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

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Active rock glaciers are periglacial landforms consisting of coarse debris with interstitial ice or ice-core. Recent studies 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 active rock glaciers with surrounding landforms to outline their ecological peculiarities is still scarce. We analysed the abiotic (ground surface temperature and humidity, soil physical and chemical parameters) and biotic (plant and arthropod communities) features of two Alpine active rock glaciers with contrasting lithology (silicate and carbonate), and compared them with the surrounding iceless landforms as reference sites (stable slopes and active scree slopes). Our data show remarkable differences between stable slopes and unstable landforms as a whole, while few differences occur between active scree slopes and active rock glaciers: such landforms show similar soil features but different ground surface temperatures (lower on active rock glaciers) and different occurrence of cold-adapted species (more frequent/abundant on active rock glaciers). Both plant and arthropod species distributions depend mainly on the geographical context as a function of soil pH and on the contrast between stable slopes and unstable landforms as a function of the coarse debris fraction and organic matter content, while the few differences between active scree slopes and active rock glaciers can probably be attributed to microclimate. The role of active rock glaciers as potential warm-stage refugia for cold-adapted species is supported by our data; however, at least in the European Alps, their role in this may be less important than that of debris-covered glaciers, which are able to host cold-adapted species even below the climatic tree line.

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Geomorphological heterogeneity at the landscape level is known to enhance biodiversity of mountain regions, providing a wide range of environmental conditions for plant and animal taxa (Brandmayr *et al.* 2003; Körner 2003; Thaler 2003). Such ecological variability may in turn have biogeographical implications within the frame of the ongoing climate changes, as specific landforms can preserve suitable microclimate conditions for cold-adapted species even when the macroclimate becomes adverse for them (e.g. warmer and drier) (Birks & Willis 2008; Stewart *et al.* 2010; Dobrowski 2011; Scherrer & Körner 2011; Ashcroft *et al.* 2012; Keppel *et al.* 2015). Glacial and periglacial landforms have been proposed to be sources of ecological variability and potential warm-stage refugia for cold-adapted species because of their microclimate features and thermal inertia (Millar & Westfall 2010; Caccianiga *et al.* 2011; Gobbi *et al.* 2011, 2014; Millar *et al.* 2013; 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 evidence of permafrost in mountain regions, particularly where the climate is cold and dry (Barsch 1977; Haeberli 1985) and the relative contribution of debris and snow at the 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 causing a cold thermal regime partially decoupled from that of the surrounding atmosphere (Harris & Pedersen 1998; Hanson & Hoelzle 2004; Juliussen & Humlum 2008). Ice deformation gives active rock glaciers a creeping movement similar to that of glaciers but slower (generally <1 m a^{-1}; Barsch 1996; Haeberli *et al.* 2006; 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; Millar & Westfall 2010; Rieg *et al.* 2012; Millar *et al.* 2013; Gobbi *et al.* 2014). Vegetation cover and plant assemblages on active rock glaciers depend on debris

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grain size and creeping activity: 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 activity 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 a^{-1} for surface creeping velocity: below this value plant cover depends on fine-grained debris availability while above it, it is heavily affected by ground instability.

Microclimate features can also play an important role in species occurrence. The low temperatures recorded in coarse-grained zones can represent not only a limiting factor for plant establishment, but also an opportunity for cold-adapted arthropods (especially ground beetles) to find suitable thermal conditions in an unfavourable environmental context outside active rock glaciers (Gobbi *et al.* 2014). In dry mountain ranges like Sierra Nevada (USA), the microclimate features of active 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 a water reserve for hydrophilic plant and arthropod species when other kinds of springs desiccate (Millar *et al.* 2013).

Even though active rock glaciers as habitat are now increasingly studied, we are still far from a comprehensive knowledge of the ecological features of such landforms. In particular, no studies have compared active rock glaciers with the surrounding landforms as reference sites; no studies have compared such landforms in areas characterized by different lithology at the same time; and no studies have clearly contextualized active rock glaciers with respect to the altitudinal zonation of mountain ecosystems (e.g. with respect to the climatic tree line) to infer their potential as warm-stage refugia for cold-adapted species.

In the present paper we analysed the abiotic (ground surface temperature and humidity, soil physical and chemical parameters) and biotic (plant and arthropod communities) features of two Alpine active rock glaciers with contrasting lithology (silicate and carbonate) and compared them with the surrounding iceless landforms as reference sites (stable slopes and active scree slopes). Our hypotheses are: (i) active rock glaciers differ from the surrounding landforms by (a) ground surface temperature/humidity and (b) soil physical/chemical parameters; (ii) active rock glaciers differ from the surrounding landforms by (a) plant/arthropod species richness/abundance, (b) cold-adapted plant/arthropod species occurrence; and (iii) soil variables drive the distribution of plant/arthropod species on the investigated landforms. Furthermore, we aimed to infer the altitudinal distribution of active rock glaciers with respect to the altitude of the climatic tree line as the lower limit of the alpine belt (Körner 2003) to constrain the role of such landforms as potential warm-stage refugia for cold-adapted species.

Study area

The analysed active 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', latitude 46°27′N, longitude 10°49′E) is located in Val d'Ultimo, lying 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', latitude 46°30′N, longitude 10°24′E) is located in Valle del Braulio, lying 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 ~32 km apart and are characterized by the typical continental climate of the inner Alps (Tampucci *et al.* 2015a). Both investigated active rock glaciers are those at the lowest elevations of their respective areas (Seppi *et al.* 2005; Scotti *et al.* 2013). The climatic tree line at the regional scale is at 2210 m a.s.l., thus ~150 and 300 m below the lowest active rock glaciers of the two study areas, respectively. The altitude of the climatic tree line was estimated as follows: 8 years (2004–2011) of mean daily temperature at 1900, 2255 and 3125 m a.s.l. were used to calculate the monthly mean altitudinal temperature lapse rate at the regional scale; 30 years (1983–2012) of mean daily temperature at 1900 m a.s.l. were used to obtain the altitude of the climatic tree line at the regional scale following Paulsen & Körner (2014) (data provided by Meteo Service of the Province of Bolzano: http://www.provincia.bz.it/meteo/home.asp).

Data collection

Sampling design

We selected three adjacent landforms for each study area, corresponding to three different ecological conditions: (i) stable slope (landform with stable fine-grained soil and no permafrost evidence, supposed to have the potential for full development of plant and arthropod communities), (ii) active scree slope (landform with unstable coarse-grained debris and no permafrost evidence), and (iii) active rock glacier (landform with unstable coarse-grained debris and permafrost evidence).

A data-logger (Tinytag TGP-4500) was placed at each landform in order to analyse the patterns of mean daily ground surface temperature and humidity during the year 2014. The devices were placed between stones at a depth ranging from 10 to 15 cm, in order to shield

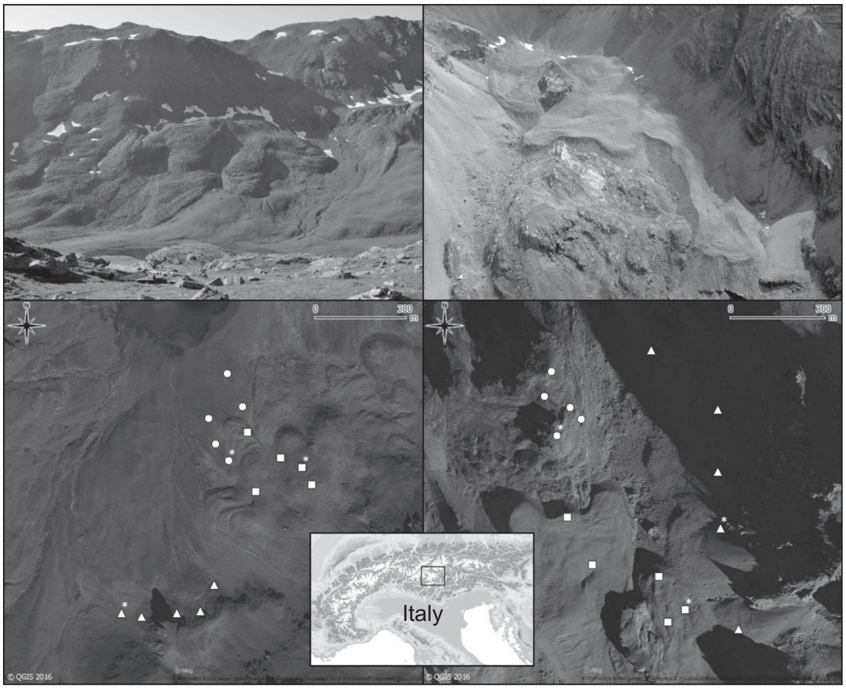

Fig. 1. Investigated landforms in Val d'Ultimo (left) and Valle del Braulio (right) with positions of the respective plots (bottom). Plots are shown depending on the landform as follows: stable slopes (circles), active scree slopes (triangles), active rock glaciers (squares). Data-loggers were placed in marked plots (*). The square in the small insert panel indicates the location of the Ortles-Cevedale massif.

them from direct solar radiation. The recording was set at 1-h intervals; 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 five plots for each landform (Fig. 1) and three sampling points for each plot, randomly placed ~10 m apart from each other. Substrate samples were taken at the surface for physical and chemical analysis: at each plot a sample of ~1 kg was taken for particle size distribution analysis; at each sampling point a sample of ~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 25 m^2 were performed, estimating the percentage of bare soil surface and the ground cover of each vascular plant species with a resolution of 5% (we conventionally assigned 1% ground cover to rare species). Arthropod species sampling was performed by 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) as their ecology is well known (Brandmayr *et al.* 2003; Thaler 2003) and they have been extensively used as bioindicators of climate change in high latitude–altitude ecosystems (e.g. Gobbi *et al.* 2007; Bråten *et al.* 2012; Moret *et al.* 2016).

Environmental and community variables

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

The landform was considered as a categorical variable with three classes (stable slope, active scree slope, active rock glacier). The following soil variables were considered: bare soil surface ('Bar.so', expressed as percentage), coarse debris fraction ('Coa.fr', sum of gravel and sand fractions expressed as percentage), soil pH ('pH'), calcium carbonate content ('Cal.ca', expressed as percentage) and organic matter content ('Org.ma', expressed in g kg^{-1}). The following community variables were considered: plant species richness ('Pla.ri', number of plant species), plant cumulative ground cover ('Pla.ab', sum of every plant species ground cover expressed as percentage), arthropod species richness ('Art.ri', number of ground beetle species plus number of spider species) and arthropod total activity density ('Art.ab', sum of ground beetle and spider activity densities: ratio between number of captured specimens and number of days of trap activity). The abundance of each plant species was expressed as ground cover percentage; the abundance of each arthropod species was expressed as activity density. Species nomenclature is after Landolt *et al.* (2010) for plants, Vigna Taglianti (2013) for ground beetles and World Spider Catalog (2016) for spiders.

Data analysis

Comparison amongst landforms

To compare the landforms in terms of microclimate features, descriptive statistics (mean value and standard deviation) of ground surface temperature and humidity 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 ground surface temperature standard deviation <0.2 °C on the basis of 1-h recording interval) and the snow-free period (period with daily ground surface temperature standard deviation >0.2 °C on the basis of 1-h recording interval). The snow-cover period includes the zero-curtain period, 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), thus the period with ground surface temperature ranging from −0.25 to 0.25 °C (Gubler *et al.* 2011). To analyse the differences in ground surface temperature and humidity amongst the landforms during the snow-cover period, 2 months during which all the landforms in both areas were snow-covered but outside the zero-curtain period were analysed: February and March 2014. To analyse the differences in ground surface temperature and humidity amongst the landforms during the snow-free period, 2 months during which all the landforms in both areas were snow-free were analysed: 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 the response variable except for landform, which was included as an explanatory one. For all soil variables and plant cumulative ground cover, quantile regression models (Cade & Noon 2003) were used; thus the median values of each variable were compared amongst landforms. To account for the correlation amongst sampling points within each plot (Gobbi & Brambilla 2016), 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 total activity density), generalized linear models with Poisson error were used. To account for the correlation amongst sampling points within each plot (Gobbi & Brambilla 2016), the models were estimated with generalized estimating equation methods (Zeger *et al.* 1988; Dormann *et al.* 2007), using an exchangeable working covariance matrix. Results from all the models were reported in terms of estimated differences between medians (quantile regression models) or mean ratios (generalized linear models) of the compared landforms, with the respective 95% confidence intervals. The confidence intervals were adjusted with the Bonferroni rule for multiple comparisons.

To identify characteristic plant and arthropod species of each landform, indicator species analysis (Dufrêne & Legendre 1997) was used. The IndVal index for abundance data was used to quantify the association between each species and each landform. Once the highest-associated landform was identified for each species, such association was assessed through a permutation test (number of permutations: 9999). In order to account for the sampling design, a restricted permutation scheme was adopted, in which the observations within each plot could not exchange with observations of other plots.

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

Relationships amongst variables and species ordination

To analyse the relationships amongst 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 ground cover for each plant species (22 plant species out of 118 were omitted because they occurred in only one plot) and the sum of activity densities for each arthropod species.

To evaluate the association amongst soil and community variables, principal component analysis methods were used. The assumption of linear correlation was checked by examining monotone correlation coefficients (Spearman's rho) and scatterplots for each pair of variables; due to the presence of some non-linear relationships, the principal component analysis was carried out on the ranks of the variables. Soil parameters were used as active variables; community parameters were included as passive variables to evaluate their association with soil parameters.

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

All analyses were performed with the R software (R Core Team 2015), with the packages FactoMineR (Husson *et al.* 2016) and vegan (Oksanen *et al.* 2015).

Results

Comparison amongst landforms

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

Unstable landforms differ from the stable slopes by 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 outlier values on the active rock glacier of Val d'Ultimo) (Fig. 3, Tables 2, S1). Similarly, unstable landforms differ from the stable slopes by lower plant species richness and cumulative ground cover (Fig. 3, Tables 2, S1). The median values of arthropod community variables at the level of plot showed no differences amongst the landforms (Fig. 3, Tables 2, S1), but the total values at the level of landform showed remarkable differences between stable slopes and unstable landforms, the former being characterized by higher species richness and total activity density (Table S1).

According to indicator species analysis result (Table S1), 48 plant species were significantly linked to the stable slopes (21 on silicate substrates and 27 on carbonate ones). The species most significantly linked (IndVal ≥ 0.90, $p \leq 0.0006$) to the stable slopes were: *Anthoxanthum alpinum*, *Potentilla aurea*, *Primula glutinosa*, *Carex curvula*, *Loiseleuria procumbens*, *Leontodon helveticus*, *Vaccinium gaultherioides*, *Soldanella alpicola* and *Ligusticum mutellina* for silicate substrates; and *Carex firma*, *Agrostis alpina*, *Dryas octopetala*, *Sedum atratum*, *Ranunculus alpestris* and *Saxifraga caesia* for carbonate substrates. Fourteen plant species were significantly linked to the active 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 substrates (*Saxifraga aphylla*, *Pritzelago alpina*, *Papaver aurantiacum*, *Arabis pumila* and *Poa minor*). Six plant species were significantly linked to the active rock glaciers: four on silicate substrates (*Poa laxa*, *Doronicum clusii*, *Senecio carniolicus* and *Saxifraga bryoides*) and two on carbonate substrates (*Arabis caerulea* and *Arabis alpina*).

According to indicator species analysis result (Table S1), four arthropod species were significantly linked to

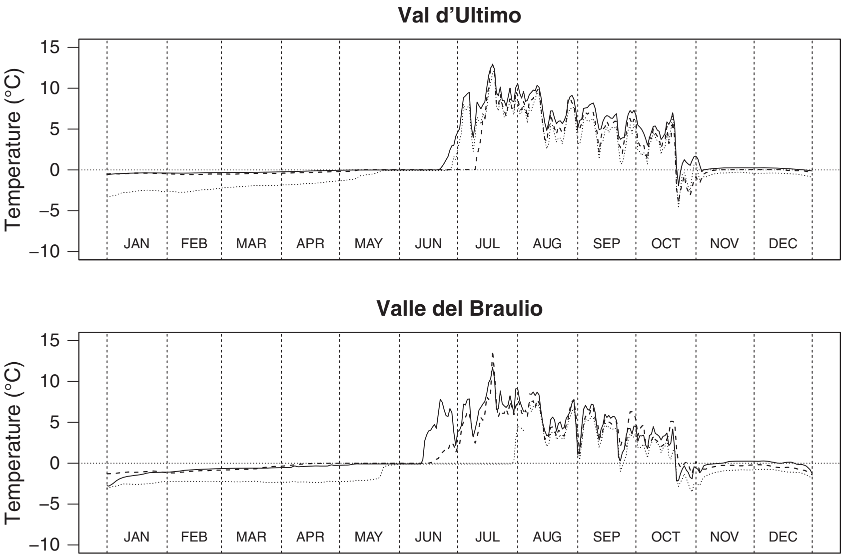

Fig. 2. Patterns of mean daily temperature of the investigated landforms over 2014: stable slopes (continuous lines), active scree slopes (dashed lines), active rock glaciers (dotted lines).

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

Landform	Altitude (m a.s.l.)	Aspect (°)	Slope (°)	Period	Length (days)	Ground surface temperature (°C)	Ground surface humidity (%)
Val d'Ultimo							
1. Stable 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)
				August–September	61	7.13 (1.68)	92.27 (7.86)
				Year	365	2.21 (3.54)	96.85 (6.57)
2. Active 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)
				August–September	61	6.12 (1.85)	95.03 (6.85)
				Year	365	1.47 (3.13)	98.54 (4.53)
3. Active rock glaciers	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)
				August–September	61	5.25 (2.00)	95.51 (6.94)
				Year	365	0.77 (3.48)	97.41 (7.33)
Valle del Braulio							
1. Stable 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)
				August–September	61	5.30 (2.09)	96.89 (4.89)
				Year	365	1.55 (3.14)	98.78 (3.60)
2. Active 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)
				August–September	61	5.09 (1.65)	96.48 (6.51)
				Year	365	1.28 (2.80)	98.69 (4.56)
3. Active rock glaciers	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)
				August–September	61	3.95 (1.86)	99.42 (2.00)
				Year	365	−0.42 (2.40)	99.91 (0.82)

the stable slopes: the ground beetles *Cymindis vaporariorum* (found both on silicate and carbonate substrates) and *Carabus sylvestris* (found only on carbonate substrates) and the spiders *Pardosa giebeli* and *Xysticus desidiosus* (both found only on carbonate substrates). One spider was significantly linked to the active scree slopes: *Anguliphantes monticola* (found both on silicate and carbonate substrates). Two spiders were significantly linked to the active rock glaciers: *Pardosa nigra* (found both on silicate and carbonate substrates) and *Sitticus longipes* (found only on carbonate substrates).

Relationships amongst 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, and 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 with the other soil variables; arthropod species richness and total activity density were positively correlated with each other but poorly correlated with the other variables (Fig. 4, Table 3).

The first two axes of the canonical correspondence analysis of the plant species (Fig. 5) explained 32.31% of the total explained inertia (18.45 and 13.86% for the first and second axes, respectively). The first axis was highly correlated with soil pH (*r* index = 0.97) and separated the two study areas, while the second axis was correlated with organic matter content and coarse debris fraction (*r* index = 0.82 and −0.59, respectively) and separated stable slopes from unstable landforms. The canonical correspondence analysis plot showed a clear partition into four main groups of sites corresponding to stable slopes and unstable landforms on silicate and carbonate substrates, respectively. No distinction was found between active scree slopes and active rock glaciers.

The first two axes of the canonical correspondence analysis of the arthropod species (Fig. 5) explained 17.78% of the total explained inertia (10.19 and 7.59% for the first and second axes, respectively). The first

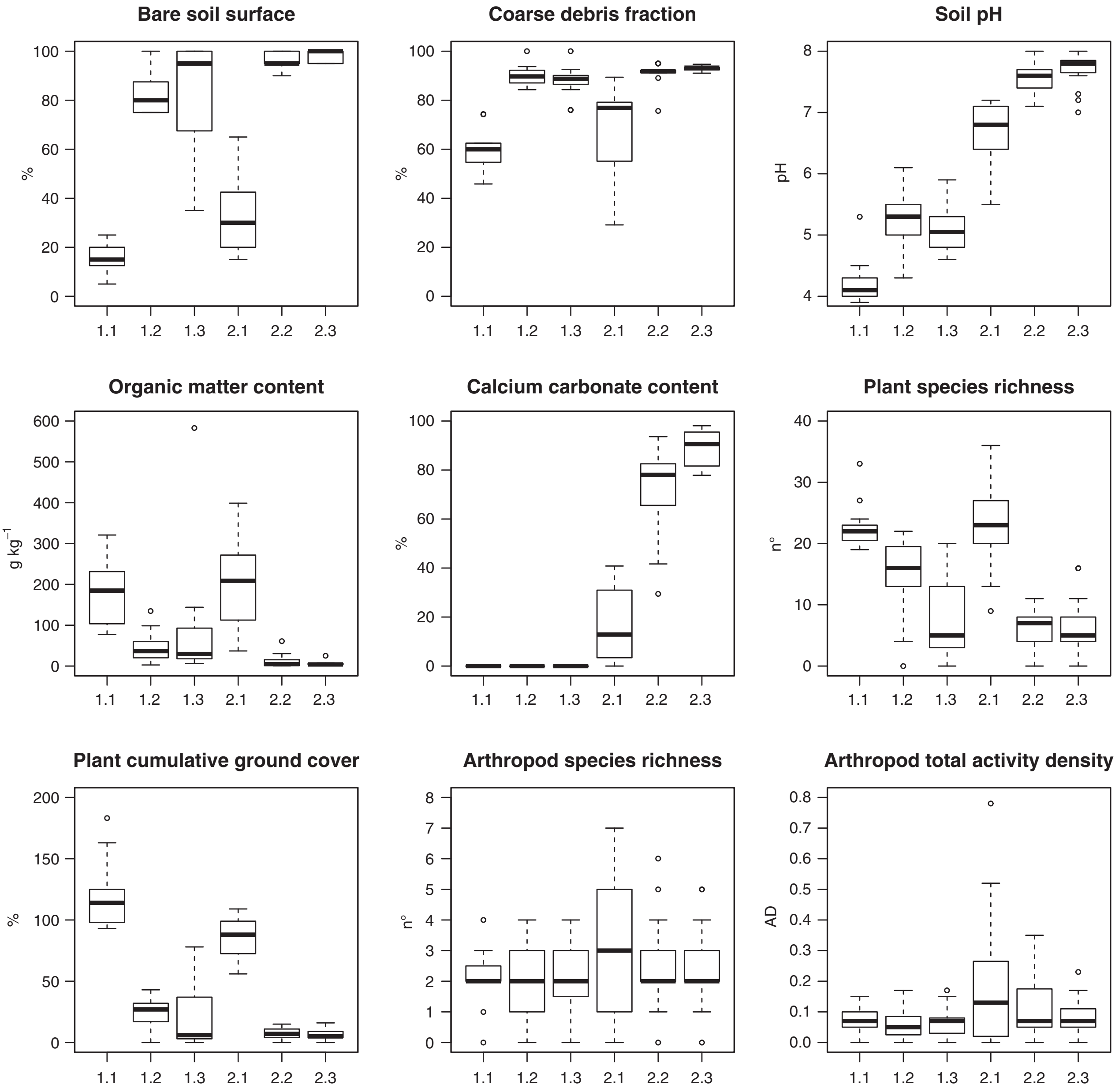

Fig. 3. Boxplot of each variable for the investigated landforms. Val d'Ultimo: stable slope (1.1), active scree slope (1.2), active rock glaciers (1.3). Valle del Braulio: stable slope (2.1), active scree slope (2.2), active rock glaciers (2.3).

axis was correlated with organic matter content (*r* index = −0.71) and separated the stable slope on carbonate substrates from the other landforms, while the second axis was highly correlated with soil pH (*r* index = 0.92) and separated the unstable landforms on carbonate substrates from the other landforms. The coarse debris fraction was fairly equally correlated with both the first and the second axes (*r* index = 0.58 and 0.64, respectively). The canonical correspondence analysis plot did not show a clear partition, but showed a cloud of sites and species in which two main gradients are recognizable: the main one occurring from stable slopes to unstable landforms and a secondary one tending to separate the two study areas. No distinction was found between active scree slopes and active rock glaciers.

Discussion

Ecology of active rock glaciers and surrounding landforms

The comparison amongst landforms in terms of abiotic and biotic features shows overall remarkable differences between stable slopes and unstable landforms (active scree slopes and active rock glaciers), while few

Table 2. Results of the multiple comparisons of variables amongst landforms: stable slopes (1), active scree slopes (2), active rock glaciers (3). All the comparisons were carried out with quantile regression models, except plant species richness, arthropod species richness and arthropod total activity density, which were carried out with generalized linear models (Poisson distribution). Results are reported as Est (95% C.I.).

Variable	3 vs. 2	3 vs. 1	2 vs. 1
Val d'Ultimo			
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})	−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)
Plant 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)
Valle del Braulio			
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})	−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)
Plant 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)

differences occur between active scree slopes and active rock glaciers.

The ground surface temperature of stable slopes is 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 with values of

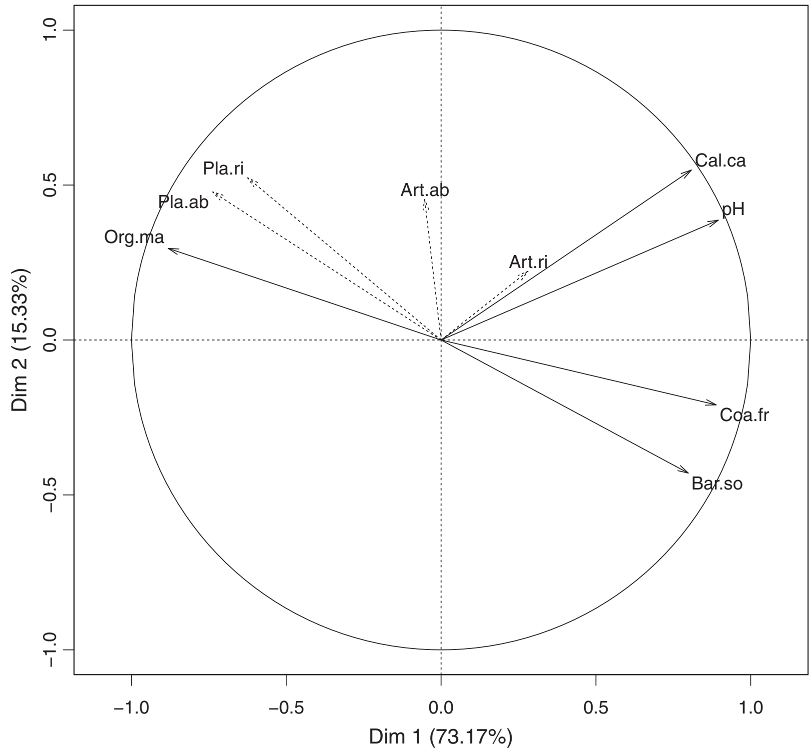

Fig. 4. Principal component analysis diagram showing the mutual relationships amongst variables: bare soil surface (Bar.so), coarse debris fraction (Coa.fr), soil pH (pH), organic matter content (Org.ma), calcium carbonate content (Cal.ca), plant species richness (Pla.ri), plant cumulative ground cover (Pla.ab), arthropod species richness (Art.ri), arthropod total activity density (Art.ab).

Table 3. Correlation amongst 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), plant cumulative ground cover (Pla.ab), arthropod species richness (Art.ri), arthropod total activity density (Art.ab). Results are reported as Spearman's index of monotone correlation (rho).

	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

approximately 0 °C due to the latent heat effect of freezing or thawing soil; and 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 active scree slopes show a ground surface temperature pattern substantially analogous to that of stable slopes, active rock glaciers are characterized by overall lower values (despite not necessarily higher ground surface humidity and longer-lasting snow cover), probably as a consequence of the thermal effect of underlying ice (Hoelzle *et al.* 1999). Hypothesis ia (active rock glaciers differ from the surrounding landforms by ground surface temperature/humidity) is thus supported by our data concerning temperature.

The soils of stable slopes can be considered more developed than those of unstable landforms, as organic matter content is higher and the coarse debris fraction, calcium carbonate content (where present) and soil pH are lower (Matthews 1992; Tampucci *et al.* 2015b). Active scree slopes and active rock glaciers show similar soil features. Hypothesis ib (active rock glaciers

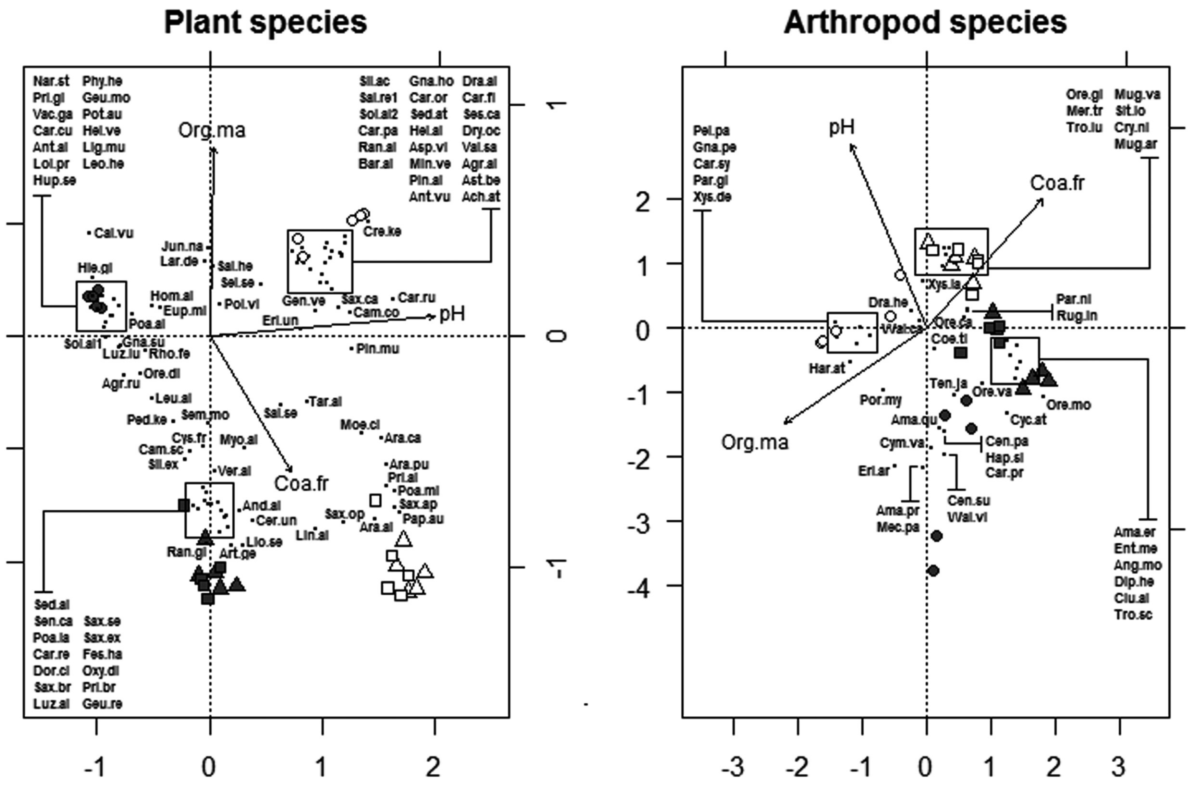

Fig. 5. Canonical correspondence analysis ordination plots of plant and arthropod species with soil variables: coarse debris fraction (Coa.fr), soil pH (pH), organic matter content (Org.ma). Areas: Val d'Ultimo (black shapes), Valle del Braulio (white shapes). Landforms: stable slopes (circles), active scree slopes (triangles), active rock glaciers (squares). Species are indicated by the codes reported in Table S1.

differ from the surrounding landforms by soil physical/chemical parameters) is thus partially supported by our data.

The stable 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 substrates (Grabherr & Mucina 1993; Oberdorfer 1998). Similarly, the arthropod communities are characterized by relatively high species richness and total 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 though plant and arthropod communities of active scree slopes and active rock glaciers show few differences in terms of species richness and abundance, some characteristic species of each of the two landforms can be identified. Active 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 substrates; Grabherr & Mucina 1993; Oberdorfer 1998) and by a spider widespread over a wide altitudinal range (*Anguliphantes monticola*; Nentwig *et al.* 2016); active 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, hypothesis iia (active rock glaciers differ from the surrounding landforms by plant/arthropod species richness/abundance) is partially supported by our data, while hypothesis iib (active rock glaciers differ from the surrounding landforms by 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, and the coarse debris fraction and organic matter content indicate the distinction between stable slopes and unstable landforms as a 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 same cannot be said for arthropods: species found only on one of the two substrates in our study (e.g. the ground beetle *Carabus sylvestris* and the spiders *Xysticus desidiosus* and *Pardosa giebeli* on the carbonate substrate) were previously found on the other substrate (e.g. Gobbi *et al.* 2006a, b, 2010, 2014). The differences in the arthropod fauna between the two study areas are thus not attributable to the substrate itself, but probably to other micro-habitat factors (the scenopoetic ones, sensus Soberón 2010). The coarse debris fraction and organic matter content explain the plant and arthropod community differences between stable slopes and unstable landforms as a whole, but soil features are not enough to discern active scree slopes and active rock glaciers. Our third hypothesis (the soil variables drive the distribution of plant/arthropod species through the investigated landforms) is thus partially supported by our data, both on silicate and carbonate substrates.

To summarize, active scree slopes and active rock glaciers show substantially analogous soil features, but different ground surface temperatures (lower on active rock glaciers) and different occurrences of cold-adapted species (more frequent/abundant on active 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 with the data collected by Gobbi *et al.* (2014) in the nearby (~30 km apart from Val d'Ultimo and ~40 km apart from Valle del Braulio) Amola active rock glacier (Val d'Amola, Adamello-Presanella Massif, central Italian Alps), to our knowledge the only previous study with a similar approach. The active rock glacier of Val d'Amola, in contrast with those of Val d'Ultimo and Valle del Braulio, is characterized by large populations of cold-adapted ground beetle species. This difference could be due to the physical peculiarities of Amola active rock glacier, in particular: (i) the occurrence of metric boulders able to prevent a uniform snow-cover (thus an efficient thermal insulation of soil from air in winter), and (ii) a mean annual ground surface temperature much lower with respect to the adjacent active 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 a limiting factor for plant survival. On the herein investigated active rock glaciers, the occurrence of smaller boulders and ground surface temperature more similar to that of active scree slopes may sustain cold-adapted plants, but are probably not enough to affect the distributions of ground beetles.

The lithological contexts in which active rock glaciers occur can affect the soil physical and chemical parameters themselves as well as the ground surface temperature as a function of grain-size distribution. Although each active rock glacier shows relatively low values of species richness and abundance, their wide distribution at a regional scale and their high variability due to lithology could provide suitable habitats for a wide range of plant and arthropod species depending on their specific ecological requirements. Even though the sample size is low (two active rock glaciers plus that described by Gobbi *et al.* 2014), the observed sites cover a broad array of substrate conditions: carbonate rocks with relatively small grain size (Valle del Braulio), metamorphic rocks with coarse debris (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 and microclimate parameters, but does not affect the coherent overall picture of active rock glaciers as cold environments decoupled from the surrounding climate conditions.

Active rock glaciers as warm-stage refugia?

Cold-adapted species are often amongst the first to be affected by current climate change as a consequence of the progressive reduction of their habitat due to temperature increases 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 & Westfall 2010; Millar *et al.* 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 active rock glaciers supports this view indicating decoupling of the local topoclimate from the regional climate, a key factor for a site to serve as a refugium (Dobrowski 2011; Keppel *et al.* 2012). A critical point lies in the capability of active rock glaciers to persist under adverse climate conditions: many studies have shown that active rock glaciers, despite their thermal inertia (Frauenfelder & Kääb 2000), tend to become climatically inactive and then relict (without ice) once the climate becomes unsuitable (Barsch 1996; Sorg *et al.* 2015). Furthermore, enhanced activity may occur at a decadal scale in correspondence with warm periods (Sorg *et al.* 2015), making active rock glaciers difficult to colonize during these critical climatic stages.

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

Conclusions

This study, performed with a multidisciplinary approach, provided a detailed explanation of the environmental correlates able to drive the plant and arthropod species richness, abundance and assemblage composition of some high-altitude Alpine landforms. Our observations confirm that in the present warm-climatic stage Alpine rock glaciers are suitable habitats for cold-adapted species, but highlight that their role as warm-stage refugia should be considered with caution, as it depends on the length of the warm-climate stage, the thermal inertia of active rock glaciers and the macroclimatic context in which they are located.

Surely, as recommended by Millar *et al.* (2013), repeated measurements of other rock glaciers, scree slopes and reference sites would allow assessment of the refugial potential of these landforms. In our opinion, a future challenge should be to apply insular biogeography concepts (Watson 2002) in order to examine the factors affecting the extinction risk of the cold-adapted species living on periglacial and glacial landforms. Such landforms can be considered suitable habitats for cold-adapted species surrounded by a matrix of unsuitable habitat; the populations of cold-adapted plants and arthropods are thus partially or completely isolated. Therefore, the extinction risk for these species is not only linked to the persistence of refugia (like periglacial and glacial landforms) in adverse climate conditions, but also to their degree of isolation (distance to the nearest neighbouring landform), the size of the island (area of the landform) and the genetic diversity of the populations, which is probably low due to the isolation and to possible bottleneck effects.

These factors emphasize the importance of periglacial and glacial landforms for organism biogeography as well as for conservation biology.

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Supporting Information

Additional Supporting Information may be found in the online version of this article at http://www.boreas.dk.

Table S1. Synoptic table at landform level. Soil and community variables are expressed as median values (with minimum and maximum values in parentheses), followed by total values at landform level (for community variables only). The abundance (Ab) of each plant species is expressed as mean value of ground cover in percent; the abundance (Ab) of each arthropod species is expressed as sums of activity densities (ara = spider; car = ground beetle). For each species the following are indicated: IndVal for each landform (IndVal), highest-associated landform (h.a.l.), significance of the association with the highest-associated landform (*p*-value, with * for significant association).