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

Duccio Tampucci^{a*}, Mauro Gobbi^b, Patrizia Boracchi^d, Erika Cabrini^a, Chiara Compostella^c, Federico Mangili^a,
Giuseppe Marano^d, Paolo Pantini^e and Marco Caccianiga^a

^aDipartimento di Bioscienze, Università degli Studi di Milano, Milano, Italy; ^bSezione di Zoologia degli Invertebrati e Idrobiologia, MUSE - Museo delle Scienze, Trento, Italy; ^cDipartimento di Scienze della Terra, Università degli Studi di Milano, Milano, Italy; ^dFondazione IRCSS Istituto Nazionale Tumori di Milano, Struttura Complessa di Statistica Medica, Biometria e Bioinformatica, Milano, Italy; ^eMuseo Civico di Scienze Naturali "Enrico Caffi", Bergamo, Italy

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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 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).

*Corresponding author. Email: duccio.tampucci@unimi.it

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 tree-line (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 m² surfaces at each sampling point. The percentage cover of rock outcrop, debris, soil, whole plant cover and of every plant species were estimated with a resolution of 5%. Arthropods data were collected through pitfall traps: a plastic cup 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

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5 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).

10 *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 assemblages 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: (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 = 1 (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 stages (c. 1–30 years since deglaciation); (2) early-successional stages (c. 31–100 years since deglaciation); (3) mid-successional stages (c. 101–150 years since deglaciation); (4) late-successional stages (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 m² 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 $-0.69\text{ °C (100 m)}^{-1}$ on the investigated landform. All soil parameters were correlated to each other (supplementary Table 1s) 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).

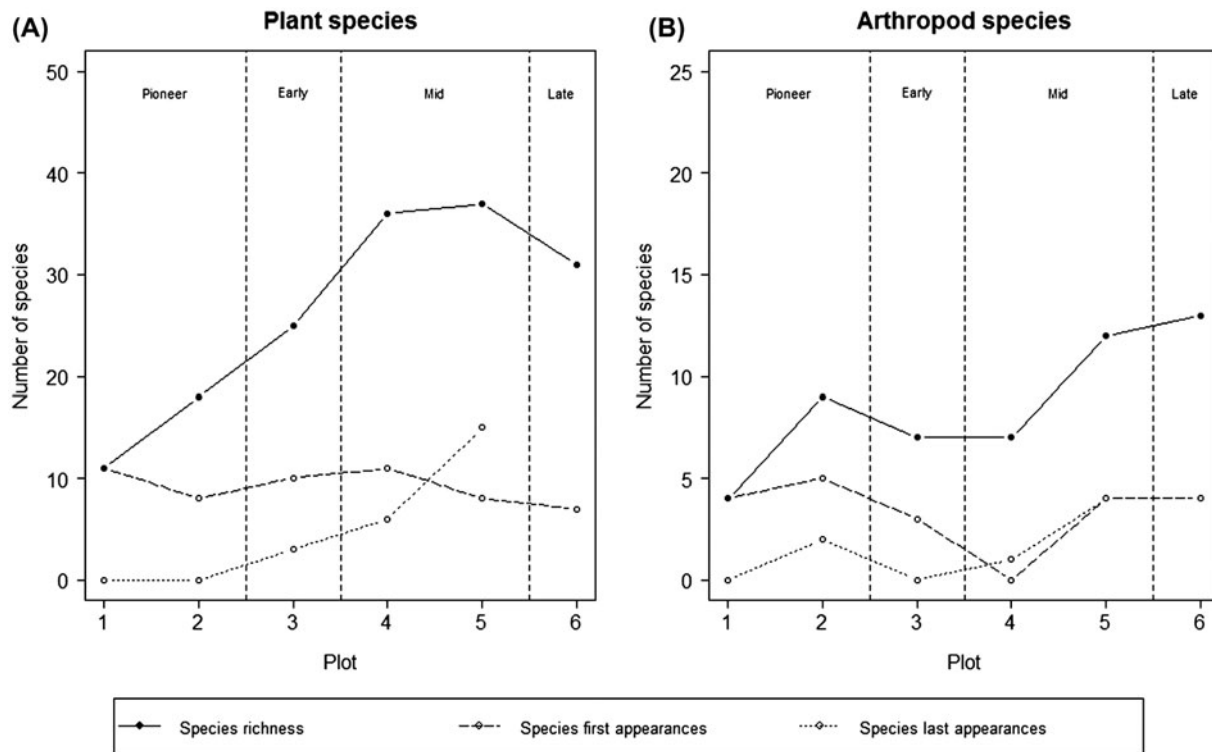
Seventy-two plant species were recorded (Table 1), among which the most frequent were *Poa alpina* and *Silene acaulis* (occurring in 83% of the sampling points), followed by *Saxifraga oppositifolia* (70%), *Androsace alpina*, *Artemisia genipi*, *Festuca quadriflora* and *Oxyria digyna* (50%). Twenty-nine 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 stages, each characterised by distinct vegetation and soil features (supplementary Figure 5 and Table 2). The first stage lasted about 95 years, 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 stage lasted 90 years at least (we are able to observe the succession only since LIA), 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 alpino-pilosa* and *Poa alpina*) and cushion species (e.g. *Saxifraga bryoides* and *Silene acaulis*). The last stage occurred on terrain ice free since LG and not involved in Holocene glacial dynamics, thus 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 1(a)) regularly increased from pioneer stages to the terrain ice-free since the beginning of the twentieth century, stabilised in the terrain ice-free since the LIA and decreased in those ice-free since the LG. 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

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5 stages lacked a specific arthropod community and were rather characterised by the overlapping of species belonging to the 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 1(b)) 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

20 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.

25 The pattern of plant species richness (Figure 2(a)) 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

2(b)), while species entrances on inner Alpine chronosequences reached the maximum in different stages depending on the glacier elevation: pioneer on Morteratsch, early-successional on Rotmoos and late-successional on Cedec. Species last appearances (Figure 2(c)) 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 (e.g. 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 2(d)): 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 2(e)) 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 2(f)) 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.

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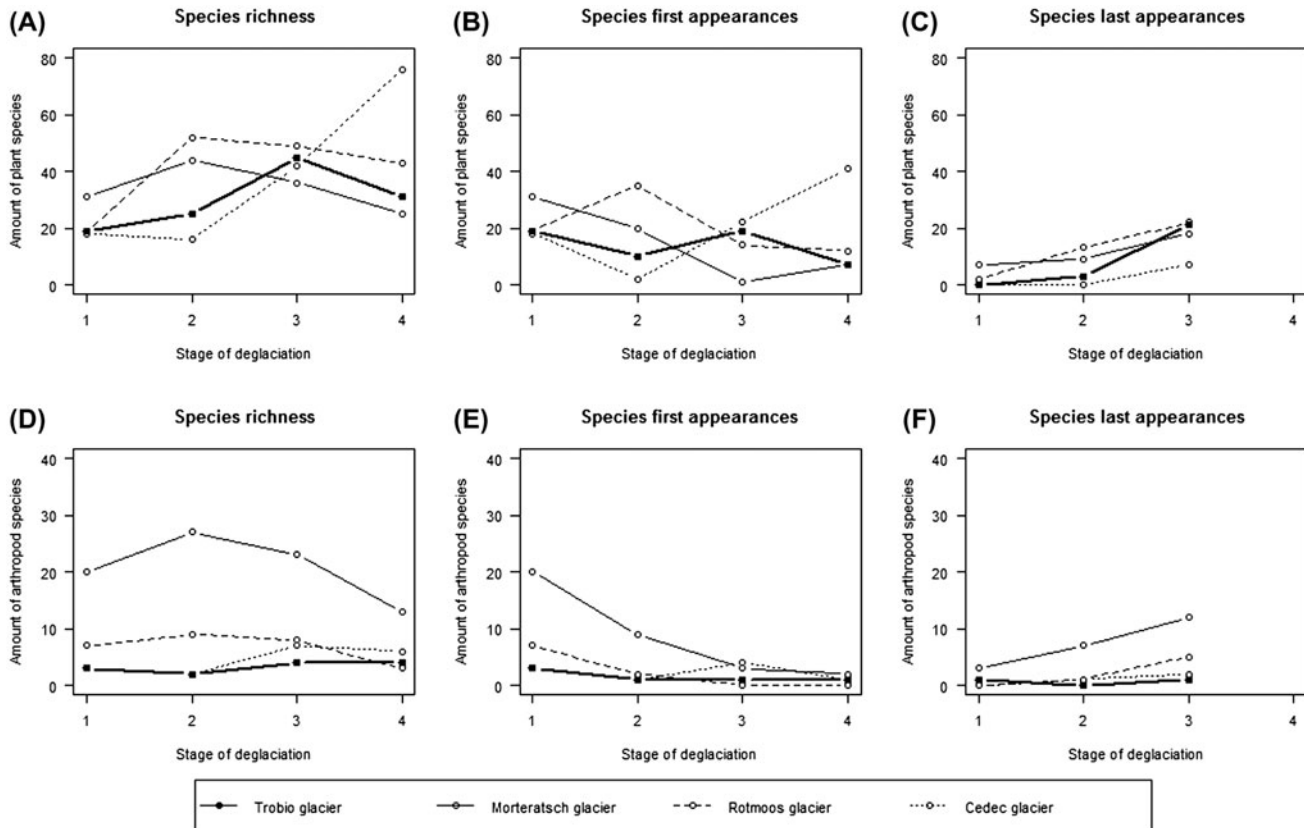


Figure 2

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 stages: 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

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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. This phenomenon is more evident for plant than for arthropod species, as for the latter the trend is similar to that of Cedec for the whole chronosequence. 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 endemic spiders were found: the most circumscribed distribution was that of *Drassodex heeri* and *Coelotes pickardi tirolensis*, both occurring on the southern-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 *Agrynetta 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 ($-0.58\text{ }^{\circ}\text{C}$

(100 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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