvatica* con *Picea excelsa* e *Abies alba* (Andreis & Sartori, 2007). Dal punto di vista fitogeografico, l'area ricade nel Distretto Lariano Sud-Orobico (Andreis *et al.*, 2005), compreso da Blasi *et al.* (2014) nell'ecoregione delle alpi centrali e orientali (*Central and Eastern Alps)*, subsezione prealpina (1A2a *Pre-Alps*). In particolare, nella partizione fitogeografica della Lombardia centro-orientale (Martini *et al.*, 2012), la Val Sanguigno si trova in prossimità della zona di transizione esoendalpica, dove si manifesta il progressivo aumento di elementi microtermi che accompagna il passaggio da Prealpi ad Alpi Orobie.

Gli esemplari di *Saxifraga presolanensis* sono stato rinvenuti in una nicchia in ombra d'acqua sulla parete nord-orientale del Monte Corte a 2210 m di quota, versante idrografico destro dell'alta Val Sanguigno (Fig.2). Il riconoscimento è avvenuto mediante le chiavi analitiche di Pignatti (1982). All'epoca del ritrovamento (19 luglio), 7 pulvini sui 10 osservati erano in antesi e in ottimo stato di salute.

Il raccordo tra la parete rocciosa e i sottostanti pascoli è costituito da un'imponente falda detritica che dà origine a un *protalus rampart* (Scotti *et al*., 2012). Il rilievo, così come il detrito sottostante, è interamente costituito da Verrucano Lombardo. L'unica possibile presenza di carbonati nelle vicinanze può essere rappresentata da arenarie e facies carbonatico-evaporitiche della Formazione di Collio, litotipi che però affiorano solo nel fondovalle e sul versante idrografico opposto (Jadoul *et al*., 2012).

La stazione è colonizzata da vegetazione casmofitica tendenzialmente acidofila. A causa delle marcate differenze geomorfologiche in uno spazio ristretto, non è stato ritenuto utile procedere all'esecuzione di un rilievo fitosociologico classico, ma sono stati redatti i seguenti elenchi floristici per le diverse morfologie della stazione:

Nicchia in ombra d'acqua: *Saxifraga presolanensis* Engler; *Cystopteris fragilis* ssp. *fragilis* (L.) Bernh.; *Viola biflora* L.

Roccia limitrofa non in ombra d'acqua: *Primula hirsuta* All.; *Rhodiola rosea* L.; *Astrantia minor* L.; *Saxifraga paniculata* Mill.; *Huperzia selago* (L.) Bernh.; *Avenella flexuosa* (L.) Parl.;

Cono detritico alla base della nicchia: *Peucedanum ostruthium* (L.) W.D.J.Koch; *Veratrum album* L.; *Cirsium spinosissimum* (L.) Scop.; *Viola biflora* L.; *Polystichum lonchitis* (L.) Roth.; *Adenostyles alliarieae* (Gouan.) A. Kern.; *Astrantia minor* L.

Al fine di inquadrare meglio le esigenze edafiche della flora compagna, si riportano di seguito gli indici ecologici relativi alla reazione del suolo secondo Landolt *et al*. (2010), di cui si riporta la legenda:

1: fortemente acido (pH 2.5 – 5.5)
2: acido (pH 3.5 – 6.5)
3: leggermente acido – neutro (pH 4.5 – 7.5)
4: neutro – debolmente basico (pH 5.5 – 8.5)
5: fortemente acido (pH 6.5 – 8.5)
I: specie stenoecia per il fattore
II: specie euriecia per il fattore

SPECIE	INDICE REAZIONE SUOLO
Saxifraga presolanensis	5 I
Cystopteris fragilis ssp. *fragilis*	4 I
Viola biflora	3 I
Primula hirsuta	2 I
Rhodiola rosea	3 I
Astrantia minor	2 I
Saxifraga paniculata	4 II
Huperzia selago	2 I
Avenella flexuosa	1 II
Peucedanum ostruthium	3 II
Veratrum album	3 I
Cirsium spinosissumum	3 II
Polystichum lonchitis	4 I
Adenostyles alliariae	3 I

Fig. 3 - Indici di reazione secondo LANDOLT *et al*. (2010) di *S. presolanensis* e della flora compagna rinvenuta.

DISCUSSIONE E CONCLUSIONI

La recente scoperta di questa nuova stazione di *S. presolanensis*, unitamente alle stazioni su substrato non carbonatico del Pilone di Montefiore, del versante meridionale del monte Corte (Federici, 1998) e del Pizzo della Corna (Martini *et al.,* 2012), riapre il problema di una migliore definizione ecologica e corologica di questa *policy species* (Rossi *et al*., 2013) stenoendemica. Si tratta, ad oggi, del quarto ritrovamento al di fuori dell'area calcareo-dolomitica prealpina, in contrasto con quanto affermato da Arietti & Fenaroli (1960), che la ritenevano esclusiva di questo settore. Nel settore esoendalpico delle Alpi Orobie (Martini *et al*., 2012) è da tempo noto il rinvenimento su substrati silicei di specie ritenute tipiche di substrati calcarei (Chenevard, 1914; Rodegher, 1929; Ravazzi & Ferlinghetti, 1986; Ferranti 1997; Martini *et. al*.), giustificato dalla vicinanza dei due contesti litologici e dalla presenza, in alcune delle formazioni geologiche orobiche di limitati quantitativi di ioni calcio e magnesio, sufficienti però allo sviluppo di specie calcifile (Ferlinghetti & Bassanelli, 2011). Non appare essere questo il caso di *S. presolanensis:* la flora compagna (Fig. 3), eminentemente silicicola secondo Landolt *et al*. (2010), con solamente altre due specie compagne in grado di tollerare occasionalmente substrati debolmente basici, esclude che la presenza di questa specie nella nuova stazione del Monte Corte sia imputabile ad una locale presenza di carbonati, ma indica invece, unitamente agli altri ritrovamenti su substrati silicei, un'effettiva capacità di crescita e sviluppo anche su substrati francamente acidi.

Questa scoperta, oltre a confermare l'elevato valore qualitativo del patrimonio floristico orobico (Martini *et. al.,* 2012), rende necessario rivedere l'ecologia di questo stenoendemita e apre alla possibilità della presenza di nuove stazioni lungo tutta la fascia di contatto tra i litotipi calcareo-dolomitici prealpini e le formazioni terrigene delle Alpi Orobie vere e proprie. Particolare attenzione andrebbe quindi posta a tutta la testata della Val Sanguigno, dove gli affioramenti di Verrucano Lombardo, oltre che sul Monte Corte, si presentano in sinistra idrografica sull'articolato spartiacque che culmina nelle Cime di Val Sanguigno - Monte Pradella - Pizzo Salina, dove non mancano nicchie e fessure adatte alla peculiare ecologia di *S. presolanensis*.

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***Galium megalospermum* All. (Rubiaceae)**

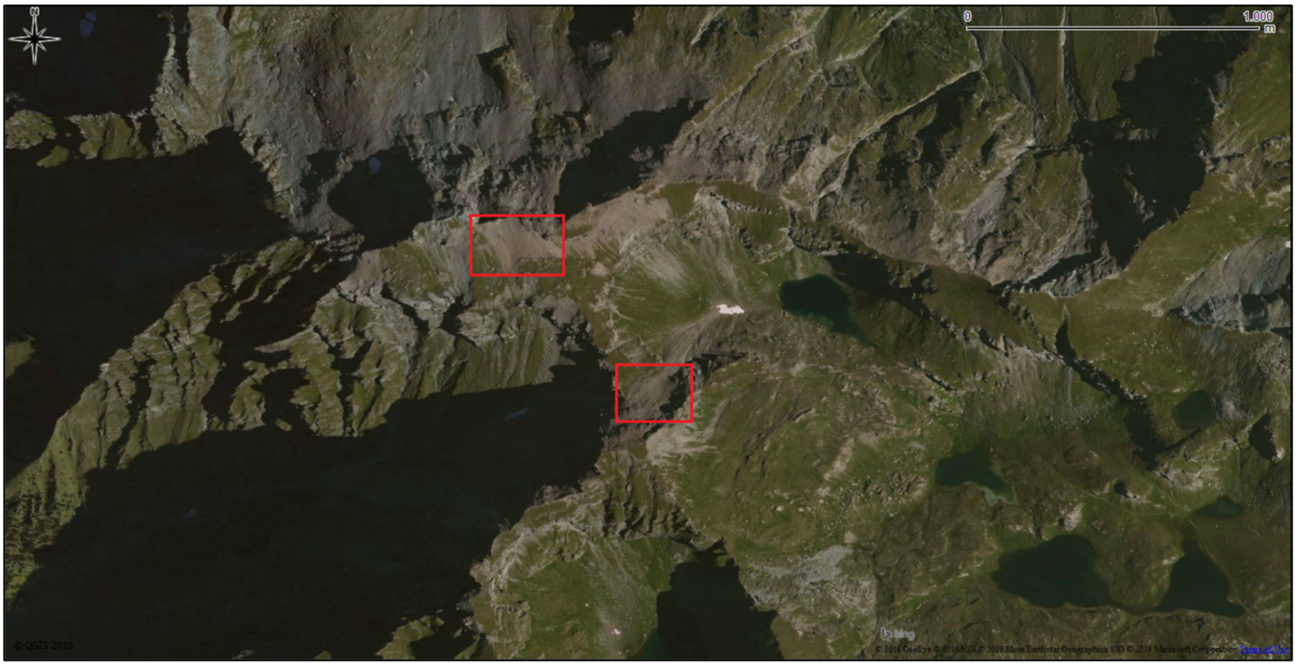
Integrazione della distribuzione regionale in Val d'Aosta (D. Tampucci)

Reperto. Val d'Ayas, Comune di Brusson (AO): presso il Colle di Bussolaz (2800m s.l.m.) e sul versante sud-orientale del Corno Bussolaz (2960-2980m s.l.m.), rupi e detriti di calcescisti. 07 agosto 2016, D. Tampucci (AO-N.SFV-3116).

Discussione. Specie endemica alpica rara ma diffusa su tutto l'arco alpino, colonizza detriti d'alta quota su substrati prevalentemente carbonatici (calcari e dolomie) e scistosi (calcescisti) (Pignatti, 1982; Aeschiman et al., 2004; Bovio et al., 2014). Pignatti (1982) riporta stazioni dai 2000m ai 3100m sia sulle Alpi occidentali (Val d'Aosta e Moncenisio) che su quelle centro-orientali (Valsugana e Giudicarie). Aeschimann et al. (2004) riportano una distribuzione pressoché continua lungo tutto l'arco alpino: nel settore occidentale sia sul versante italiano che su quelli francese e svizzero, nei settori centro-orientali su tutto il versante settentrionale e nelle sole province di Trento e Belluno sul versante meridionale. Bovio (2014) indica la specie come localizzata e rara in Val d'Aosta, generalmente distribuita dai 2000m (ma raramente sotto i 2300m) ai 3020m (Passo di Invergneux, Cogne), storicamente segnalata fino a 3164m (Rosa dei Banchi, Champorcher). La presenza in Val d'Aosta è finora accertata solo per le valli delle Alpi Graie orientali da Champorcher a Cogne, mentre sarebbero da verificare segnalazioni storiche per altre località, soprattutto nelle Alpi Pennine occidentali (Bovio et al., 2014).

Si segnala la presenza di cospicua popolazioni di *Galium megalospermum* All. in località Palasinaz (Comune di Brusson, AO), sulle Alpi Pennine orientali. Sono state individuate due stazioni principali caratterizzate da pulvini discretamente sviluppati (circa 5-15cm) e perfettamente vitali (osservati sia in fioritura che in fruttificazione). La popolazione maggiore si trova sulle pendici sud-orientali del Corno Bussolaz, su rupi e detriti di calcescisti (2960-2980m) assieme a *Herniaria alpina*, *Silene acaulis*, *Draba dubia*, *Petrocallis pyrenaica*, *Saxifraga oppositifolia*, *Campanula cenisia*, *Campanula cochlearifolia*, *Achillea nana*, *Artemisia genipi*, *Taraxacum* sp., *Festuca* cfr. *violacea* e *Trisetum distichophyllum*. Una popolazione più ridotta è stata invece localizzata sulle falde detritiche a sud-ovest del Passo di Bussolaz (2800m), in comunità strettamente glareicole con *Campanula cenisia*, *Cerastium latifolium* e *Saxifraga biflora*.

Dal punto di vista biogeografico, la presente segnalazione è coerente con l'areale noto per la specie a scala alpina, ma consente di estendere la distribuzione di *Galium megalospermum* in Val d'Aosta alle Alpi Pennine orientali, dove non era mai stata segnalata in precedenza. Dal punto di vista ecologico, la stazione è coerente con la quota e la litologia indicate in letteratura; da notare comunque una certa attitudine a colonizzare cenge rupicole oltre a detriti incoerenti. La segnalazione di *Galium megalospermum* in zona Palasinaz arricchisce ulteriormente il patrimonio floristico di una zona già ampiamente nota come una delle più ricche e interessanti della Val d'Aosta (Bovio et al., 2014).



Localizzazione di *Galium megalospermum* in località Palasinaz: a nord la stazione sul versante sud-orientale del Corno Bussolaz (2960-2980m), a sud la stazione del Passo di Bussolaz (2800m).

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