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Epigean Arthropod Succession along a 154-year Glacier Foreland Chronosequence in the Forni Valley (Central Italian Alps)

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Abstract

The 154-year (1850–2004) chronosequence of the Forni Glacier foreland has been studied by sampling ant, centipede, ground beetle, and spider species assemblages. Species numbers increase with terrain age along the chronosequence from 2 to 26 on the oldest soils. Thirty-nine species were collected; species richness and diversity (Shannon's Index) of communities are correlated to the year of soil deglaciation. Shannon Index values increase with sites deglaciated between 1 and 61 years ago; sites deglaciated between 61 and 78 years ago produce similar values, and those deglaciated 78 to 154 years ago show a further increase in diversity. Ground beetles and spiders are found at all sites, while ants and centipedes were associated with mature forest soils. On the glacier surface, pioneer species such as the wolf-spider *Pardosa saturatior* and the ground beetle *Oreonebria castanea* permanently inhabit the supraglacial detritus surviving on trophic resources. Wingless ground beetle species are associated with mature soils, especially those with high hydric stability. Open land species typical of primary succession are found in the pioneer and intermediate stages, while community assemblages found on older terrain are linked to forest vegetation structure and dynamics.

Introduction

After the most recent phase of glacier advance known as the Little Ice Age (LIA; 16th–19th centuries), the alpine region has been affected by accelerated glacier retreat. This process has been interrupted by periods of minor readvance. Such fluctuations are documented by moraine deposits which can be dated to reconstruct past glacier behaviors. A multi-proxy approach including primary succession of vegetation (Matthews, 1992; Caccianiga et al., 2001; Caccianiga and Andreis, 2004), invertebrates (Kaufmann, 2001, 2002), and dendrochronological studies (Pelfini, 1992b) should also be considered when interpreting past glacier dynamics. Such methods are useful instruments for studying glacier dynamics where geomorphological evidence has been destroyed.

High altitude habitats where organisms live under unfavorable or extreme conditions are considered particularly sensitive to low intensity climatic changes. Vegetation and animals therefore represent an archive of data containing information about past climatic changes, which enables us to predict likely impacts from current global warming. Arthropods represent a new and significant field of research. Recent studies carried out on invertebrate community assemblages along proglacial chronosequences highlight the potential to use animals to understand the responses of living organisms to environmental and climatic changes (Hodkinson et al., 1998, 2002, 2004; Kaufmann, 2001, 2002).

In the Italian Alps, the Holocene maximum coincided with the LIA maximum, where the majority of glaciers reached a climax position during the first two decades of the 19th century (Pelfini and Smiraglia, 1992; Orombelli and Mason, 1997). Several studies have been carried out investigating Holocene fluctuations of alpine glaciers. Some 30 glaciers have been studied in detail; research was concentrated on the most glaciated sectors of the Monte Bianco (Orombelli and Porter, 1982), Monte Rosa (Diolaiuti et al., 2003), Bernina (Orombelli, 1987), Ortles-Cevedale (Pelfini, 1992a), and Adamello-Presanella (Baroni and Carton, 1991) mountain groups (Casartelli et al., 1996). At these sites glacier fluctuations have been reconstructed using geomorphological, dendrochronological, and lichenometric methods on frontal and lateral moraines.

Terminal moraines also provide the opportunity to study the modality of invertebrate colonization in primary succession and community assemblages. Therefore, knowledge of glacier foreland colonization by invertebrates is an important instrument for understanding the community reaction to climate and environment changes and for understanding glacier dynamics during the past (Harte et al., 2004; Hodkinson et al., 2004; Kaufmann, 2001, 2002). Moreover, arthropod communities could be used to underline the ecological value of glacial geomorphosites (Pelfini and Gobbi, 2005). There have been many studies on the impacts of global change on arthropods of alpine ecosystems (Meyer and Thaler, 1989; Brandmayr et al., 1997a, 1997b; Thaler, 1997), but in Italy there is only one study by Focarile (1976), which considers the beetle assemblages of proglacial and periglacial environment in Breuil (Valtournanche, Western Italian Alps).

In this paper data are presented on arthropod species assemblages of a primary succession studied in a glacial foreland of Italian Alps (Forni Valley, Ortles-Cevedale Group). The aims of this paper are: (1) to characterize the general succession of arthropod epigean fauna on an alpine glacier foreland chronosequence, and (2) to show the potential use of glacier foreland arthropod communities in predicting the future impacts of climate changes on alpine environments. Although this is a local study, it may serve as a model with potential application to other Italian glacier forelands and larger scale studies.

Study Site

The study area chosen focuses on the necessity to research a zone of the Italian Alps at high altitude, marked by the presence of a large proglacial foreland and a strongly retreating glacier. The Forni Valley, located in the Central Italian Alps (Ortles-Cevedale Group) contains

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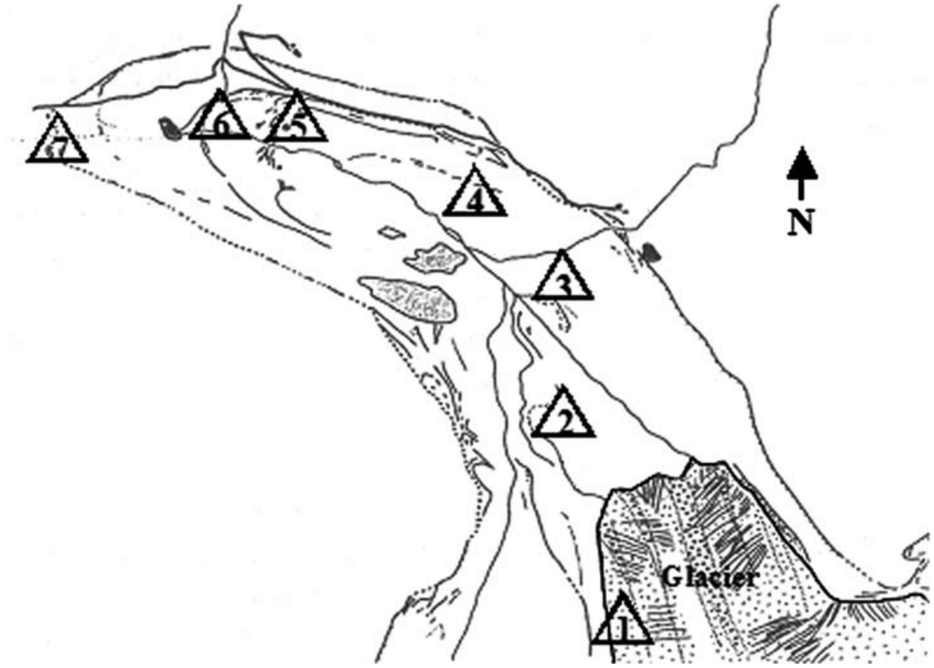

FIGURE 1. Collecting stations: (1) glacier surface; (2) 1980 moraine; (3) 1953 glacier position; (4) 1943 glacier position; (5) 1926 moraine; (6) 1904 moraine; (7) 1850 moraine. Adapted from Pelfini (1992a).

the largest Italian valley glacier, the Forni Glacier, with an approximate surface area of 12 km^2. There is no strong altitudinal gradient in the valley, but there is evidence that the retreating glacier crossed the present tree line. The proglacial area covers an altitudinal range of 2150–2500 m with dated moraines marking the retreat of the glacier since the LIA. In the last 150 years the glacier has retreated an estimated 2.5 km. Numerous studies have investigated the present-day geomorphological, glaciological, and climatological aspects of the area (Casartelli et al., 1996; Pelfini, 1992b; Pelfini and Smiraglia, 1992; Merli et al., 2001).

Collecting stations (Fig. 1) were positioned on (1) the glacier surface (2600 m); (2) the terminal moraine, deglaciated since 1980 and therefore devoid of vegetation and soil (2348 m); (3) the 1953 glacier position (2335 m), characterized by stony, wet soils on a *Festucetum halleri* prairie, scattered with *Salix caprea* trees (Credaro and Pirola, 1975) and *Salix herbacea* scrubs; (4) the 1943 glacier position (2240 m), marked by stony soils with *F. halleri* grass, a sparse cover of *S. caprea* (Credaro and Pirola, 1975) and *S. herbacea*; (5) a terminal moraine deglaciated in 1926 (2203 m) (this area is marked by pastured *Rhododendro-Vaccinetum* and *Juniperion nanae* vegetation with small trees and shrubs covering approximately 95% of the area); (6) the terminal moraine that has been ice free since 1904 (2190 m), which has a similar vegetation cover to that of station 5; (7) the terminal moraine dating to around 1850 (2150 m) (this station is characterized by a pastured *Larix decidua* and *Pinus cembra* forest with sparse trees [*Rhododendro–Vaccinietum cembretosum*] and dwarf shrubs [*Rhododendro–Vaccinetum*] covering about 100% of the soil).

Pelfini (1992b) highlights the difficulties associated with dating morainic deposits. Historical evidence suggests the 1850 moraine underwent complete deposition during 1819–1921. Lichenometric data, however, indicate deposition in 1856, somewhat later than the majority of Italian glaciers (Orombelli and Pelfini, 1985; Pelfini, 1987, 1992b). We therefore tried to establish an approximate date around 1850. Station 6 moraines were denoted as formed at the beginning of the 20th century. These measurements are affected by glacial stream activity, and it is possible that Forni Glacier fluctuated near to this position in 1902–1903 and again in 1913–1914. In this example, we established an approximate and hypothetical date around 1904. The fifth collecting station moraine is well documented by Ardito Desio, where photographs are dated to 1926. The most recent moraine (Station 2) is associated with the general cold phase of the 1960–1970s, with deposition occurring around 1980 at the end of this cold period (Rossi et al., 2003). Stations 4 and 3 have been dated using various sources of evidence including reports, photographs, rich iconography, and records of glacial retreat made over the last 100 years.

Material and Methods

Epigean arthropods were sampled using pitfall traps. Six traps, 10 m apart, were used at each sampling station with no protective covering. Each trap (a 7 cm plastic cup) contained 2/3 standard mixture of wine vinegar and salt. A small hole was made approximately 1/3 of the way down the cup to allow excess rain water to drain away. Trapping was carried out during the snow-free season from July to October 2004, where traps were emptied after periods of 20 days.

Surface-active predatory arthropods were selected for this study, including ants, centipedes, ground beetles, and spiders. These taxa, in the high mountain environments, show diversity not only with increasing vegetation structure, but also with more complex soil and bedrock properties.

Communities were analyzed using species richness and diversity (Shannon's Index) techniques. Shannon's Index measures the heterogeneity of communities by evaluating the distribution of specimens of different species (MacArthur, 1965). To analyze changes of the local heterogeneity of communities within the glacier foreland, a species-sites matrix was ordered using reciprocal averaging (RA). Sites with the most similar species combinations are positioned in close proximity, and species with the most similar distribution are again positioned together. We used the macro developed in Excel by Leibold and Mikkelson (2002) to perform the ordination.

The dispersal power of ground beetles was analyzed separately to investigate soil stability. Dispersal power is deduced by the analysis of wing morphology (brachypterous and macropterous species as well as morphs). Species colonizing new sites *per pedes* show a reduction of metathoracic wings (brachypterous species, "B"), and thus consequently have a low dispersal ability. These species are mostly connected to stable environments, whereas flying species (macropterous

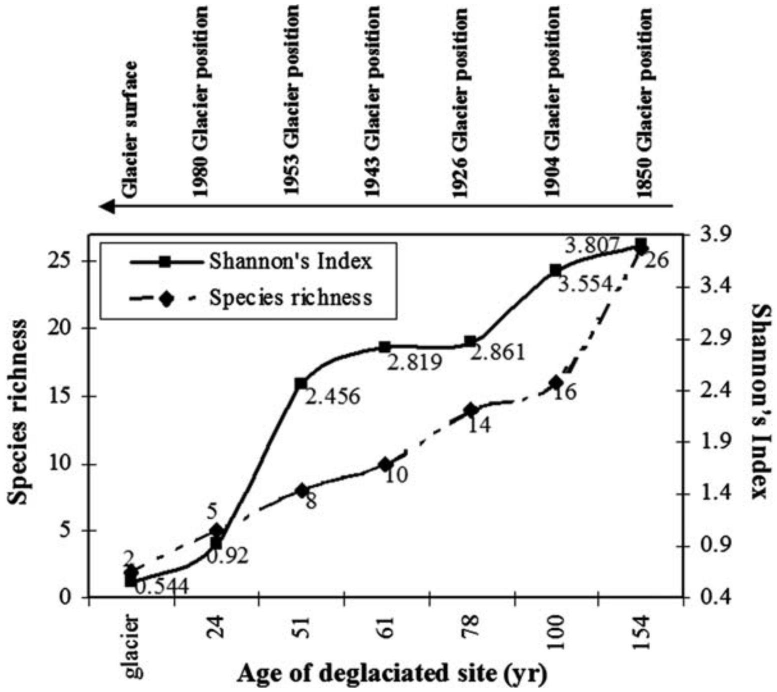

FIGURE 2. Relation between species richness, Shannon's Index, and age of deposition of moraines.

species, "M") are able to disperse further owing to their fully functional wings (Brandmayr, 1991; Nilsson et al., 1993). Dispersal power of communities was calculated using the B/M species ratio. Correlation between these two species types was tested using the Spearman's rank correlation.

Results

Thirty-nine species of epigean arthropods were collected. The richest groups of epigean predators were represented by Coleoptera Carabidae (18 species), Arachnida Araneae (15 species), Hymenoptera Formicidae (4 species), and Chilopoda (2 species). Species numbers increased from 2 on the most recently deglaciated terrain, to 26 on the most mature ground (Fig. 2). Species richness and Shannon Index values are highly correlated to the chronosequence of the glacier foreland (species richness: $r^2 = 0.99$; $p < 0.01$; Shannon's Index: $r^2 = 0.93$; $p < 0.01$) (Fig. 2). A steep increase in Shannon Index values is seen from the glacier border to areas which have been ice free for approximately 61 years. Sites abandoned by the glacier between 61 and 78 years ago do not have a substantial increase, while surfaces deglaciated between 78 and 154 years ago show a continuous, gradual increase in diversity.

The ordination of species-site matrix (Fig. 3) shows two important results: the first is that ground beetles and spiders are found in all stations, while ants and centipedes are associated with older soils. Recently deglaciated stages differ from older ones; not only in relation to the number of ground beetles and spider species, but a high species turnover is also observed across the chronosequence. The second is that sites 7, 6, 5, and 4 are highly variable, whereas sites 3, 2, and 1 are extremely similar with very low within-trap variability.

The ground beetle *Oreonebria castanea* (Bonelli, 1810) and the wolf spider *Pardosa saturatior* Simon, 1937 were the only species captured on the glacier surface and on the debris covering the glacier (Fig. 3). The ground beetles *Amara quenseli* (Schönherr, 1806) and *Carabus sylvestris* Panzer, 1793 appear on terrain after approximately 24 years of deglaciation. On older terrain, the abundance of ants decreases when soils change from forest to alpine grassland. On the other hand, the ground beetles *Cymindis vaporariorum* (Linnaeus, 1758) and *Calathus melanocephalus* (Linnaeus, 1758) show peak abundance on these alpine soils (Fig. 3).

Figure 4 shows the significant correlation between soil age and the ratio of brachypterous and macropterous species (B/M ratio) within site communities ($r_s = 0.901$; $p = 0.006$). The B/M rate increases steadily, with low values recorded on the most recently deglaciated soils and generally higher values gained on older ground.

Discussion

Data analysis shows how a faunal succession of epigean arthropods on glacier forelands could be described as a sequence of distinct assemblages with characteristic species. Species turnover along the chronosequence gives emphasis to the influence of length of terrain exposure which ultimately affects the structure of the communities.

Results are compared with invertebrate community data from the Rotmoos glacier foreland (Tyrol, Central Austrian Alps) as reported by Kaufmann and Raffl (2002). This work is considered owing to its pioneering contribution to primary succession on European glacier forelands and its similarities to the study site selected for this research. Both the Rotmoos and Forni forelands have northern exposures, similar altitudinal ranges, as well as similar foreland length and comparable glacial histories.

According to Kaufmann's (2001) hypothesis, species diversity increases in relation to terrain age and associated soil stability. Results gained from the Shannon's Index analysis (Fig. 5) show close agreement with the successional stage sequence observed at the Rotmoos foreland ($r_s = 1$; $p < 0.01$). The area in front of the Forni Glacier, deglaciated approximately 61 to 78 years ago, produces Shannon's Index values which remain stable, possibly as a result of the onset of species turnover. In the older stages of succession, Shannon Index values increase slightly, suggesting a moderately stable environment.

Only a few pioneer species such as *Oreonebria castanea, Pardosa saturatior*, and *Amara quenseli* are adapted to live in the wet, cold, unstable environments near and on the glacier. Thaler (1997) pointed out that *P. saturatior* lives frequently on bare ground close to glaciers. In addition, *O. castanea* is a nocturnal, hygrophilous, and

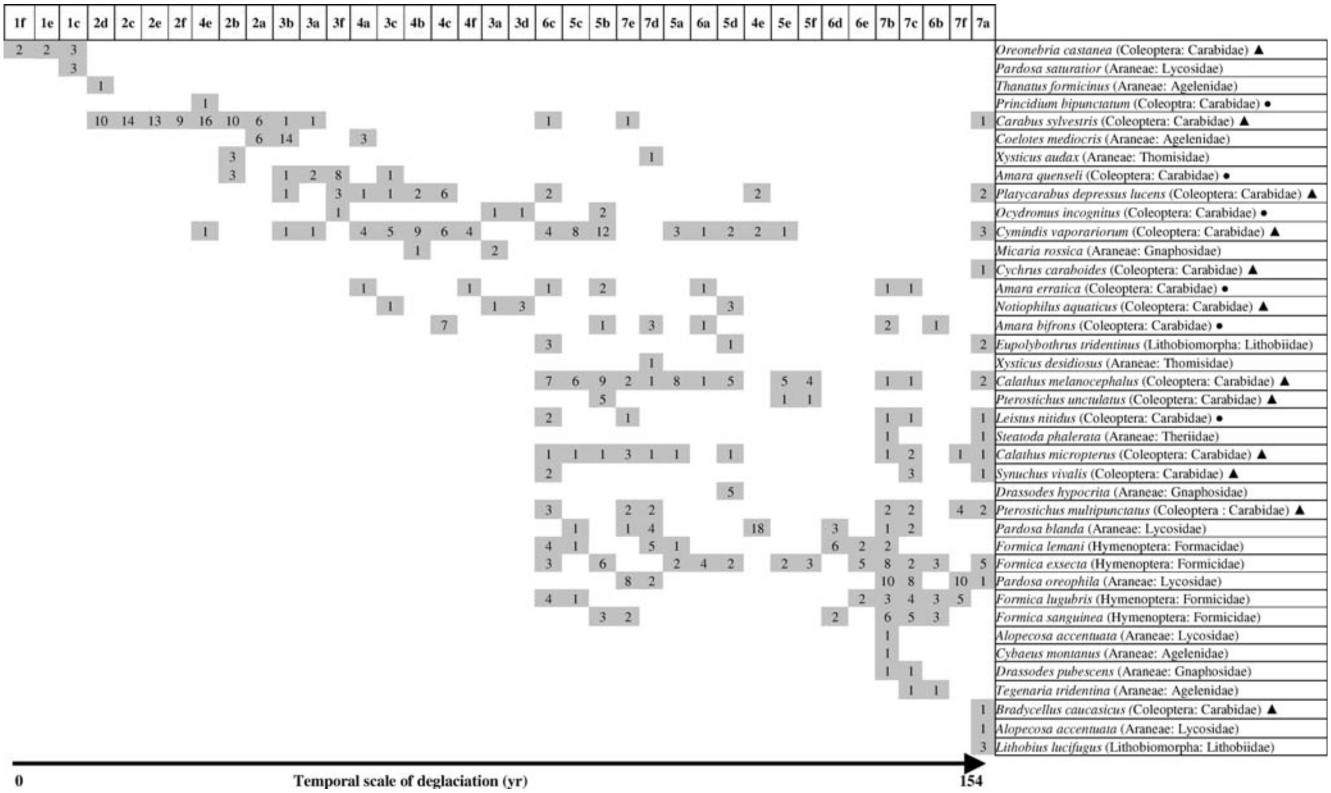

FIGURE 3. Species-sites matrix using reciprocal averaging (RA). Sites are presented with their number and letter code. Macropterous Carabidae species are denoted by (●) while brachypterous species symbolized by (▲).

microtherm species, typical of pioneer and wet "high-alpine" environments (Focarile, 1976; Brandmayr and Zetto Brandmayr, 1988; Gereben, 1995; Kaufmann and Juen, 2002). It is suggested that the lateral moraines and detritus covering the glacier may be an important habitat for microtherm species refuge, as the glacier surface represents an important and stable trophic resource. The cold surface of the glacier functions as a sink collecting allochthonous animals, driven up the foreland by glacial winds. The presence of a stony detritus layer on the glacier seems to enhance the presence and survival of the two previously mentioned species. *A. quenseli*, with its particular metabolic (Hodkinson, 2003) and ecological characteristics (Brandmayr et al., 1997b) is well adapted to live in these pioneer environments on frontal moraine deposits (site 2), where vegetation development is poor and soils are unstable.

The ordinate species-sites matrix shows that pioneer specialists are replaced by species typical of mature and structured environments. The older sites show similar community composition likely to be a result of stabilizing environmental conditions along the chronosequence. This hypothesis is supported by the ratio of B/M species of ground beetles. The "evolutionary pathway" (*sensu* Brandmayr, 1991) of dispersal power describes a progressive reduction of wingless species that is connected to an increase of ecosystem instability. In this example, the presence of glacial outwash and young soils could be considered as a limiting factor for dispersal capacity (Brandmayr, 1991). We observed a high B/M rate in mature, older stages and low rates in younger stages, as expected by this model. In the older stages, we can identify two species assemblages. The first is marked by ground beetles tied to mature soil and structured vegetation, characterized by the presence of *Cymindis vaporariorum* and *Calathus melanocephalus*. Both species are attributed to alpine pastures or mesophilic alpine grasslands. The second, an association of ants belonging to the genus *Formica*, is restricted to montane or subalpine forest soils.

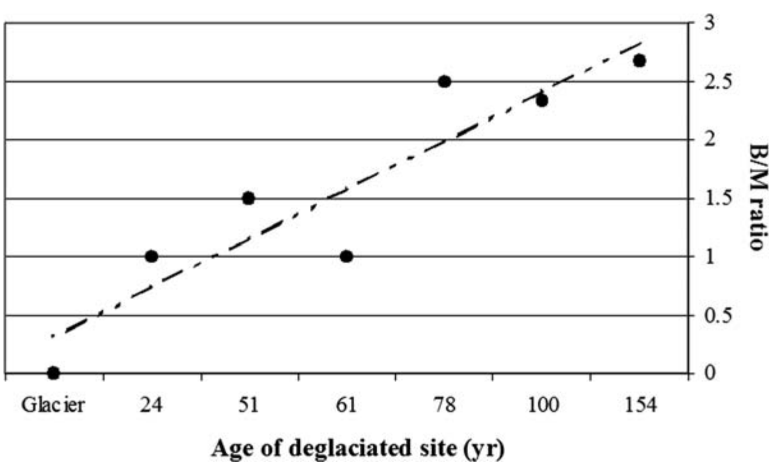

FIGURE 4. Relationship between brachypterous (B) and macropterous (M) ground beetles along the chronosequence.

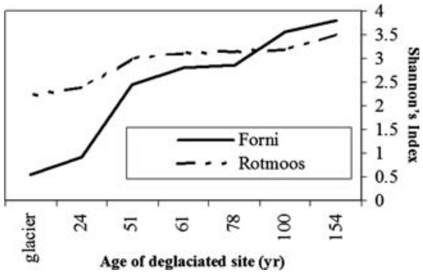

FIGURE 5. Comparison between Shannon's Index values from the Forni and Rotmoos forelands.

In conclusion, the epigean arthropod succession along the chronosequence is characterized, for the first 61 years of deglaciation, by pioneer species. Between 61 and 78 years, species turnover is greater, and finally, terrain aged >78 years is characterized by alpine grassland and forest communities (coniferous). On more mature soils, forest community colonization is somewhat delayed by grazing and perhaps other abiotic factors.

On the most recently deglaciated terrain, abiotic factors such as soil stability and grain size seem to have a significant impact on community assemblages. In the later stages of succession, where more stable conditions prevail, biotic factors have more dominant control on the potential community assemblage (e.g., vegetation diversity and structure). Comparisons between Rotmoos foreland and that of Forni foreland reinforced the evidence found at the two proglacial areas (High Arctic) studied by Hodkinson et al. (2004). Close similarities are seen between community composition and species richness, with respect to the same successional stage, which suggests deterministic and directional community development.

The data presented in this paper indicate that glacier retreat connected to climatic warming induces a species succession which therefore influences local distribution of alpine species. The environmental evolution of high altitude environments could therefore restrict taxa to progressively narrower alpine zones at the summit of mountains (Chapin and Körner, 1989). Finally, if glacial retreats continue, those species tied to such environments will be at risk from habitat loss and, consequently, at risk from extinction.

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