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ORIGINAL ARTICLE

Carabid diversity in alpine environments: Investigating biogeographic and ecological traits of the communities living in the Dolomites (Italy)*

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Abstract. In the landscape of the Dolomites, within the protected area of the Paneveggio – Pale di S. Martino Park in the Eastern Alps of Italy, a study was conducted to explore the distribution of carabid beetles. To achieve this, pitfall traps were placed along a 1000-m elevation gradient, following the bioclimatic gradient from spruce forests to the resilient pioneer vegetation in the extreme high-altitude environments. The research revealed that both community diversity and biogeographic diversity exhibited a clear correlation with the bioclimatic gradient. As one ascended to higher altitudes, the composition and distribution of carabid beetle communities shifted, reflecting the bioclimatic gradient. The chorological spectrum of the communities showed that Pleistocene paleoclimatic events provided the triggering factors affecting the postglacial recolonization of alpine ecosystems of the Dolomites region. Most of the sampled species displayed specific life strategies that enabled them to thrive in this harsh setting, responding to the selective pressures imposed by ecological factors. An extensive dataset encompassing the diversity of carabid beetles in these high-altitude domains was created. Given that the studied environments are widely distributed along the Italian Eastern Alps, the dataset serves a crucial purpose as it can be used as a reference for other research campaigns conducted in similar environments. Furthermore, it could act as a temporal benchmark for future researches on insects living in extreme environments, e.g. the Dolomites, or for comparing changes in climate that may be detected by future studies in the same geographic area.

INTRODUCTION

Mountain environments represent an element of the ecological and geographical landscape increasingly at the center, in recent times, of activities aimed at their economic exploitation, and therefore increasingly involved in processes that jeopardize the conservation of the natural resources that characterize these high altitude environments.

From a scientific point of view, the mountain is certainly an ideal "laboratory in nature" for studying fundamental issues related to the evolution and adaptation of living organisms, but also ecological problems relating to the relationships between abiotic variables and plant and animal diversity (Soldati, 2010). There are at least three research topics applicable to the study of mountain environments, which relate to the altitudinal species distribution, evolutionary and life strategies focus of the study approach.

One of the most evident environmental factors that indirectly influences species distribution in mountain environments is the decrease in temperature as a function of increasing altitude, because, together with the slope exposure variation, they influence the local incidence of meteorological activity throughout the seasons, giving rise to the altitudinal series of bioclimatic zones.

Given the habitat heterogeneity linked to the bioclimatic series, mountain environments host high species diversity, where such diversity is likely detectable as group of species or communities (Hodkinson, 2005; Körner, 2007; Rassmann et al., 2014; Corcos et al., 2018).

From an evolutionary point of view, the mountain can be considered an island in which evolutionary radiations lead to the current biogeographic features (Habel et al., 2010). The mountain represented a refuge for living organisms subjected to selective pressures during past extreme climatic changes (glaciations), and in this sense the mountain is a source of biogeographic diversity, because the pressure imposed by the glaciations induced new evolutionary lines that, thanks to specific morpho-functional characteristics, adapted to different mountain ecosystems during inter-glacial times. Currently, these evolutionary lines are represented by endemic species, which constitute an exclusive faunal resource and thus form the peculiar component regarding the biogeographic features of mountain ecosystems, and can therefore be seen as a conservation area for certain phylogenetic groups (Lomolino, 2001; Körner et al., 2007; Schmitt et al., 2010).

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From the life strategies point of view, it is probable that different animal species respond similarly (convergent evolution) to the altitudinal gradient, so that the study of suitable ecological indicators can provide important information on the main factors characterizing mountain ecosystems (Hodkinson, 2007; Saha et al., 2020; Seeber et al., 2022), and a powerful tool with which to compare present vs. past data in the perspective of climate change (Pizzolotto et al., 2014). From this perspective, the effects of the ecological pressures are mirrored by the presence (vs absence) of different species traits.

The phenomena described are not independent of each other, rather, they interact and affect species presence in such a way that species exhibit characteristic responses to the selective pressures found in mountain environments, where it is likely that groups of species characteristic of mountain environments form, sensitive to their alterations. More generally, given the importance of high-altitude ecosystems both for the fauna they host and for the impact of climate change on them, it is of paramount importance to study or monitor their status using model organisms well adapted to their ecological features.

Carabid beetles have been widely used as model organisms in several fields, and have a large literature to support them. The species diversity of this group is the result of a great adaptive radiation which has allowed these insects to colonize numerous environments, from deserts to glaciers, including habitats subjected to conditions of strong anthropic disturbance. They are good model organisms and potential indicators suitable for long-term environmental monitoring and for environmental characterization based on the identification of taxocoenoses (Boer, 1977; Stork, 1990; Desender et al., 1994; Brandmayr et al., 2000; Lövei & Toft, 2005; Brandmayr et al., 2005; Vanbergen et al., 2005; Kotze et al., 2011; Turin et al., 2022).

Sensitivity to climate change was documented by studies relating to the Quaternary fossil carabid fauna (Foddai & Minelli, 1994; Ashworth, 1996), from works relating glacial dynamics to changes in the distribution of carabid species (Gobbi et al., 2007; Gobbi et al., 2017), and from a series of observations on the northward range-shifts of different carabid species (Drees et al., 2011; Brandmayr et al., 2013; Pizzolotto et al., 2014).

Studies on the fauna of alpine soils are progressively increasing, but require great research effort, because mountain ecosystems show a high diversity of facies even within the same ecological landscape (Guerra et al., 2020; Steinwandter & Seeber, 2023). This is why gathering ecological data about such environments is welcome and badly needed (Lomolino, 2001).

The aim of this work is to provide a dataset as complete as possible on carabid beetles living along a bioclimatic altitudinal gradient that goes from forests to extreme high-altitude environments. This dataset aims to serve as a temporal benchmark for future research campaigns in the Dolomites area. Furthermore, I aim to answer three questions: (i) Does the distribution of the groups of species change with ecosystems (community diversity)? (ii) Do chorological categories change according to ecosystems (biogeographic diversity)? (iii) Are there adaptive strategies concentrated in extreme high-altitude environments (species traits diversity)?

METHODS

Sampled sites

Detailed features of the sampled sites are in Table 1, and Fig. 1 (see also Pizzolotto et al., 2016). The Appendix (at the end of the article) contains list of the 25 sites and the NAT2000 vegetation category characterizing them.

Data collection

The data used in this work are the result of various collection campaigns carried out between 2008 and 2014. Every year different locations were sampled leading to a total of 25 sampling sites (see Table 1).

Quantitative sampling was carried out at each site using an average of 6 pitfall traps (see Table 1). The traps were positioned by selecting an area that was as homogeneous as possible regarding the ecological characteristics of the sampled environment. These traps consist of a plastic glass of about 9 cm in diameter at the mouth and 7 cm at the base, about 11 cm high, containing a solution of commercial wine vinegar saturated with table salt. A small hole (0.5 cm in diameter) was made in each glass about 4 cm from the rim to prevent content overflow by any rainwater. Traps were buried up to the brim, spaced about 10 m from each other, taking particular care to eliminate any empty space between the rim and the ground.

Pitfall traps don't give the whole assemblage of species that occur in the sample sites, rather they give a quantitative set of data to compare sites, and to give a picture of the differences among species assemblages. In this sense pitfall traps gave valuable results in past studies not only from mountain environments, as e.g. in Niemelä et al. (2000), Ribera et al. (2001), Turin et al. (2022).

The traps were kept in operation for the entire season of activity of the carabid fauna, which in alpine environments is between the end of June and mid-September. The sampled material was collected approximately every 30 days, also providing for the renewal of the bait.

To allow data comparison between the sites, even when the days of capture and the traps number vary, it was necessary to standardize for trapping effort the quantitative data of the captured number of individuals per species, according to the so-called Activity Density (AD) as follows:

$$AD = [\text{nr individuals} / (\text{traps} * \text{days})] * 10$$

where nr individuals is the number of individuals captured in a given time, the ratio is then multiplied by 10 to obtain a value that indicates the number of active individuals that fall into a trap in the space of ten days during that time of the year.

The AD is calculated for each sampling period, and it evaluates the carabid activity throughout the season. The data used for the synecological analysis is instead the annual AD (aAD), which is based on the total annual number of individuals caught and on the total annual sampling effort unit (EU) used:

the effort unit (eu) for each single sampling period is
$eu = (\text{traps} * \text{days})/10$

from which the total annual capture effort is given by the sum of

$EU = \sum eu$
and therefore

Table 1. Main features of the sampled sites, grouped on the basis of vegetation physiognomy (second column).

Site ID	Veg. physiog.	Altitudine m a.s.l.	Aspect	Slope °	Bedrock	Vegetation %	Traps	Traps avg	Year
Rs	pioneer vegetation	2680	E	20	D-d	10	6	5.8 ± 0.5	2013
Alp1		2651	N	10	D-d	5	6	5.8 ± 0.5	2014
Alp2		2625	S	25	D-d	5	6	5.3 ± 1	2014
Alp3		2537	E	25	D-d	10	6	5.9 ± 0.3	2014
Alp4		2566	E	10	D-d	40	5	5.2 ± 0.6	2014
Cf1		2575	S	40	D-d	40	6	4.2 ± 1	2013–2014
VN1		2512	S	10	D-d	80	5	5 ± 0	2013–2014
F1		2200	N	30	D-d	60	6	5 ± 0	2008
F2		2250	N	35	D-d	20	6	4.8 ± 0.4	2008
VV1		2000	W	35	D-d	10	5	5 ± 0	2009
VV2	transition vegetation	1950	W	10	D-d	50	5	4.3 ± 0.9	2009
Se1	sesleria grasslands	2200	N	5	Werf	90	6	4.8 ± 0.5	2011
Se2		2200	N	20	Werf	90	6	3.2 ± 0.9	2011
Se3		2200	N	15	Dol	100	6	3.4 ± 2.6	2011
NA1	nardus pastures	2170	SSW	10	Werf	100	6	3 ± 1.3	2009
NA2		1910	S	15	Gard	100	6	5.3 ± 1.1	2009
FH1	festuca grasslands	2230	WSW	10	Ign	95	6	6 ± 0	2012
FH2		2245	WSW	25	Ign	70	6	6 ± 0	2012
FH3		2175	WSW	5	Ign	100	6	5 ± 1.4	2012
L	alpine forests	1900	W	25	Dol	50	6	5 ± 0	2013
RM		1970	W	25	D-d	70	6	6 ± 0	2013
VV3	subalpine forests	1800	NW	30	Dol	100	5	5.2 ± 1.5	2009
VV4		1850	SE	40	Dol	95	5	4.5 ± 0.6	2009
PS1		1650	NW	20	Ign	80	6	4 ± 1.3	2008
PS2		1780	NNE	25	Ign	65	6	4.5 ± 0.5	2008

Bedrock: D-d and Dol – dolomia where the first is incoherent and the second solid; Werf – werfen sandstones; Gard – "Val Gardena" sandstones; Ign – ignibrite (i.e. metamorphic); Traps avg – average number of active traps ± standard deviation.

aAD = total number of individuals / EU

Biological features

During the determination phase, the status of the species was assessed in relation to certain biological and biogeographical features (Brandmayr & Zetto Brandmayr, 1988; Brandmayr et al., 2005). The species biological features mirror their greater or lesser adaptation to factors characterising the sampled ecosystems. From a general point of view eurytolerant species have greater possibility to spread the extinction risk over wide ranges of environmental factors than stenotolerant species (Boer den, 1968). The biological features considered include wing morphology (brachypterous vs. macropterous species), where wing dimorphic species were included with macropterous into a high dispersal power group, and dietary type (specialized zoophages, generalist zoophages, mixed diet, seed predators). In extreme environments of high altitude, dispersal power and feeding strategy are key factors in colonizing these environments, where short-winged and specialized-zoophages species indicate stable environmental conditions, subjected to risk of extinction in case of climatic change (Gobbi et al., 2017).

The geographic distribution range is linked to the adaptive strategies that lead a species to live in a given environment, and in this sense a narrow range means a strict adaptation to that environment (Kirkpatrick & Barton, 1997; Costa et al., 2008). This is particularly true in alpine environments, where the richness of stenoendemic species reflects the greater or lesser faunistic peculiarity of the investigated area. Here, the extent of the distribution range was evaluated according to the following categories: I – stenoendemic Alpine species; II – montane Central European species; III – European species; IV – Eurasian, Eurosiberian species; V – Palearctic, Holarctic species (Pizzolotto, 2009; Pizzolotto & Brandmayr, 2014).

Data analysis

To analyse the relationships between carabids and habitat, i.e. the composition of the species groupings characterizing the different environments, cluster analysis of data was applied to sites and species. Sites were classified on the basis of the Bray-Curtis distance, with the method of the minimum variance within groups (Ward distance). The species classification method was applied by calculating the Jaccard index and the Ward distance (Pielou, 1984). Site clustering helps to see what species concentrate their activity in a similar way, while species clustering helps to highlight if species are distributed in a similar way. The evidence for clusters was graphically evaluated on the basis of the dendrograms. Data analysis was done in R (version 4.1) software (https://cran.r-project.org/) by means of libraries vegan (Oksanen et al., 2022) and cluster (Maechler et al., 2022).

The information thus highlighted by the site and species classifications was further integrated by analysing the concentration trend of each species in relation to the sampled sites. Quantitative data (in our case aAD) reflect the influence that environmental factors (e.g., temperature, snow duration, summer climate severity, soil structure) exert on the abundance of species in relatively recent times. In this sense quantitative data provide an estimate of the degree of affinity that species exhibit towards different ecosystems, especially in cases where the same species has been recorded in more than one ecosystem. Thus, the peak of aAD can be taken as a proxy of the "preference" by a species for an ecosystem (actually to the complex of ecological factors), so it is useful to observe in which site the maximum aAD value falls, which here will be called central value of the species (see also Chemini & Pizzolotto, 1992; Pizzolotto et al., 2016, 2018). Most of the carabid species show relatively high values of aAD within ecosystems they "tolerate" to live in also, and these here will be called nuclear values, given by those aAD values above the average when computed on the sites where the species is present. In

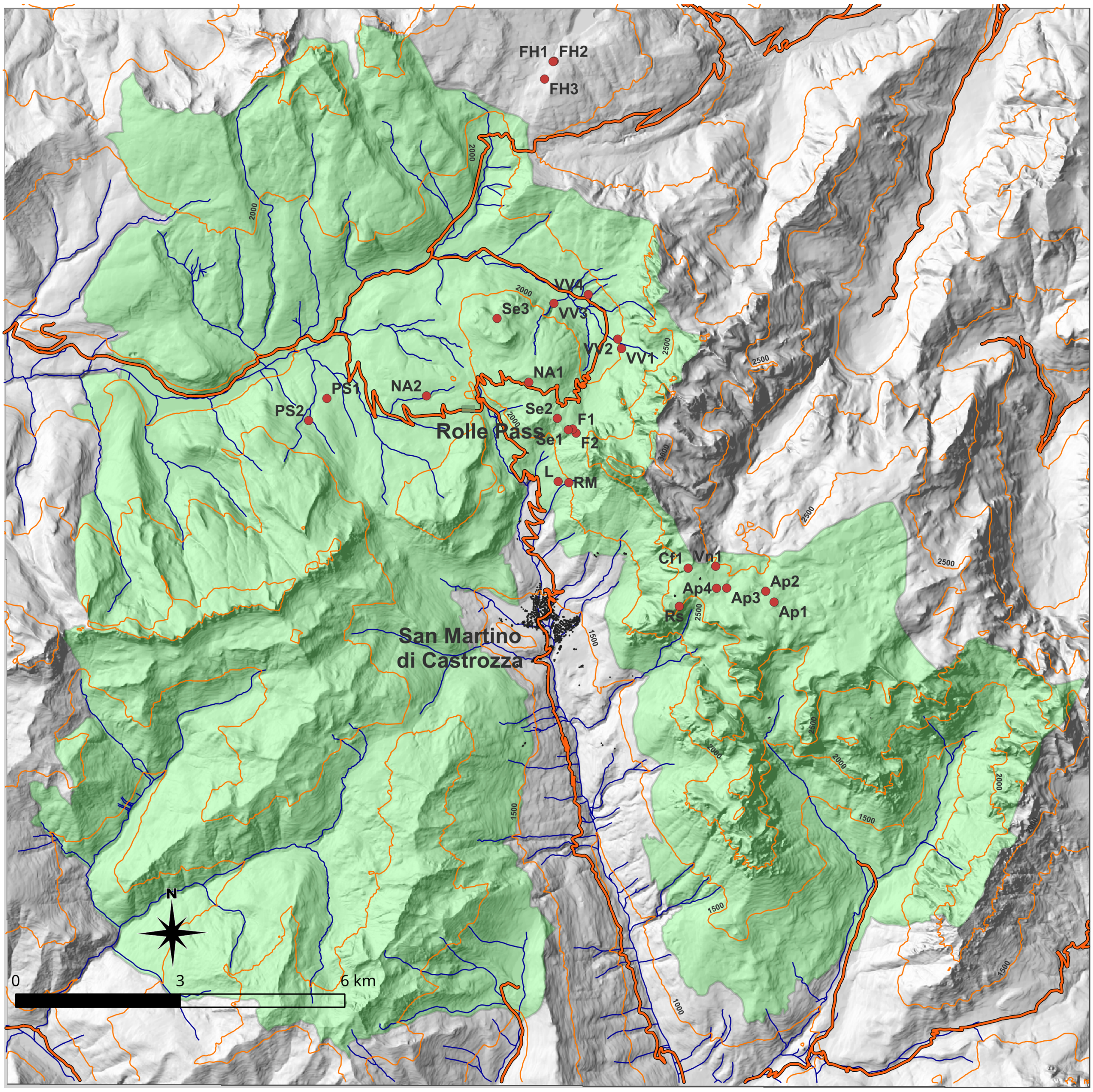

Fig. 1. The study area and the sample sites, with the area of the Paneveggio Park marked in green. Detailed description of sites are in Table 1 and Appendix.

cases where the aAD is equal or lower than the average, here they will be called orbital values, leaving the doubt open wether the orbital value indicates a "traveler" (i.e., intentionally crossing that site) or "tourist" (i.e., arrived by chance) species.

Under ideal conditions, specialist species well adapted to particular environmental conditions, will have few nuclear values and a high central value, while for generalist species the nuclear values should be increasingly numerous according to the greater ecological tolerance of the species, up to having numerous values lower than the average (orbital values) when the tolerance is very large.

The ideal case would be that of a species whose nuclear values are all concentrated in a single cluster of sites, where the central value also falls. If such cluster is really the one presenting the best conditions for the species, then sampling other habitats (e.g. in the future) will only add orbital values to the data table.

To graphically emphasize the central, nuclear and orbital values may be of help on the interpretation of the data table, by suggesting the habitat choice of the species within the study area.

RESULTS AND DISCUSSION

Cluster analysis

The study campaign was conducted from 2008 to 2014 and involved 25 sampling sites (Table 1) where 7691 individuals belonging to 46 species were collected. The data were synthesized in Table 2.

The dendrogram of the sampling sites based on quantitative data (aAD) of the sampled species showed that group A is the most heterogeneous, characterized by high-altitude environments without true vegetation cover (Fig. 2). Within Group A, sites from the Altopiano delle Pale (Rs and

Table 2. Zoosociological table of the sites sampled along a bioclimatic altitudinal gradient that goes from forests to extreme high-altitude environments. In the first row, A, B and C refer to the cluster of Fig. 2, while in the first column, 1, 2 and 3 refer to the cluster of Fig. 3. Symbols refer to the status of each species in each sample site, ◘ – central value of the species (i.e., the maximum aAD value); ● – nuclear value of the species (aAD values higher than the average of the sites where the species is present); ∞ – orbital value of the species (aAD equal or lower than the average). Black and gray rows and columns mirror the cluster analysis of Figs 2 and 3. Species names from https://www.gbif.org/species/1.

		A										C								B						
		Alp2	Alp4	Alp1	Alp3	Rs	Cf1	F2	VN1	VV1	F1	Se2	Se1	Se3	FH2	FH1	FH3	NA1	NA2	PS1	VV3	L	PS2	RM	VV4	VV2
1	*Nebria germarii* Heer, 1837	●	●	●	◘	∞	∞		∞																	
	Nebria diaphana K. & J.Daniel, 1890	∞	∞		∞	∞	◘	●	∞	∞	∞															
	Trechus dolomitanus Jeannel, 1931	●		◘		∞	∞	∞																		
	Carabus bertolinii (Kraatz, 1878)	∞	∞		∞	●	◘	∞	∞	∞	∞	●	∞	∞	●	●	●	∞						∞		∞
	Carabus creutzeri Fabricius, 1801	∞		∞	∞	∞	∞	●	●	●	◘		∞	∞							∞	∞	∞			∞
	Bembidion glaciale Heer, 1837					◘	∞		∞																	∞
	Leistus punctatissimus Breit, 1914					◘			∞																	
	Pterostichus morio (Duftschmid, 1812)							◘	∞		∞	∞														
	Cychrus caraboides (L., 1758)										∞	◘														
	Amara alpestris A. & G.B.Villa, 1833										◘	∞	∞	●												
	Pterostichus schaschli (Marseul, 1880)									◘	∞															∞
	Trechus pallidulus Ganglbauer, 1891					∞					◘															
2	*Calathus melanocephalus* (L., 1758)										∞	●	◘		●	∞	●	∞	∞							
	Dyschirius globosus (Herbst, 1784)											∞	∞		◘	∞	●	●	●							
	Amara erratica (Duftschmid, 1812)								∞			∞	∞	∞	∞	∞	◘	●	∞							
	Carabus germarii Sturm, 1815											●	∞	●	∞	●	●	◘	∞				∞			
	Notiophilus aquaticus (L., 1758)											∞	◘	∞	●	∞	∞									
	Amara lunicollis Schiödte, 1837												●	∞		∞	◘	∞	●							
	Amara praetermissa (C.R.Sahlberg, 1827)										∞	●	∞		●	◘	∞	●								
	Nebria gyllenhali (Schönherr, 1806)										∞		∞		∞	∞	◘	∞								
	Cymindis vaporariorum (L., 1758)														◘	∞	●									
	Bembidion incognitum G.Müller, 1931														◘	∞	∞									
	Bembidion bipunctatum (L., 1760)												◘		∞	∞	∞									
	Amara quenseli (Schönherr, 1806)														∞		◘									
	Stomis rostratus (Duftschmid, 1812)																◘									
	Trechus obtusus Erichson, 1837																	◘								
	Clivina fossor (L., 1758)																	◘								
	Bembidion lampros (Herbst, 1784)														∞				◘							
	Poecilus versicolor (Sturm, 1824)																		◘							
3	*Dromius agilis* (Fabricius, 1787)																					◘				
	Carabus linnaei Panzer, 1812																					◘				
	Trichotichnus laevicollis (Duftschmid, 1812)																					◘		∞		
	Pterostichus burmeisteri Heer, 1837																					◘		∞		
	Harpalus laevipes Zetterstedt, 1828																					∞		◘		
	Cychrus angustatus Hoppe & Hornschuch, 1825																					◘		∞		
	Abax pilleri Csiki, 1916																					∞		∞		◘
	Trichotichnus knauthi (Ganglbauer, 1901)									◘												∞		●		∞
	Pterostichus unctulatus (Duftschmid, 1812)											●	∞	∞	∞	∞	∞	∞		◘	●	●	●	∞	∞	
	Pterostichus jurinei (Panzer, 1802)													●				∞	∞	∞	●	∞	◘			
	Leistus nitidus (Duftschmid, 1812)																			∞	●	◘	∞	●		
	Cychrus attenuatus (Fabricius, 1792)																			∞	●	◘	∞	∞	∞	
	Calathus micropterus (Duftschmid, 1812)													∞						●	∞	∞	◘	∞	∞	∞
	Notiophilus biguttatus (Fabricius, 1779)								∞		∞				∞					●	∞	∞	◘	∞	∞	
	Carabus auronitens Fabricius, 1792																				∞	∞	◘			
	Leistus piceus Frölich, 1799																				◘					
	species number	5	3	3	4	8	6	5	9	5	12	11	13	10	15	13	15	12	8	6	9	16	9	12	4	7
	total aAD	6.22	5.3	5.54	6.56	6.46	9.99	6.97	2.27	2	5.7	7.49	7.5	6.14	6.86	5.78	8.54	5.26	2.86	11.5	10.6	15.7	26.5	1.81	1.05	2.23

Alp1, 2, 3, 4) are well aggregated in one subgroup, while in another subgroup are sites from scree slopes, including those not exclusive to the Altopiano (Cf1, VV1, F1, 2), and a snow-filled valley (VN1). Group A also includes, in addition to VV1, two sites external to the Altopiano that are located on the edge of the scree slope of the Travignolo glacier, below Cimon della Pala, F1, and F2 (see Fig. 1). The site F1 is characterized by pioneer herbaceous vegetation (Seslerietum), and F2 by *Dryas* cushions on scree. Overall, Group A represents the clusters of carabid beetles that have colonized summit environments (Altopiano delle Pale) and the talus slopes surrounding the rocky walls.

Group B comprises subalpine forest sites ranging from spruce forests to the tree line. Two subgroups are evident: one composed of forest sites with sparse canopy cover (RM-14 and VV2) or artificially planted (VV4), and the other subgroup consists of forest sites with high canopy cover (L-14, VV3, PS1-08, PS2-08) and an alpine meadow (SS3, which closely borders spruce forests). It is likely that the aAD of *Pterostichus jurinei* and the presence of *Calathus micropterus* have led to the inclusion of this site in the forest group.

Group C is the most structurally homogeneous, represented by a series of progressive staircase-like bifurca-

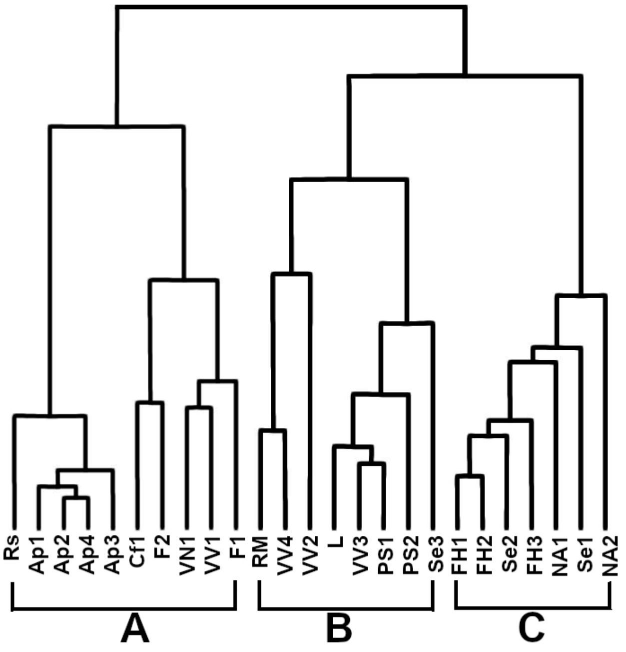

Fig. 2. Classification of the sampled sites, based on Bray-Curtis distance and minimum variance clustering. Detailed description of sites are in Table 1 and Appendix.

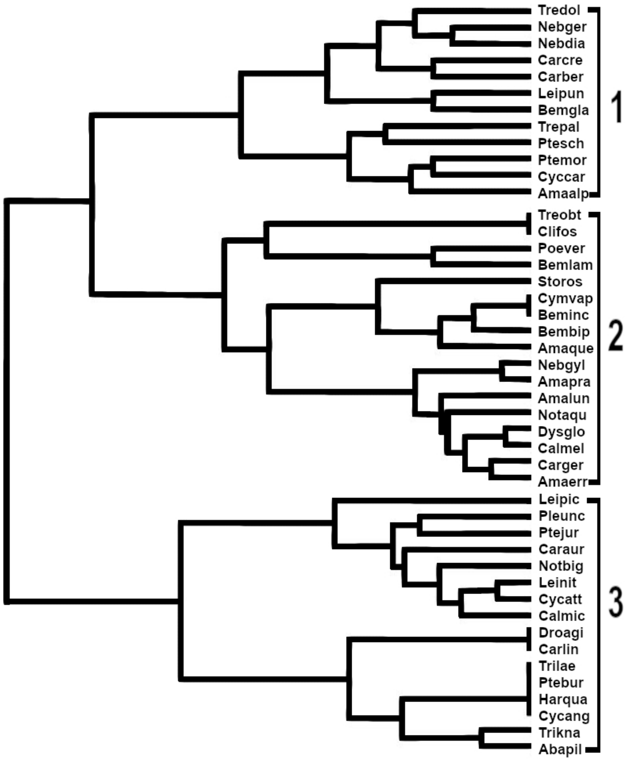

Fig. 3. Classification of the sampled species, based on Jaccard index and minimum variance clustering. The groups are in the sequence 1, 2, 3, in line with the altitudinal arrangement of the sampled sites.

tions. It is characterized by high-altitude meadows on both limestone and siliceous substrates, as well as *Nardus* grasslands. From a quantitative perspective, there are no subgroups since species of the genus *Amara* are abundant and present in almost all sites in the group. Group C may therefore represent high-altitude climax meadows, where rocky substrates likely exert a considerable influence on species diversity, but other factors such as grazing (NA1 and NA2) or proximity to forests (as in the case of Se3) may interact with substrate features to affect species diversity.

The dendrogram of the classification of species distinguishes three major groups of species (Fig. 3).

Group 1 is characterized by twelve species concentrated in sites belonging to group A, namely the summit environments (Altopiano delle Pale) and the debris slopes surrounding the rocky walls. Many species have been found exclusively in these environments, and only two (*Carabus bertolinii* and *C. creutzeri*) are not exclusive and are widespread in most of the sampled sites, where they don't show central values of aAD. In the dendrogram it is easy to recognize (see also Table 2) two subgroups, suggesting the existence of a group of species well adapted to the extreme conditions of the plateau (sites Alp1-4, Rs), but also capable of following the debris slopes to colonize lower altitudes where they join the second group of species that, on the contrary, has an altitudinal limit in these debris slopes. All species, except for *C. bertolinii*, *Cychrus caraboides*, and *Amara alpestris*, show only central values or nuclear values always within the sites of group A.

Group 2 is the largest group, and shows a clear concentration in group C sites, namely high-altitude meadows on both limestone and siliceous substrates, as well as *Nardus* meadows. Similarly, in this case it is possible to identify two subgroups that divide the central species of meadows on limestone or siliceous substrates from those of *Nardus* meadows.

Group 3 classifies species that are concentrated almost exclusively in forest ecosystems, i.e., in the sites of group B. Half of these species are distributed only in *Larix decidua* and *Pinus mugo* forest sites, corresponding to the altitudinal limit of the trees, while the other half of the species are present in all forests that extend from the valley floor to the tree line.

Species-environment relationships

In the following sections, on the basis of cluster analysis and species "centrality", the main species communities characterizing the sampled environments will be identified, and the relationship between community and ecosystem will be higlighted following the altitudinal gradient from top to down.

Mountain environments above the vegetation line

Community of the limestone pavements and scree slopes above 2500 m in altitude (sites Alp1-4, Rs, CF1, VN1, see Fig.1)

The area corresponding to the Altopiano delle Pale shows geomorphological characteristics that allow the establishment of ecosystems in extreme ecological conditions, especially regarding temperature and snow cover duration, which limit the favorable season for living organisms to just a few months (from late June to early September). It represents a unique and peculiar element of the Park's ecological landscape, resembling a high-altitude island due to its elevation and the configuration of the surrounding geomorphology. A true vegetation cover is only present in the little snowy basins, while patches of vegetation can be observed throughout the area among the rocks and clastic debris dominating the landscape.

Colonization by carabid beetles was influenced by factors affecting feeding and the development of eggs and larvae, in other words, the ability to complete their biological cycle (Gereben, 1995; Gobbi et al., 2010, 2017; Valle et al., 2020). These characteristics are highly fragmented across the entire Altopiano, with noticeable variations even within a few meters. Therefore, the distribution of species is likely to appear as a random mosaic pattern, actually shaped by the high microclimatic variation, and by the dynamic of the vegetation patches over space and time.

The microclimatic features produce highly selective limits for the establishment of stable populations, as evidenced by the low number of species characterizing the carabid community associated with limestone pavements (sites Alp1-4). Here, the number of species ranges from three to five, probably influenced by slope exposure, since the highest diversity was recorded in south-facing Alp2. The role of slope exposure is further supported by the greater species diversity found in sites Rs and Cf1 (six and eight species, respectively), where the presence of more developed vegetation cover and East and South exposure promote carabid activity, despite the steeper slopes compared to sites Alp1-4. It is likely that when well-developed soil is added to thick vegetation cover and exposure, as in the case of little snowy basins, species diversity reaches values comparable to those in alpine meadows, as recorded in site VN1, where ten species were recorded.

Given the uniqueness of these environments and the low number of species inhabiting them, *Nebria germari* can be indicated as a characteristic species, accompanied by *Trechus dolomitanus*, even though the latter is found at lower elevations than the Altopiano. The role of indicator species, closely associated with these environments, could be played by *Leistus punctatissimus*, as described in Pizzolotto & Brandmayr (2018).

In general, brachyptery (wings reduction) is the most widespread species trait in high-altitude environments, as also observed in this community where brachyptery characterizes the majority of species (95% of species), which are also the most abundant (98% of aAD).

The dominant feeding trait in the community is generalized predation (82% of species), while only *Carabus creutzeri* is a specialized snail predator, but it is not a typical species of these environments.

The composition of the community based on the distribution area (chorological spectrum) of each species is the most typical example of high-altitude community resulting from the selective pressure of glaciations. In fact, the community is exclusively (except *Bembidion glaciale*) composed of stenoendemic species, i.e., with an extremely limited distribution area, as a consequence of their isolation during glacial periods when only the highest peaks within the Alpine arc remained ice-free (Holderegger & Thiel-Egenter, 2009).

Overall, the mountaintop community shows substantial uniformity with few possibilities for variations in species diversity, while their abundance can also be significantly influenced by both geomorphological factors (e.g., southern exposure of slopes) and edaphic factors (e.g., developed soil). In this sense, site CF1 perhaps represents a variant of this community, associated with high-altitude limestone scree slopes, where *Nebria diaphana* and *Carabus bertolinii* are more abundant.

Community of the talus slopes and pioneer vegetation below 2500 m (VV1, F2, F1).

An important aspect of the alpine ecological landscape is given by the talus slopes that mainly cover the slopes below the rocky walls of the mountains, where they also have a significant altitudinal extent. Generally, these environments undergo a transition into the vegetation of Rhododendro-Mugetum thickets and *Larix* forests at their lower boundary, where the latter are at their upper altitudinal limit and in suboptimal soil conditions, resulting in a fragmented appearance, often resembling a colonizing plant cover characterized mainly by *Rhododendron*, *Dryas*, and *Vaccinium*. The scree slopes come into contact with the *Sesleria* grasslands when geomorphological factors allow the settlement of this vegetation at higher altitudes.

These environments present critical conditions due to the unstable nature of the substrate, low availability of nutrients, strong temperature fluctuations, and soil aridity (Ellenberg, 1988). However, these conditions are not uniformly distributed, so more favorable and less favorable situations are often arranged in a mosaic-like pattern, creating isolation conditions in which long-term micro-evolutionary speciation phenomena can occur, which have indeed mainly affected the invertebrate component during the Plio-Pleistocene era (Minelli & Stoch, 2006; Schuldt & Assmann, 2009).

This phenomenon was already highlighted by Darlington (1943), who discussed the importance of reduced wings in mountain environments, where species live ecologically isolated. Isolation and low dispersal power in high altitude environments strongly reduce, or even stop, the genetic flow among populations, leading to local evolutionary lineages, as discussed by Ikeda et al. (2012), who found that flightlessness in isolated environments promotes the evolution of new species. Similarly, Schoville et al. (2012) discussed the alternance of glacial vs. inter-glacial phases as of paramount importance for the evolution of new species, given the cyclical dynamics of range shift, population reduction and isolation.

The community in these environments is characterized more by the absence of species from extreme environments than by the presence of indicator species. In fact, talus slopes, due to their geomorphological position, represent the lower distribution limits of species from summit environments and, at the same time, the upper limits of species from meadows. This phenomenon is probably well represented in those scree slopes that cover extensive altitudinal gradients with elevation differences of up to 700 m. However, there is at least one species that is abundant in scree slopes, *Pterostichus schaschli*, which characterizes them along with *Pterostichus morio* and *Trichotichnus knauthi*. As elevation increases, the latter two likely disappear, giving way to *Nebria diaphana* and *N. germari*, while descending in altitude, the community is more influenced by *Amara alpestris*, *Carabus creutzeri*, and *Trechus pallidulus*.

In these habitats, the carabid fauna is represented by a relatively low number of species but with a significant percentage of specialized elements (Minelli & Stoch, 2006). In fact, only five species were collected in sites F2 and VV1, while 12 species were recorded in F1. In the case of F1, the fragmented plant cover is located on well-developed soil, and the site is continuous with the *Sesleria* grasslands at lower altitudes.

The ecosystem of lithosols and the extreme ecological conditions of these environments have likely favored the reduction of wings as an adaptive strategy. Therefore, the community is characterized by low dispersal power, represented by the majority of species and almost all sampled individuals. Less extreme conditions in the part of the scree slopes interconnected with alpine meadows probably facilitate the presence of a greater number of macropterous species, although not abundant as shown by the macropterous aAD of only 4% in F1.

The dominant feeding trait within the sampled species is predation (over 80% of the species), and more than 20% of species are specialized predators. A trophic niche for species with a mixed diet is present where the herbaceous cover can develop and become a feeding area for the genus *Amara* (17% of zoophytophagous species in F1).

The chorological spectrum of the community (Fig. 4) includes species from all chorological categories, with the dominance of alpine endemics. It is interesting to observe the variation in the spectrum along the altitudinal bioclimatic gradient, where the talus slopes represent a sort of threshold between vegetation vs. non-vegetation zone. Here, the species distribution can be interpreted based on the drastic selection imposed by paleoclimatic changes during glaciations (Holderegger & Thiel-Egenter, 2009). Some species adapted to refugial high-altitude ecological conditions have currently been able to expand their ranges slightly, probably because they can only exploit the upper parts of the scree slopes as a dispersal route, which are very isolated between valleys. Conversely, the areas at the base of the scree slopes in contact with alpine meadows represented the upper altitudinal limit for the expansion of species with wider ecological tolerance. Such species have had access to a dispersal route with less fragmented habitats from one valley to the other, encountering a limit only in the altitudinal direction where lithosols affected edaphic ecology, preventing the uphill rise of eurytopic species (Holdhaus, 1954; Schmitt, 2007; Drees et al., 2010). In this sense, it is possible to interpret the wide ecological spectrum that characterizes especially site F1, where endemics are dominant quantitatively.

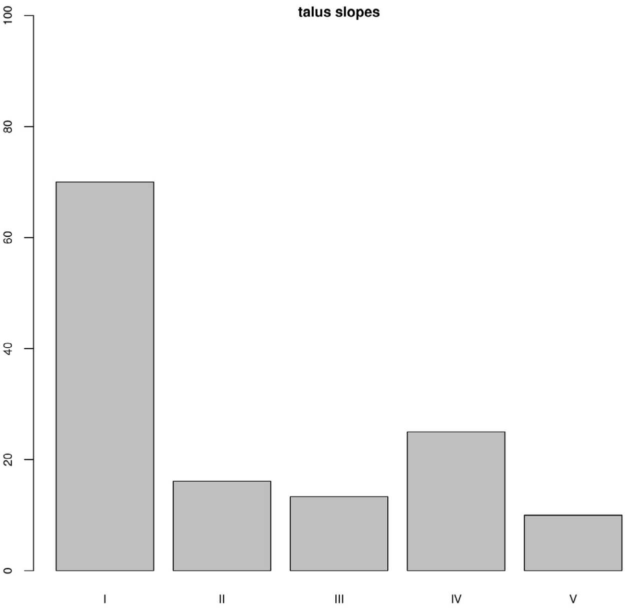

Fig. 4. Chorological spectrum of the talus slopes below 2500 m. Y axis: species percentages, x axis: I, stenoendemic Alpine species; II, montane Central European species; III, European species; IV, Eurasian, Eurosiberian species; V, Palearctic, Holarctic species.

The overall picture that emerges from the surveys of scree environments is one of a substantial overlap among different faunal aspects that are difficult to delineate with precise boundaries. These environments are strongly influenced, even in their biogeographic history, by factors related to slope exposure, soil structure, temperature fluctuations, and snow cover duration.

Regarding the scree community, it is worth noting a group of species that likely characterizes the interface with shrub and sparse tree environments, identifiable in the rhododendron and juniper heaths with scattered larches. In these areas, the biological characteristics of carabids are similar to those of scree slopes, with a dominance of brachypterous species, endemics, and zoophagous species. However, species from the mountain tops are absent, while *Pterostichus schaschli* and *Trichotichnus knauthi* are present, and *Abax pilleri*, on the other hand, comes from forest ecosystems.

Alpine meadow communities

Alpine meadows contribute to the physiognomy of the landscape, imparting a sense of uniformity to the vegetation cover. However, their extent has sometimes been indirectly modified by livestock grazing activities. Indeed, the historical increase in livestock farming, through the creation of new pastures on sunnier slopes and the expansion of natural alpine pastures downhill, has led to imbalances in soil stability and alterations in vegetational equilibria. New durable secondary herbaceous associations (mowable meadows, nardetum) have indirectly caused the lowering of alpine herbaceous associations (such as *Sesleria* grasslands) below their bioclimatic limits (Boiti & Boiti Saffaro, 1988). Subsequent abandonment of mountain areas has triggered secondary successional dynamics, raising the forest margin and reshaping ecotonal boundaries among different ecosystems (Ciolli et al., 2007; Tattoni et al., 2010).

Community of meadows on carbonate substrates (Se1-3)

The carbonate substrates of the Park host a wide variety of environments, many of which fall under the category of *Sesleria* grasslands (*Seslerio-Caricetum sempervirentis*) and their pioneer stages (Brandmayr & Zetto Brandmayr, 1988).

The three sampled *Sesleria* grasslands exhibit homogeneous characteristics: they are located at the same altitude, have the same exposure, and similar slopes. Species diversity is high, with an average of 11 species.

It seems possible to characterize *Sesleria* grasslands based on the presence of *Amara alpestris* and *Carabus creutzeri*, which, although not very abundant, are the only species not shared with other meadows. In addition to these, *Calathus melanocephalus* and *Notiophilus aquaticus* can be included due to their peak of aAD, as they are also widespread in other types of alpine meadows.

The *Sesleria* grassland community differs from the communities of *Nardus* meadows, primarily in terms of dispersal power, which is evenly divided between the two strategies of brachyptery (54% of species) and macroptery (46% of species). Species with specialized zoophagous feeding strategies (18% of species) are well represented, and along with other zoophagous species (53%), they represent the dominant feeding strategy. The chorological spectrum (Fig. 5) is still well characterized by the presence of endemics (24%), as well as by all chorological categories.

The adaptive strategies of the *Sesleria* grassland community, and meadows in general, have been selected by postglacial ecological processes when these habitats served as important dispersal routes for species pushed to the margins of the Alps during the glacial period. Species with wide ecological tolerance, emerging from the glacial refuges surrounding the Alpine chain, gradually spread first following grassland ecosystems and then forest ecosystems, and succeeded in recolonizing the interior of the Alpine chain (Holdhaus, 1954; Varga & Schmitt, 2008; Drees et al., 2010).

Therefore, the *Sesleria* grassland community is quite heterogeneous (as found by Steinwandter et al., 2022), as it can easily show species from spruce forests, such as *Pterostichus jurinei*, which is abundant in Se3, a site very close to the tree line, as well as species from other herbaceous formations, such as *Amara lunicollis*.

Meadows on siliceous substrates (FH1-3)

The sampled sites were *Festuca* grasslands homogeneous in terms of vegetation type and geomorphological characteristics, which correspond to substantial homogeneity in the carabid beetles recorded. In fact, these three sites share the majority of species. Furthermore, these environments have recorded some of the highest values of species diversity, with 15 species for FH2 and FH3 sites and 13 for the FH1 site.

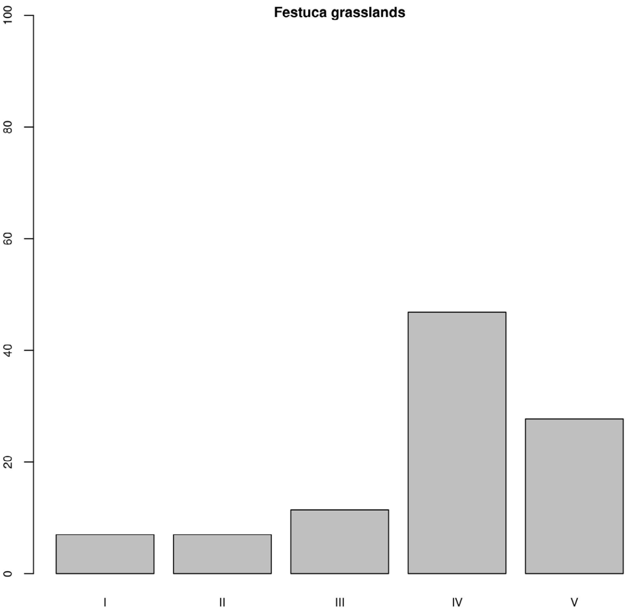

Fig. 5. Chorological spectrum of the *Sesleria* grasslands. Y axis: species percentages, x axis: I, stenoendemic Alpine species; II, montane Central European species; III, European species; IV, Eurasian, Eurosiberian species; V, Palearctic, Holarctic species.

The preference of some carabid beetles for siliceous substrates is not so much exclusive to the *Festuca* grassland but rather evident in their aAD values, which are higher compared to other environments where these species have been collected. Characteristic of *Festuca* grasslands are the *Amara* beetles, which are zoospermophagous. In fact, several species have central values, and among them, *Amara quenseli* is exclusively recorded in these environments, along with *Cymindis vaporariorum* and *Stomis rostratus*. *Amara praetermissa* was suggested as an orophilic specialist in the alpine region (Brandmayr & Zetto Brandmayr, 1988) and holds a central position in *Festuca* grasslands but is also abundant in Se2 and NA1. *Amara lunicollis*, which is reported as typical of *Nardus* grasslands (Brandmayr & Zetto Brandmayr, 1988), is indeed abundant in NA2, but it is central in FH3, as is *Amara erratica*. *Dyschirius globosus* also appeared to be typical of *Nardus* grasslands (Brandmayr & Zetto Brandmayr, 1988). However, in our case, the highest aAD values are found in *Festuca* grasslands, even though the nuclear values characterize *Nardus* grasslands. *Nebria gyllenhali* is generally found in herbaceous formations on siliceous or marly rocks, where there can be some surface water runoff (Brandmayr & Zetto Brandmayr, 1988), and it seems to strongly favor the FH3 site. Other carabid beetles in this community associated with the presence of water stagnation are *Bembidion bipunctatum*, *Notiophilus aquaticus*, and *Notiophilus biguttatus*. The affinities with *Nardus* grasslands are probably a consequence of moderate grazing by horses in the sampling area.

In the sampled sites, the biological traits of the species are very similar regarding wing development, dietary preferences, and chorotype. Flying species predominate, un-

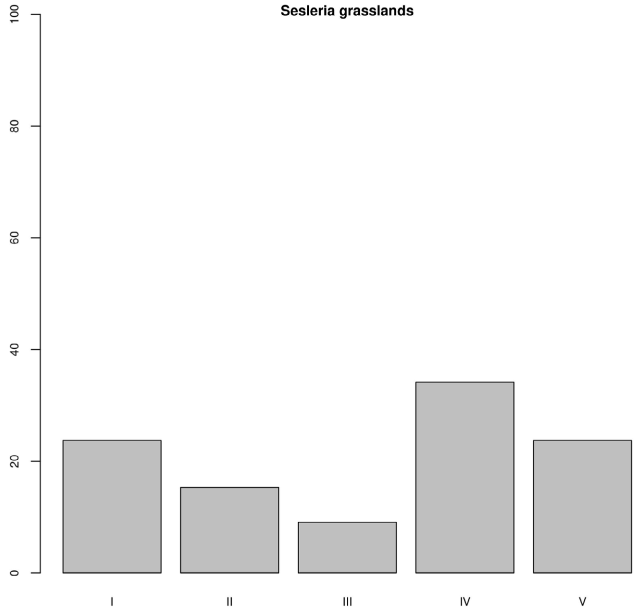

Fig. 6. Chorological spectrum of the *Festuca* grasslands. Y axis: species percentages, x axis: I, stenoendemic Alpine species; II, montane Central European species; III, European species; IV, Eurasian, Eurosiberian species; V, Palearctic, Holarctic species.

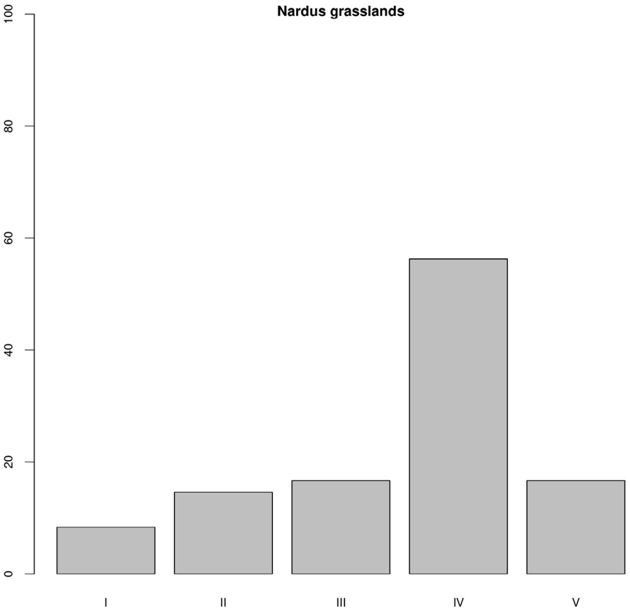

Fig. 7. Chorological spectrum of the *Nardus* grasslands. Y axis: species percentages, x axis: I, stenoendemic Alpine species; II, montane Central European species; III, European species; IV, Eurasian, Eurosiberian species; V, Palearctic, Holarctic species.

like the *Sesleria* community, with an average of over 70% of the species. The feeding strategy is almost similar to that of the *Sesleria* species, with 68% of the species being zoophagous, followed by zoospermophages with an average of 23%, while the specialized zoophagous species are less represented (less than 10%). The chorological spectrum is clearly skewed in favor of categories corresponding to broad ranges (Fig. 6), from which it emerges that there are few endemic species, representing an average of 7% of the total species for each site, while most species belong to the Euro-Asian/Euro-Siberian and Palaearctic chorotypes, and the same is mirrored by the high values of aAD.

Pastures on *Nardus* meadows (NA1, NA2)

One of the widespread components of the ecological landscape of the Park is represented by the *Nardus* meadows, derived both from meadows and high-altitude moorlands (as NA1) and from historical deforestation (as NA2). The fact that they have been classified within the same group (Fig. 2) is probably indicative of the strong influence that grazing exerts in homogenizing potentially different environments. The *Nardus* meadow community does not appear to be influenced by the coexistence of species linked to the *Sesleria* meadows community, while it is probably affected by the diversity of altitude and origin of the areas in which it has settled. For example, *Trechus obtusus* remains associated with the higher-altitude horizons of the *Nardus* meadows (site NA1), while *Bembidion lampros* here shows a preference for the lower and perhaps more grazed horizons (site NA2). Unlike other Bembidini, *Bembidion lampros* is not strictly ripicolous and tends to prefer open habitats on at least partially bare soils in the Alps (Brandmayr & Zetto Brandmayr, 1988). Apart from a single specimen collected in FH2, we find this species only in NA2, thus associated with the lower-altitude horizons of the *Nardus* meadows, along with *Poecilus versicolor*. *Trechus obtusus*, another species found exclusively here, is probably linked to higher-altitude horizons, not only to the *Nardus* meadows.

Based on the sampled sites, it is difficult to delineate a clear taxonomic distinction between the Nardetum and Seslerietum communities, but it becomes clearer when evaluating biological characteristics. The dispersal power of the community reflects the disturbance conditions generated by grazing and is composed on average of few brachypterous species (29% of species, with 15% of aAD), while macropterous species dominate both in terms of species number (72%) and abundance (aAD 86%). The dominant feeding strategy is still mainly predator-based (75% of species), with an average of 25% of species having a mixed diet, while no species with a specialized diet were recorded. The chorological spectrum is different from that of other grassland communities and is perhaps influenced by the difference in altitude (or origin) of the two surveyed sites because only NA1 has an endemic species (*Carabus bertolinii*), which represents only 0.4% in aAD, while species of chorological category II are only slightly more abundant (5%), and in NA2, the influence of species with a wide chorological category is greater.

The *Nardus* community does not exhibit the biological characteristics that make other communities faunistically valuable, and this is not at all unexpected, because it is compatible with an acidified soil and poor water stability, where bovine trampling is a strong disturbance element for the carabidocenosis. Despite the fact that the *Nardus* meadows have high species richness (14 species), the carabid community consists of generalist elements, which are not very distinctive from an ecological and biogeographical perspective.

Forest communities

Larch forests and mugo pine shrublands (sites L, RM)

Larch and/or mugo pine vegetation is distributed within the Park's territory based on geomorphology and altitude. These environments do not occupy a specific altitudinal bioclimatic zone but rather occur in areas where exposure and substrate allow their establishment.

The mugo pine forest, which often marks the limit of arboreal vegetation, typically grows at higher altitudes on unstable substrates and steep slopes with prolonged snow cover, probably because it does not face competition from other species for the same territories. Within it, the soil forms sporadically, mainly in small depressions, and develops slowly due to low average annual temperatures.

Despite their high-altitude location in contact with scree slopes and uneven vegetation cover, no significant faunal influence from non-forest habitats was found in the sampled mugo pine shrubland, except for *Trichotichnus knauthi* and a single specimen of *Carabus bertolinii*. The species characterizing this environment seem to originate from habitats at lower altitudes, where the mugo pine shrubland connects with the larch forest. None of the species common in forest environments show central values in RM, with the highest aAD recorded for *Leistus nitidus* and *Abax pilleri*.

In terms of carabid biological characteristics, there is a certain resemblance between mugo pine and larch forest, suggesting that the carabid species living in these two forest formations can be identified as the same community, which becomes less species-rich going from the larch forest to the mugo pine shrublands.

The number of species populating these environments is among the highest observed for all the sampled sites, with 16 species in the larch forest and 12 in the mugo pine shrubland, but with a clear difference in aAD between the two types, as the total aAD in site L is 15.74, compared to 1.81 in RM, where no species reaches the value of 1 aAD. Perhaps this, along with the abundance of brachypterous species, is the characteristic that differentiates the two species groups the most. The central species with maximum aAD values among those sampled are *Carabus linnaei* and *Cychrus attenuatus*, accompanied by *Leistus nitidus* and *Cychrus angustatus*.

In site RM, *Carabus auronitens* was also found, which seems to have expanded the altitudinal limits of its range, most likely due to climate change (as discussed in Pizzolotto et al., 2014).

The high species diversity of this community probably is mainly related to the physiognomy of the larch forest, which appears as a rather sparse forest with very large larch trees, as well as numerous other tree species and a dense grass ground cover. It is therefore likely that the high diversity of ecological niches allows for the success of different adaptive strategies, so that both brachypterous and macropterous species are almost equally represented (60% and 40%, respectively). However, their aAD highlights an environmental difference, as low dispersal power is the dominant strategy in the larch forest (97% of aAD). The feeding strategy seems to respond to the availability of various food resources, as there are 22% of species with a mixed diet, but probably more resources are available for zoophagous species, as suggested by the small number of zoophytophagous individuals (4% of aAD).

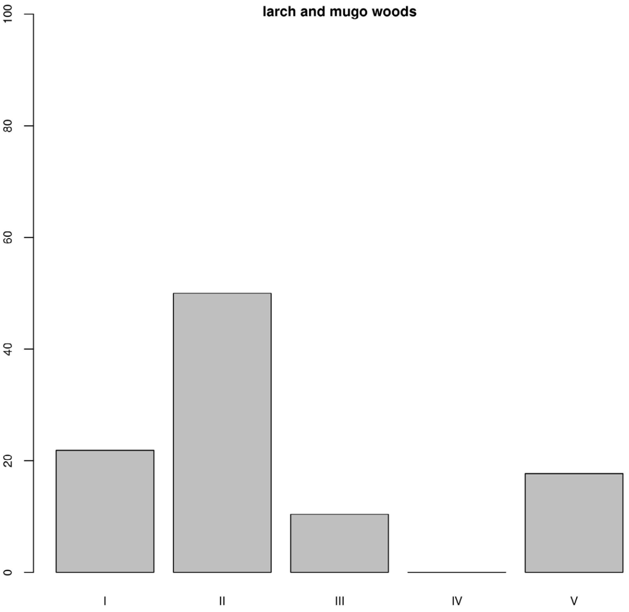

Fig. 8. Chorological spectrum of the larch and mugo woods. Y axis: species percentages, x axis: I, stenoendemic Alpine species; II, montane Central European species; III, European species; IV, Eurasian, Eurosiberian species; V, Palearctic, Holarctic species.

The proximity to the Southern limit of the Dolomites that served as refuge during the glaciations is likely the factor determining the presence of some endemic species that settled here by expanding their range during postglacial recolonization (the dynamics linked to the "Massifs de refuge", see Holdhaus, 1954; Tribsch & Schönswetter, 2003; Hewitt, 2004; Schmitt, 2009; Habel et al., 2010), exploiting both the soil heterogeneity in the mugo pine shrublands (*Carabus bertolinii*, *Trichotichnus knauthi*, and *Abax pilleri*) and the extensive clearings in the larch forest (*Carabus creutzeri*). The postglacial gradual expansion of forest ecosystems has also allowed the recolonization of high-altitude marginal environments by species with a wide distribution range but always with ecological preference centered on forest ecosystems (Fig. 8).

Forests of spruce (sites PS1, PS2, VV3, VV4)

The ecosystem of spruce forests is found along the slopes of the valleys up to a maximum altitude of about 2000 m and is one of the elements that most characterizes the ecological landscape of the Park, along with meadows and pastures, and scree slopes.

Among the sampled forest sites, a high degree of similarity has been observed, despite their geographical distance and different physiognomy, so they have been clearly separated by cluster analysis from non-forest environments (Figs 2 and 3). The species recorded are all shared with

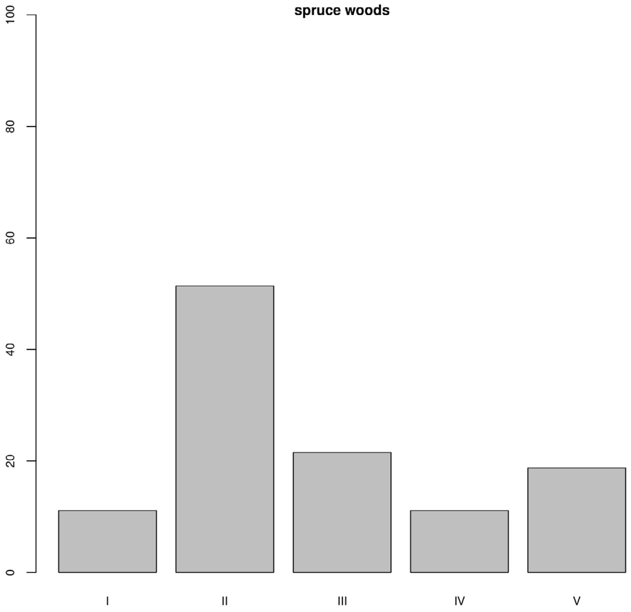

Fig. 9. Chorological spectrum of the spruce woods. Y axis: species percentages, x axis: I, stenoendemic Alpine species; II, montane Central European species; III, European species; IV, Eurasian, Eurosiberian species; V, Palearctic, Holarctic species.

other forest sites, and only *Calathus micropterus* shows a clear preference for spruce forests, where it is present with the highest aAD recorded among all species sampled in all Park sites. *Leistus nitidus* and *Cychrus attenuatus* are widespread in forest ecosystems, but not exclusively in spruce forests. It is possible to hypothesize that a new species could assume the role of characteristic species, i.e. *Carabus auronitens*, known to be associated with forest ecosystems (Turin et al., 2003), which has only been found at such high altitudes thanks to recent sampling and it seems widespread up to the larch forests.

The data from site VV4, where only four species with low aAD were recorded, probably represent a particular aspect of the community, which is disadvantaged by the artificial nature of the wood, where moreover a high density of ants was recorded.

The spruce forests represent a stable stage in ecological succession, a condition also reflected in the dispersal ability of the carabid beetle community, which is composed on average by 74% of brachypterous species corresponding to an aAD of 95%.

The structure and composition of the vegetation are probably the factors that make the trophic niches more suitable for predator or specialized predator strategies, as no species with a mixed diet were recorded.

The chorological spectrum (Fig. 9) reflects the distance both in altitude and ecological factors from refugial conditions, as the current bioclimatic zone of the forests did not play such a role during glaciations and was not included in the habitat of many endemic species during interglacials. The only endemic species recorded is *Carabus creutzeri*, eurytopic, while montane Central European species (category II) represent the characteristic aspect of the chorological spectrum (an average of 51% of species).

CONCLUSIONS

This research on carabid beetles in high-altitude environments of the Dolomites mountains found the presence of different communities of species correlated with the studied altitudinal bioclimatic gradient. On the basis of the aAD central value of the species and of the cluster analysis, some of these species can be considered characteristic of the community and ecosystem in which they were sampled. In particular, *Nebria germari* and *Trechus dolomitanus* for pioneer vegetation environments above 2500 m in altitude, while *Pterostichus schaschli* and *Pt. morio* for the same environments below 2500 m in altitude. *Amara alpestris* and *Carabus creutzeri* characterize meadows on carbonate substrates, while *Amara quenseli* characterizes meadows on siliceous substrates. It seems that the other studied environments don't host characteristic species, even if peaks in the aAD of some species have been recorded within those environments.

The collected data showed that community diversity and biogeographic diversity follow the altitudinal diversity of ecosystems, at least for the investigated area. Furthermore, the diversity of species traits reflects the selective pressures of ecological factors in high-altitude extreme environments, where stenoendemic species with a predatory feeding strategy and limited dispersal power are more common.

The studied environments are widely distributed along the Italian Eastern Alps, so the collected data can be used as a reference for other research campaigns conducted in similar environments, or as a benchmark for comparing changes that may be detected by future research campaigns in the same geographic area or similar environments.

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Appendix. List of the sample sites and the NAT2000 vegetation category characterizing them.

See also Pizzolotto et al. (2016), and https://cdr.eionet.europa.eu/help/natura2000/Documents/Int_Manual_EU28.pdf

Some of the data have already been published (Pizzolotto et al., 2014), but most of them are unpublished. They are gathered here in order to obtain an exhaustive description of the carabid distribution in the main ecosystems of the Park.

RS – Small patches of vegetation on limestone bedrock. NAT2000: 8240, 8120
Ap1 – Small patches of vegetation on limestone bedrock. NAT2000: 8240, 8120
Ap2 – Small patches of vegetation on limestone bedrock. NAT2000: 8240, 8120
Ap3 – Small patches of vegetation on limestone bedrock. NAT2000: 8240, 8120
Ap4 – Small patches of vegetation on limestone bedrock. NAT2000: 8240, 8120
Cf1 – Small patches of vegetation on limestone scree. NAT2000: 8240, 8120
VN1 – Snow bed. NAT2000: 6170
F1 – Fragments of alpine meadow and scree vegetation. NAT2000: 8120
F2 – Pioneer scree vegetation. NAT2000: 8120
VV1 – Pioneer scree vegetation. NAT2000: 8120
VV2 – Vegetation with dwarf bushes and sparse willows, mainly Rhododendron, Dryas and blueberry. NAT2000: 4060, 4070
Se1 – Alpine meadow with Sesleria varia and Carex sempervirens. NAT2000: 6170
Se2 – Alpine meadow with Sesleria varia and Carex sempervirens. NAT2000: 6170
Se3 – Alpine meadow with Sesleria varia and Carex sempervirens. NAT2000: 6170
NA1 – Pasture of Nardus derived from trampling of Rhododendron moors. NAT2000: 6150

NA2 – Pasture of Nardus resulting from the deforestation of a larch-cember wood. NAT2000: 6150
FH1 – Acidophilic pasture of Festuca. NAT2000: 6150
FH2 – Acidophilic pasture of Festuca. NAT2000: 6150
FH3 – Acidophilic pasture of Festuca. NAT2000: 6150
L – Larch forest with abundant Erica undergrowth. NAT2000: 9420
RM – Mountain pine forest. NAT2000: 4070
VV3 – Mixed forest dominated by spruce. NAT2000: 9410
VV4 – Man-planted spruce forest.
PS1 – Subalpine spruce forest with dense blueberry undergrowth and soil rich in sphagnum moss. NAT2000: 9410
PS2 – Subalpine spruce forest with blueberry undergrowth and soil with sphagnum moss. NAT2000: 9410