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Article · June 2023

DOI: 10.13133/2284-4880/1442

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Sapienza Università Editrice

E-ISSN 2284-4880
ISSN 0429-288X

Fragmenta entomologica, 55 (1): 45–56 (2023)

Research article
Submitted: September 23rd, 2022 – *Accepted*: January 10th, 2023 – *Published*: June 30th, 2023
DOI: 10.13133/2284-4880/1442

Sex-ratio and body size plasticity in two cold-adapted ground beetles co-occurring in a periglacial area of the European Alps (Coleoptera: Carabidae)

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Abstract
Differences in the sex-ratio and morphometric parameters in cold-adapted ground beetles were analysed to investigate environmental heterogeneity at small scale in a periglacial contest of the European Alps. Four hundred and thirty specimens of two cold-adapted ground beetles – *Nebria germarii* (Heer, 1837) and *Nebria castanea* (Bonelli 1810) – were analysed in order to test the presence of variation in sex-ratio, sexual dimorphism and morphometric parameters in relation to the occurrence of ice, and other environmental variables. Specifically, the populations found on an ice-related landform (active rock glacier) were compared with those on ice-free landforms (a fossil rock glacier and a scree slope). Both species experience sex-dependent morphometric plasticity. In addition, sex-ratio is female-biased, supporting female pioneering tendency in all the studied landforms. Two morphometric parameters resulted indirectly affected by the presence/absence of ice in the terrain: the head width decreases, while elytra width increases passing from ice-free to ice-related landform. Both these morphometric differences may be related to the increase of intra/interspecific competition and to the lower trophic availability. This study highlights that even if these high altitude cold-adapted species are able to survive on ice-free landforms, they probably find more favourable conditions on ice-related landforms. Since the two species show different sensitivity to the ice-presence, it is not always possible to detect this preference through abundances variability (e.g for *N. castanea*), but it necessary to use more detailed morphometric analysis. Head width and elytra width are good candidates as response traits of interstitial ice occurrence in stony terrains.

Key-words: ice, morphometric parameters, *Nebria germarii*, *Nebria castanea*, permafrost, rock glacier, plasticity.

Introduction

The occurrence of high geomorphological heterogeneity in the Alpine environment is one of the most important variables determining high biodiversity in Alpine ground beetle assemblages and their maintenance over time (Gobbi et al. 2021a). Some examples of these heterogeneous environments are represented by glaciers, proglacial plains, debris-covered glaciers, active rock glaciers and scree slopes. In particular, rock glaciers are the best expression of permafrost (i.e. soil, rock or sediment that is frozen for more than two consecutive years (Haeberli et al. 2006)) occurrence on the European Alps. They consist of coarse surface debris that insulates an ice-core or ice-debris mixture. In the European Alps they represent a fragmentary habitat, linked to discontinuous and azonal permafrost that locally determines existence of micro-thermal environments (Seppi 2006). Also among/within rock glaciers a further heterogeneity is given by the different debris size: when it consists of large blocks, a negative thermal anomaly originates which determines a colder microclimate on the surface (Juliussen & Humlum 2008).

Active rock glaciers, like debris-covered glaciers, allow cold-adapted species (i.e. animal and plant species closely related to alpine and nival belt) to survive, by acting as refuge areas in the current warm-stage period (Tampucci et al. 2017; Brighenti et al. 2020; Valle et al. 2020; Gobbi et al. 2021b; Valle et al. 2021).

On Alpine rock glaciers, springtails (Collembola), ground beetles (Coleoptera: Carabidae), spiders (Araneae) and centipedes (Chilopoda) are among the most abundant taxa, in terms of species richness and abundance of individuals (Gobbi et al. 2011; Gobbi 2020; Gobbi et al. 2020; Gobbi & Lencioni 2020). Specifically, ground beetles are the most studied from the ecological point of view, due to their sensitivity to local-scale climate change, large percentage of endemic species, low dispersal capacity and ability to respond clearly to different environmental conditions (Brandmayr et al. 2003; Gobbi et al. 2011; Pizzolotto et al. 2016; Gobbi 2020). In addition, an increasing number of papers that used a species-trait approach highlighted the existence, in several species, of a certain morphological plasticity, linked to different factors such as temperature, trophic availability, intra and interspecific competition (Kingsolver & Huey 2008; Talarico et al. 2020; Sukhodolskaya et al. 2021). Previous studies on ground beetles proved the existence of morphometric variability at different scales, reflecting the response to different environmental conditions: at large scale along latitudinal or altitudinal gradient (Sukhodolskaya 2016; Sukhodolskaya & Ananina 2017; Cvetkovska-Gjorgjievska et al. 2017), or at smaller spatial scale, like along glacier forelands (Gobbi et al. 2010).

The present study focuses on two cold-adapted ground beetle species, *Nebria germarii* (Heer, 1837) and *Nebria castanea* (Bonelli 1810), co-occurring on a periglacial area of the European Alps. The goal of this article is to evaluate at small scale (i.e. comparing neighboring landforms) the variations in sex-ratio and morphological parameters within the populations of these two species living on ice-related (active rock glacier), and ice-free (fossil rock glacier and scree slope) landforms. In particular, in this paper we aim to test if: i) sex-ratio and sexual dimorphism of the two cryophilic species change in relation to the landforms analysed, ii) the presence of ice indirectly influences the morphological parameters of the investigated populations.

Material and methods

Study area

The study was performed in the glacial cirque Lazaunkar (Val Senales, Trentino-Alto Adige, Eastern Rhaetian Alps (SOIUSA classification), 46.44.49N, 10.45.20E.). Three landforms were analysed: an active rock glacier, a fossil rock glacier and a scree slope (Fig.1).

The selected ice-related landform is an active rock glacier classified as a "tongue-shape rock glacier" (Whalley & Martin 1987); it occupies an area of 0.12 Km^2 and it develops for 660 m with a NE aspect, covering the altitudinal range between 2700 m and 2480 m (2005 data from Krainer et al. 2015). Being active it has an ice-core that determine its dynamicity and morphology: flow velocities are low along edges and increase towards the central part of the rock glacier (mean velocity from 2 to 6 mm/day), where the transverse ridges and the furrows are well developed (Fey & Krainer 2020).

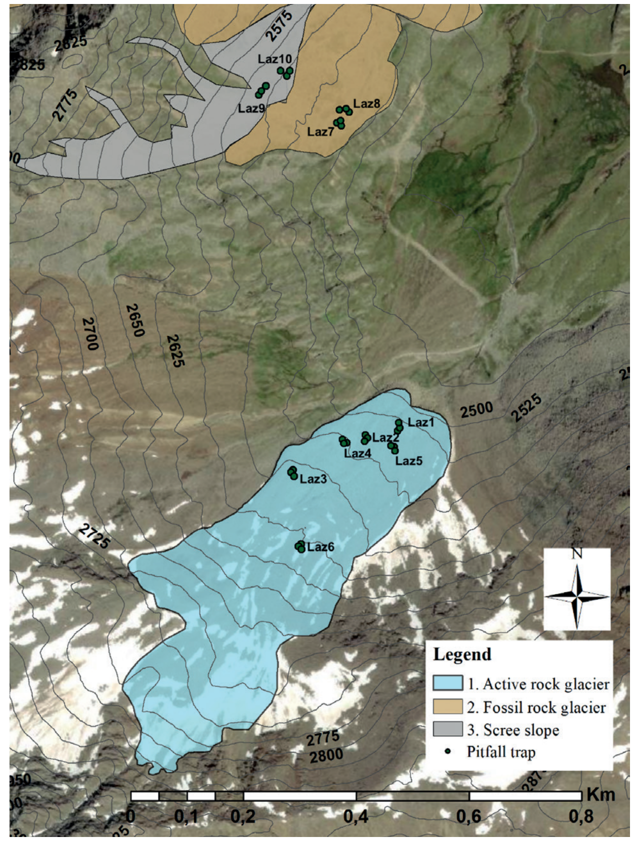


Fig. 1 – Sampling plan: distribution of pitfall traps at the Lazaunkar site.

The selected ice-free landforms are a fossil rock glacier and a scree slope that do not have permafrost. The fossil rock glacier is a former rock glacier that lost its ice core and is located about 400 m North from the active rock glacier and occupies an area of 0.05 km^2 (calculated in QGIS 3.26.2). The scree slope is located upstream the fossil rock glacier and occupies an area of about 0.05 km^2 (calculated in QGIS).

The surface of the three geomorphological landforms is characterized by coarse-grained debris with scattered large boulders (> 1 m), with the exception of sparse isles of fine debris. Herbaceous plants are present on the active rock glacier, specifically on fine stony debris islands. On the other hand, on fossil rock glacier and scree slope fine debris islands with small shrubs (*Vaccinium* spp., *Juniperus communis* and *Rhododendron ferrugineum*) are also present.

Sampling design

The sampling design (Fig. 1) consisted of six plots located on the surface of the active rock glacier (Laz1, Laz2, Laz3, Laz4, Laz5, Laz6), while two plots on the surface of the fossil rock glacier (Laz7 and Laz8) and two plots on the surface of the scree slope (Laz 9 and Laz 10) were selected due to the limited extent of these landforms. Each plot was represented by three pitfall traps (Gobbi 2020; Gobbi & Lencioni 2020) distanced each other about 10 m. Each pitfall trap consisted of a plastic vessel (diameter 7 cm, height 10 cm) baited with a mixture of wine-vinegar, salt and few drops of soap (Gobbi 2020). All traps were active over the entire snow-free period, specifically from the 14 Jul – 4 Sep. 2020 and collected and reset every ca. 20 days (Supplementary Table 1). In proximity of each traps a sample of about 200 g was taken to measure substrate pH (in 1:2.5 substrate:water) and organic matter content. Coordinates, altitude and vegetation cover (percentage coverage estimate) were also recorded in correspondence of each trap.

Morphometric parameters
All the sampled arthropods were counted, sorted and stored in the collections of MUSE-Science Museum of Trento (Italy). Ground beetles were identified to the species level using a stereomicroscope and dichotomous keys reported in Ledoux & Roux (2005) and Pesarini & Monzini (2010, 2011). In addition to species identification, vital stage and sex of each specimen were also annotated through the analysis of the genital organs and/or secondary sexual characteristics. Species identification of the larval stage was not carried out; thus larvae are excluded from the analysis.

Finally, morphometric data of the ground beetles belonging to *Nebria germarii* (215 specimens) and *Nebria castanea* (215 specimens) were measured. A stereomicroscope equipped with a micrometric objective was used for

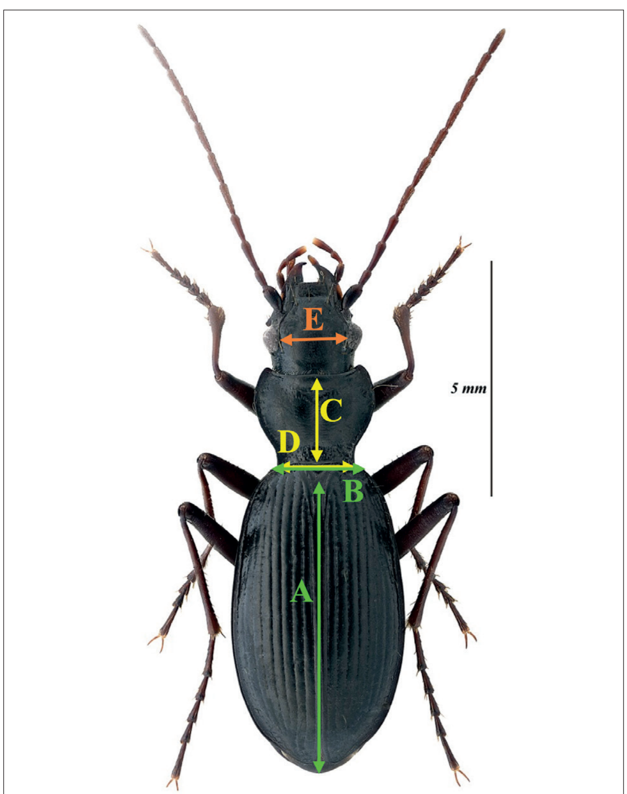


Fig. 2 – Dorsal view of *Nebria germarii* and representation of the measured body parameters. For the meaning of the letters see the text (Photo by A. Carlin).

Correlation test (plot)	**Correlation coefficient**	**p-value**
Elytra width ~ altitude	0.110	0.310
Elytra width ~ pH	0.239	0.026*
Elytra width ~ vegetation cover	0.159	0.141
Elytra width ~ springtail abundance	0.298	0.005*
Elytra width ~ spider abundance	-0.108	0.318

Table 1 – Correlation coefficients and p-value of the correlation analysis between the elytra width of *Nebria castanea* females, of the significant plot specimens, and the environmental variables. Asterisk highlights significant values.

the measurements. Following Sukhodolskaya et al. (2020) five, of the six, morphometric parameters were recorded (Fig.2) (the trait "head length" was not used due to the bias in the measurement: the occipital suture was not always visible, and we avoided its evagination in order to limit the risk of damage of the museum specimens):

A) Elytra length as distance between posterior end of scutellum and terminus of right elytron (in absence case of intact right elytron, left one is acceptable).
B) Elytra width as interhumeral distance.
C) Pronotum length measured along of central furrow pronotum.
D) Pronotum width as distance between posterior corners of pronotum.
E) Head width as distance between proximal innermost sides of eyes.

Data analyses
Each analysis was performed at pitfall trap level, thus considering each trap separately.

An analysis of variance (ANOVA, because of the normal distribution – assessed by the Shapiro-Wilk test – of the male and female abundance data) was performed to test the differences of the sex-ratio in *N. germarii* and *N. castanea* among each landform type and each plot. A total of 118 females and 97 males for *N. germarii* and a total of 127 females and 88 males for *N. castanea* were analysed.

Then, an analysis of variance was performed using the Kruskal-Wallis test (because of the non-normal distribution of the data assessed by the Shapiro-Wilk test) to verify the existence of sexual dimorphism in *N. germarii* and *N. castanea* on the whole study site. When the model is significant, the Dunn test with Benjamini-Hochberg correction (Benjamini & Hochberg 1995) was performed, to define which landforms or plots have significant differences.

A principal component analysis (PCA) was carried out to identify the main variation gradients of the morphometric parameters and their relationship with the analysed landforms.

A morphometric analysis was performed using the Kruskal-Wallis test in order to evaluate the presence of significant differences in body size between landforms

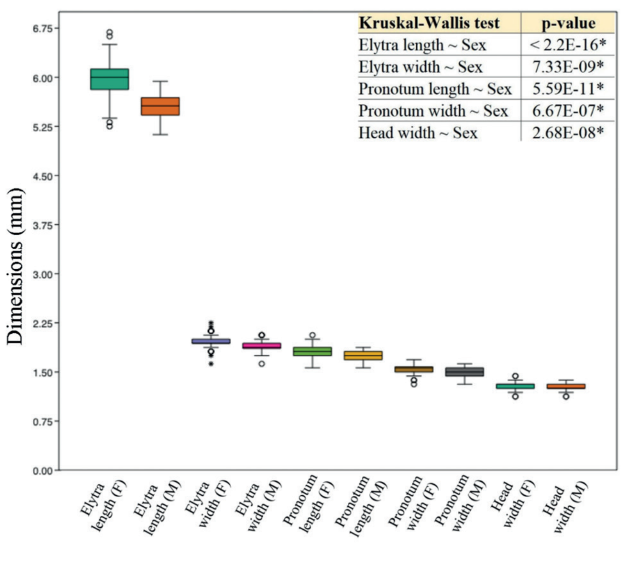


Fig. 3 – Boxplot of *Nebria germarii* body parameters as a function of sex (F=female; M=male). p-value of the Kruskal-Wallis tests for *N. germarii* body size as a function of sex. Asterisk highlights significant values.

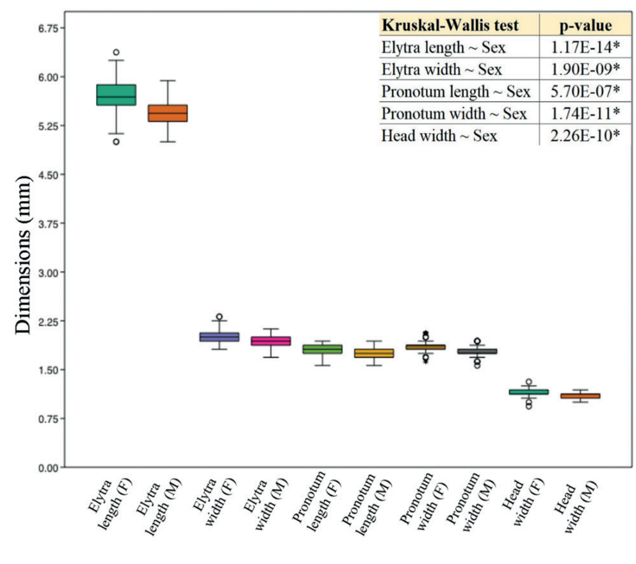


Fig. 4 – Boxplot of *Nebria castanea* body parameters as a function of sex (F=female; M=male). p-value of the Kruskal-Wallis tests for *N. castanea* body size as a function of sex. Asterisk highlights significant values.

for *N. castanea* and *N. germarii*. The analysis was carried out by comparing the specimens of the landform with ice (active rock glacier) with those of the landforms without ice (fossil rock glacier and scree slope). For the morphometric analysis, body measurements of 426 ground beetles were used, instead of 430, because of four damaged specimens (one *N. castanea* and three *N. germarii*). The analyses were performed considering only one sex at a time to avoid differences related to sexual dimorphism.

For females of *N. castanea*, a correlation analysis (using Pearson coefficient) was carried out, to evaluate which environmental variables between pH, vegetation cover, altitude, springtails (Collembola) abundance and spiders (Arachnida: Araneae) abundance determine the significant differences found in the morphometric analysis. Through preliminary analysis (with Pearson test) a high autocorrelation between organic matter and pH was observed (Correlation coefficient = -0.8). Therefore, only pH was used in the correlation analysis as soils variable. This correlation analysis was not performed for *N. germarii*, due to the small number of specimens sampled on fossil rock glacier and scree slope.

ANOVA test and Kruskal-Wallis tests were performed with R software (version 4.1.1) (R Core Team, 2020), while the PCA and the correlation analysis were performed with PAST software (version 4.03) (Hammer et al. 2001).

Results

Abundances of ground beetle species in the considered landforms

A total of four ground beetle species (432 individuals) were collected in the study area: *Nebria germarii*, *Nebria castanea*, *Pterostichus unctulatus* (Duftschmid, 1812) and *Cychrus attenuatus* (Fabricius, 1792). *Nebria germarii* and *Nebria castanea* resulted the most abundant species.

Specifically, two-hundred and one *N. germarii* specimens were sampled on landform with ice (sampling with 18 traps divided into six plots; 11.2 specimens/trap on average) and 14 specimens on ice-free landforms (sampling with 12 traps divided into four plots; 1.2 specimens/trap on average). As regards *N. castanea*, 123 specimens were sampled on the landform with ice (sampling with 18 traps divided into six plots; 6.8 specimens/trap on average) and 92 specimens on the ice-free landforms (sampling with 12 traps divided into four plots; 7.7 specimens/trap on average). The sampling revealed the presence of *N. germarii* in almost ten times higher abundances on landforms with ice than those present on ice-free landforms (11.2 specimens/trap vs 1.2 specimens/trap). As regards *N. castanea*, the abundances present in the two landforms are similar (6.8 specimens/trap vs 7.7 specimens/trap).

Ground beetle community detected includes also two *Pterostichus unctulatus* sampled on fossil rock glacier and one specimen of *Cychrus attenuatus* sampled on scree slope. Therefore, both these two species were collected only on ice-free landforms.

Sex-ratio

For both species no significant differences in sex-ratio were observed as a function of landforms and plots. A total of 118 females and 97 males of *N. germarii* were sampled. The average sex-ratio in the whole study area is slightly female-biased (percentage of females = 55%; χ^2 = 14,475; p <0.01). About *N. castanea*, 127 females and 88 males specimens were sampled. Similarly to *N. germarii*, also for this species the populations are slightly female-biased (percentage of the females = 59%; χ^2 = 16,999; p <0.01).

Sexual dimorphism
For both species the existence of sexual dimorphism was assessed, with significant differences for all body measurements, specifically female specimens resulted bigger than male specimens (Fig.3; Fig.4).

Main gradients of morphometric variables
For both species it was observed that the morphometric parameters linked respectively to the width and to the length are not strongly correlated because the former vary along axis 2, the latter along axis 1. In addition, through this analysis, no clear distinction was observed between the specimens of the analysed landforms (Fig.5).

Morphometric analysis of N. germarii
By comparing the morphology of the specimens sampled on the active rock glacier (landform with ice) with the specimens collected on both the fossil rock glacier and scree slope (landforms without ice), a significant effect of the landform type in relation to the ice-presence on the width of the head was found (p-value = 0.026). In particular, the head of specimens found on the active rock glacier resulted significantly narrower with respect to the head of the specimens on the landforms without ice (Fig.6).

Morphometric analysis of N. castanea
Significant differences were found in the elytra width of female specimens as a function of landform type (p-value = 0.007); in particular the elytra of the active rock glacier specimens are significantly wider than the elytra of the specimens on the landforms without ice (Fig.7).

Correlation analysis for N. castanea
The morphometric parameter which showed the greatest significant variation in relation to the landform type is the elytra width of female specimens of *N. castanea*. The analysis showed a weak, but positive and significant correlation between elytra width and soil pH (p-value = 0.026) and springtail abundance (p-value = 0.005) (Table 1, Fig.8, Fig.9). The analysis was not performed for males because no significant differences were found in males' analysis.

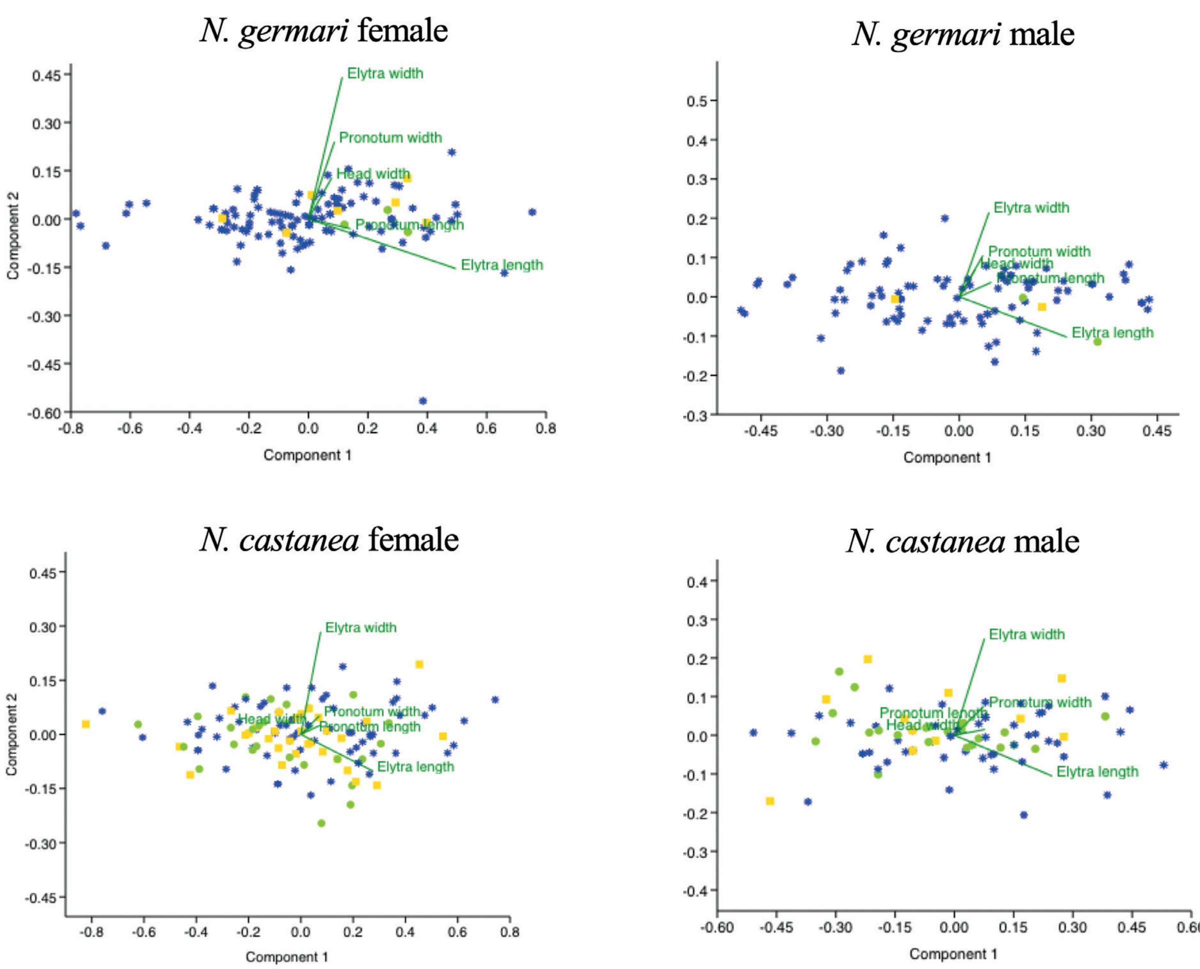
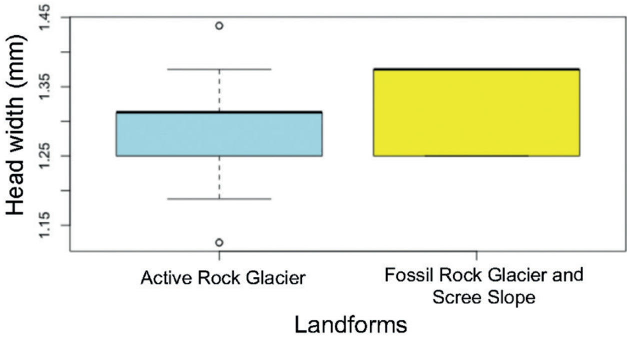
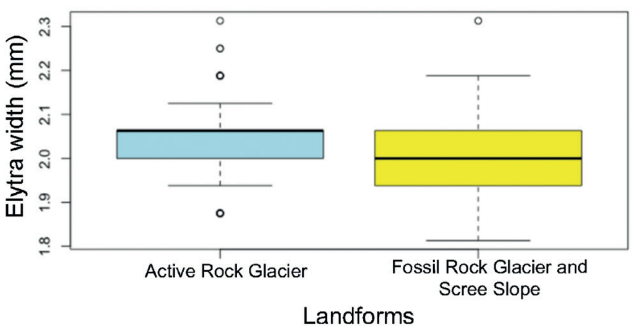


Fig. 5 – PCA analysis graphs. Blue stars=active rock glacier specimens; Gold squares=fossil rock glacier specimens; Green dot=scree slope specimens.



Nebria germarii	Females	Males
Elytra length	0.052	0.136
Elytra width	0.082	0.772
Pronotum length	0.158	0.664
Pronotum width	0.170	0.618
Head width	0.026*	0.643

Fig. 6 – Boxplot of head width of *Nebria germarii* females as a function of landform. p-value of *N. germarii* morphometric analysis with Kruskal-Wallis test, that evaluate the presence of significant differences in body size between landforms with ice (active rock glacier) and without ice (fossil rock glacier and scree slope). Asterisk highlights significant values.



Nebria castanea	Females	Males
Elytra length	0.122	0.093
Elytra width	0.007*	0.897
Pronotum length	0.889	0.372
Pronotum width	0.786	0.745
Head width	0.156	0.232

Fig. 7 – Boxplots of elytra width of *Nebria castanea* females as a function of landform. p-value of *N. castanea* morphometric analysis with Kruskal-Wallis test, that evaluate the presence of significant differences in body size between landforms with ice (active rock glacier) and without ice (fossil rock glacier and scree slope). Asterisk highlights significant values.

Discussion

Sex-ratio and sexual dimorphism in N. germarii *and* N. castanea *populations*

On Alpine debris-covered glacier and along its proglacial area it has been observed for the species *N. germarii* and *N. castanea* the tendency to have female-biased populations (Tenan et al. 2016). Specifically, it has been observed that the presence of female-biased populations is linked to the greater propensity of females to disperse with respect to males, useful for colonizing pioneering environments with less interspecific competition (Tenan et al. 2016; Hågvar et al. 2020). In our case the populations of *N. germarii* and *N. castanea* sampled in the study area resulted only slightly female-biased. Therefore, the presence or absence of ice in the investigated landforms does not affect the sex-ratio in *Nebria* populations suggesting the presence of almost stable and close populations.

In general, for *N. germarii* and *N. castanea* sexual dimorphism has been assessed, in which females are significantly bigger than males; this is a common pattern already documented in ground beetles populations (with the exception of some subsocial ground beetles (e.g. Ditomina; Brandmayr & Talarico 2021) and the ecological significance concerns the greater accumulation of biomass by the females useful for the production of a great number of eggs (Marshall et al. 2013). On the other hand, large sizes imply an increase in the duration of development of larval stages, a greater food needs/consumption, and a significant risk of mortality due to the higher exposure to predators (Nylin & Gotthard 1998; Sukhodolskaya et al. 2021).

Variation in N. germarii *and* N. castanea *abundance in relation to the ice presence*

Differently to *N. castanea* that occurred both on ice-free and ice-related landforms, *N. germarii* showed a marked preference for the considered ice-related landform (active rock glacier). This preference can be explained by *N. germarii* occurrences on terrains with high humidity and low average annual temperatures as highlighted in other researches (Kaufmann & Juen 2001; Pizzolotto et al. 2014; Valle et al. 2020; Panza & Gobbi, 2022).

Morphometric variations of N. germarii *and* N. castanea *in relation to the ice presence*

Interestingly, head and elytra width resulted the most related parameter to the landform type, specifically this variation is sex-related. More in details, female individuals of *N. germarii* living on the ice-free landforms (fossil rock glacier and scree slope) resulted with a wider head, compared to the specimens of the ice-related landform (active rock glacier). This was also observed for *N. castanea*, for both

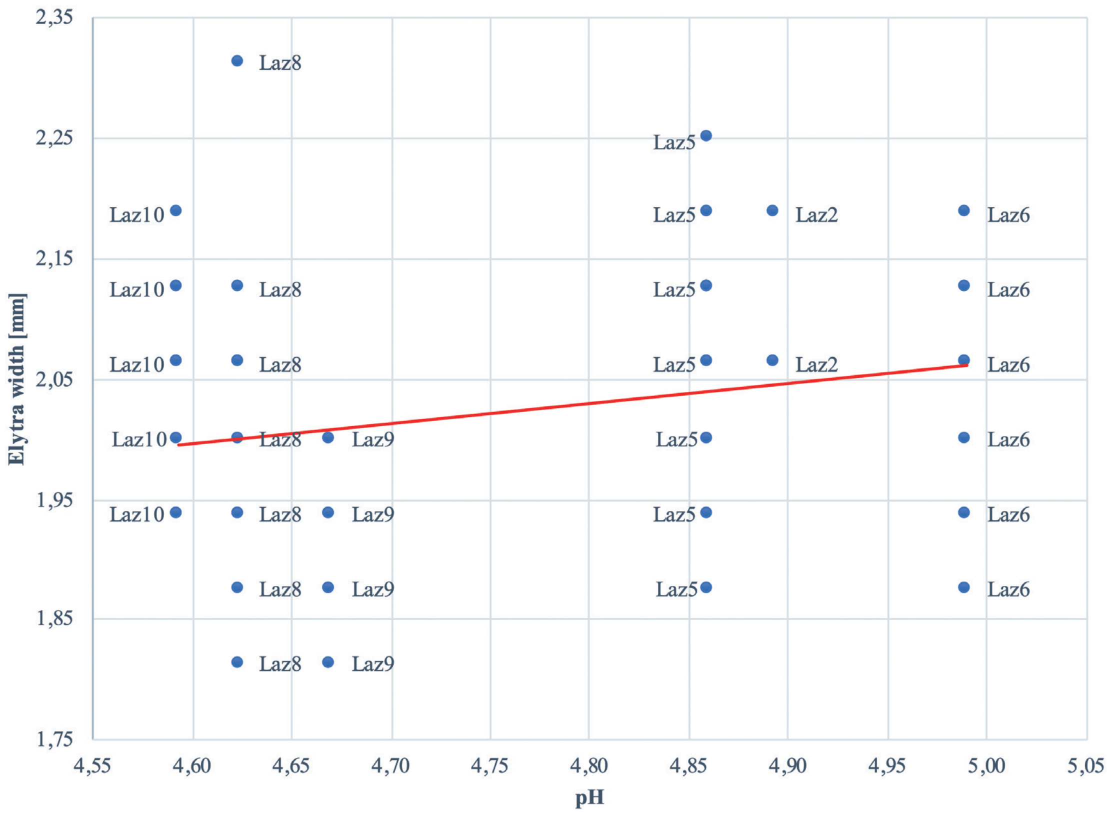


Fig. 8 – Linear regression graph between elytra width of *Nebria castanea* females and the soil pH.

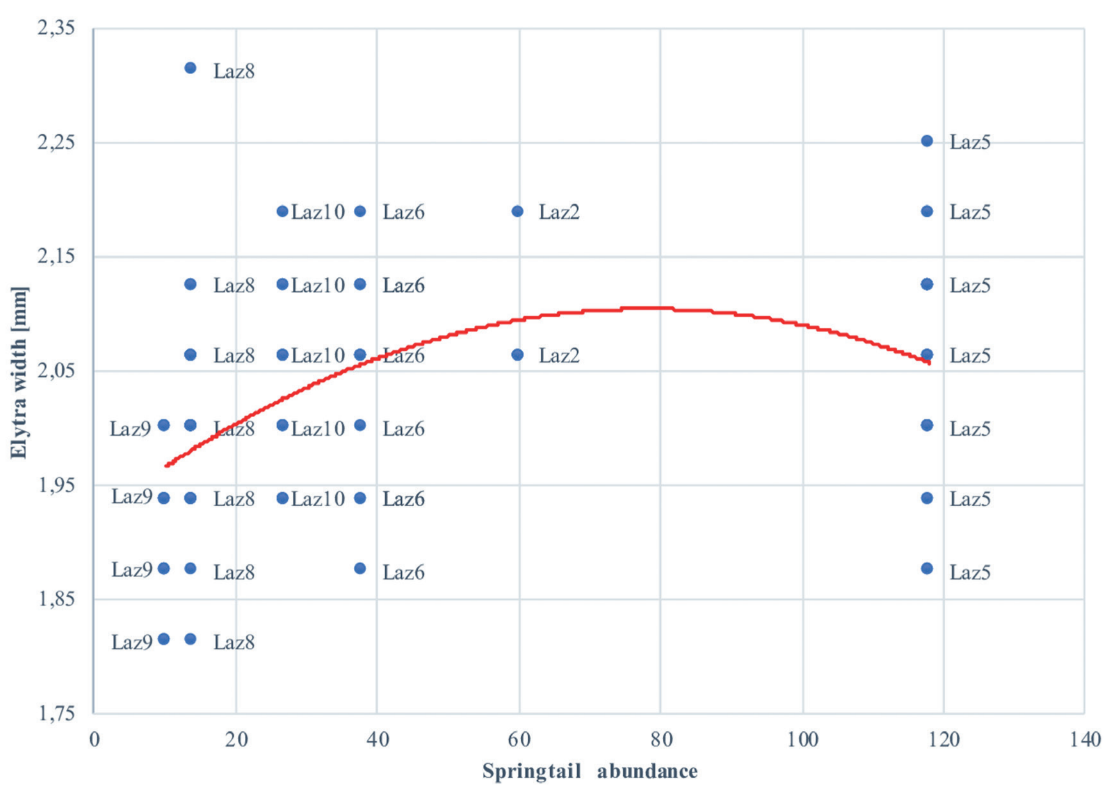


Fig. 9 – Polynomial regression graph between elytra width of *Nebria castanea* females and the springtail abundance.

males and females. Springtails represent the main trophic resource for ground beetles in glacial habitat (Raso et al. 2014; Valle et al. 2020); our data on springtails showed that their average abundance for trap is lower on ice-free landforms (10.3±2.5 individuals on ice-free landforms vs 40.8±5.4 on the ice-related landform). It is known that trophic availability is a factor determining greater or lesser intra- and interspecific competition among alpine ground beetles (Tenan et al. 2016). Thus, we can suppose that, in the ice-free landforms only the most competitive *Nebria* specimens, thus those with larger head size, are better adapted to live in habitats with limited trophic resources (springtails) and great intra and interspecific/inter-taxa competition or greater intra and inter-guild competition. About the inter-taxa competition it is also important to highlight that in these high-altitude environments, spiders represent the direct competitors of ground beetles (Gobbi et al. 2017; Sint et al. 2019). The wider head could allow a more efficient ingestion in larger quantities of food with respect to other competitors (Forsythe 1982), like for instance, spiders, and could also allow a more efficient inter guild predation (e.g. spiders vs ground beetles), in particular in landforms, like the ice-free, with low availability of preys (collembola).

In *N. castanea* significant morphometric variations were found also for the female elytra width between the analysed landforms; this difference was confirmed by the correlation analysis: a positive relationship was observed between springtail abundance and female elytra size of *N. castanea*. The greater size of the elytra of the specimens on active rock glacier may be linked (as suggested also by head morphometric variations) to greater abundance of springtails present on ice-related landform. In fact, the greater abundance of springtails determines a greater trophic availability, therefore a greater biomass accumulation (Raso et al. 2014). Morphological plasticity has already been documented for other ground beetle species (Talarico et al. 2020; Sukhodolskaya et al. 2021) and specifically in *N. castanea* (Gobbi et al. 2010), also in relation to the prey size (Komuna et al., 2013; 2014). In this species it might be considered an adaptive capacity that allows to survive even in extreme conditions such as those of glacial and periglacial areas. Individuals of those populations display different body size, related to the environment stability in which they live. A stable environment allows a longer larval development, and a high trophic availability allows high foraging rates; the action of these two effects determines the presence of larger specimens (Blake et al. 1994; Gobbi et al. 2010).

The positive relationship between the female elytra width of *N. castanea* and soil pH can be a proxy of soil degree of evolution. Specifically, on micaschists – the bedrock type of the study area – higher pH and lower organic matter values in soils on the ice-related landforms respect to soils on ice-free landforms could indicate the presence of a more immature substrate (Ji et al. 2014). The presence of environment on the landform with ice with less competition and more trophic availability causes the presence of larger ground beetle specimens, compared to the specimens present on ice-free landforms (fossil rock glacier and scree slope).

Ice-related landforms support optimal microclimatic conditions for cold-adapted arthropod species (Brighenti et al. 2020; Gobbi 2020; Valle et al. 2021). The result obtained by our study allowed to advance the hypothesis that ice-related landforms, respect to ice-free landforms, host less inter- and intra-specific competition for cold-adapted species. Thus, even if some cold-adapted *Nebria* species manage to survive also on neighbour ice-free landforms, they probably find more favourable conditions on landforms with ice, and this preference is detectable through morphometric analysis.

This is an important step ahead on the knowledge about the relationship between species traits plasticity in climate-depending species in relation to their environment.

Conclusions

This work represents the first study that analyses morphometric parameters in high altitude ground beetles and shows how the morphology is influenced by environmental factors, in particular the ice presence. Furthermore, it allowed to increase the knowledge regarding the cryophilic species *Nebria germarii* and *N. castanea* in their pioneering characteristics in colonizing ice-related landform (i.e. with female-biased populations). However, we highlighted different sensitivity to ice presence in these two high altitude cold-adapted species. For some organisms, morphometric analysis result fundamental to detect with a high sensitivity cold-adapted species response to ice presence, thus suggesting the effectiveness of this method for investigating in detail the ecology of the endangered periglacial habitat.

Acknowledgements – Authors thank Mr. Peter Tumler (Agriturismo Vieshof) and Anna Invernizzi for the support given to the field activity. The authors also thank two anonymous reviewers for their useful comments.

References

Baquero M.E., Ledesma E., Gilgado J., Ortuño V., Jordana R. 2017. Distinctive Collembola communities in the Mesovoid Shallow Substratum: First data for the Sierra de Guadarrama National Park (Central Spain) and a description of two new species of *Orchesella* (Entomobryidae). PLoS ONE, 12(12): e0189205. Doi: https://doi.org/10.1371/journal.pone.0189205. 10.1371/journal.pone.0189205

Benjamini Y., Hochberg Y. 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. Journal of the Royal Statistical Society. Series B (methodological), 289–300.

Blake S., Foster G.N., Eyre M.D., Luff M.L. 1994. Effects of habitat type and grassland management practices on the body size distribution of carabid beetles. Pedobiologia, 38: 502–512.

Brandmayr P., Pizzolotto R., Scalercio S., Algieri M.C., Zetto T. 2003. Diversity patterns of carabids in the Alps and the Apennines. Pp 307–317 In: Nagy L., Grabherr G., Korner Ch., Thompson D.B.A. (eds), Alpine Biodiversity in Europe (vol. 167). Springer, Berlin.

Brandmayr P., Zetto, T., Pizzolotto R. 2005. I Coleotteri Carabidi per la valutazione ambientale e la conservazione della biodiversità. Manuale operativo. APAT-Agenzia nazionale per la protezione dell›ambiente e per i servizi tecnici, Roma.

Brandmayr P., Talarico F. 2021. Study on behavioural ecology of *Ditomus calydonius* Rossi (Coleoptera: Carabidae: Ditomina), a strictly granivorous ground beetle with brood care. Russian Entomological Journal, 30(4): 455–467. Doi: 10.15298/rusentj.30.4.08

Brighenti S., Hotaling S., Finn D., Fountain A., Hayashi M., Herbst D., Saros J., Tronstad L., Millar C. 2020. Rock glacier and related landforms: overlooked climate refugia for mountain biodiversity. Global Change Biology, 27(8): 1504–1517. Doi: 10.32942/osf.io/84ydq

Brygadyrenko V., Reshetniak D.Y. 2014. Morphological variability among populations of *Harpalus rufipes* (Coleoptera, Carabidae): What is more important – the mean values or statistical peculiarities of distribution in the population? Folia Oecologica, 41: 109–133.

Brygadyrenko V., Korolev O. 2015. Morphological polymorphism in an urban population of *Pterostichus melanarius* (Illiger, 1798) (Coleoptera, Carabidae). Graellsia, 71(1): e025. Doi: 10.3989/graellsia.2015.v71.126

Cvetkovska-Gjorgjievska A., Hristovski S., Prelić D., Šerić Jelaska L., Slavevska-Stamenković V., Ristovska M. 2017. Body size and mean individual biomass variation of ground-beetles community (Coleoptera: Carabidae) as a response to increasing altitude and associated vegetation types in mountainous ecosystem. Biologia, 72(9): 1059–1066. Doi: https://doi.org/10.1515/biolog-2017-0114

Fey C., Krainer K. 2020. Analyses of UAV and GNSS based flow velocity variations of the rock glacier Lazaun (Ötztal Alps, South Tyrol, Italy). Geomorphology, 365: 107261. Doi: 10.1016/j.geomorph.2020.107261

Forsythe T.G. 1982. Feeding Mechanisms of Certain Ground Beetles (Coleoptera: Carabidae). The Coleopterists Bulletin, 36(1): 26–73. Doi: http://www.jstor.org/stable/4007976

Gobbi M., Caccianiga M., Cerabolini B., De Bernardi F., Luzzaro A., Pierce S. 2010. Plant adaptive responses during primary succession are associated with functional adaptations in ground beetles on deglaciated terrain. Community Ecology, 11: 223–231. Doi: https://doi.org/10.1556/ComEc.11.2010.2.11

Gobbi M., Isaia M., De Bernardi F. 2011. Arthropod colonisation of a debris-covered glacier. The Holocene, 21(2): 343–349. Doi: 10.1177/0959683610374885

Gobbi M., Ballarin F., Brambilla M., Compostella C., Isaia M., Losapio G.M., Maffioletti C., Seppi R., Tampucci D., Caccianiga M.S. 2017. Life in harsh environments: carabid and spider trait types and functional diversity on a debris-covered glacier and along its foreland. Ecological Entomology, 42: 838–848. Doi: https://doi.org/10.1111/een.12456

Gobbi M., Lencioni V. 2020. Glacial Biodiversity: Lessons from Ground-dwelling and Aquatic Insects. Pp:1–23. In: Kanao M., Godone D., Dematteis N. (eds), Glaciers and the Polar Environment, IntechOpen, London, 10.5772/intechopen.92826

Gobbi M. 2020. Global warning: Challenges, threats and opportunities for ground beetles (Coleoptera: Carabidae) in high altitude habitats. Acta Zoologica Academiae Scientiarum Hungaricae, 66: 5–20. Doi: 10.17109/azh.66.suppl.5.2020

Gobbi M., Caccianiga M., Compostella C., Zapparoli M. 2020. Centipede assemblages (Chilopoda) in high-altitude landforms of the Central-Eastern Italian Alps: diversity and abundance. Rendiconti Lincei. Scienze Fisiche e Naturali, 31: 1071–1087. Doi: https://doi.org/10.1007/s12210-020-00952-4

Gobbi M., Armanini M., Boscolo T., Chirichella R., Lencioni V., Ornaghi S., Mustoni A. 2021a. Habitat and landform types drive the distribution of carabid beetles at high altitudes. Diversity, 13: 142. Doi: https://doi.org/10.3390/d13040142

Gobbi M., Ambrosini R., Casarotto C., Diolaiuti G., Ficetola G.F., Lencioni V., Seppi R., Smiraglia C., Tampucci D., Valle B., Caccianiga M. 2021b. Vanishing permanent glacier: climate change is threatening a European Union habitat (Code 8340) and its poorly known biodiversity. Biodiversity and Conservation, 30: 1–10. Doi: 10.1007/s10531-021-02185-9

Haeberli W., Hallet B., Arenson L., Elconin R., Humlum O., Kääb A., Kaufmann V., Ladanyi B., Matsuoka N., Springman S., Vonder Mühll D. 2006. Permafrost Creep and Rock Glacier Dynamics. Permafrost and Periglacial Processes, 17: 189-214. Doi: 10.1002/ppp.561

Hågvar S., Gobbi M., Kaufmann R., Ingimarsdóttir M., Caccianiga M., Valle B., Pantini P., Pietro P., Fanciulli, Vater A. 2020. Ecosystem Birth Near Melting Glacier: A Review on the Pioneer Role of Ground-Dwelling Arthropods. Insects, 11(9): 644. Doi: 10.3390/insects11090644

Hammer Ø., Harper D.A.T., Ryan P.D. 2001. PAST: Paleontological statistics software package for education and data analysis. Palaeontologia Electronica, 4(1): 1–9.

Ji C., Yang Y., Han W., He Y., Smith J., Smith P. 2014. Climatic and Edaphic Controls on Soil pH in Alpine Grasslands on the Tibetan Plateau, China: A Quantitative Analysis. Pedosphere, 24: 39–44. Doi: 10.1016/S1002-0160(13)60078-8

Juliussen H., Humlum O. 2008. Thermal Regime of Openwork Block Fields on the Mountains Elgåhogna and Sølen, Central-eastern Norway. Permafrost and Periglacial Processes, 19: 1–18. 10.1002/ppp.607

Kaufmann R., Juen A. 2001. Habitat use and niche segregation of the genus *Nebria* (Coleoptera: Carabidae) in the Austrian Alps. Mitteilungen der Schweizerischen Entomologischen Gesellschaft, 74: 237–254

Konuma J., Sota T., Chiba S. 2013. Quantitative genetic analysis of subspecific differences in body shape in the snail-feeding carabid beetle *Damaster blaptoides*. Heredity, 110: 86–93.

Konuma J., Yamamoto S., Sota T. 2014. Morphological integration and pleiotropy in the adaptive body shape of the snail-feeding carabid beetle *Damaster blaptoides*. Molecular Ecology, 23: 5843–5854. Doi: 10.1111/mec.12976

Krainer K., Bressan D., Dietre B., Haas J., Hajdas I., Lang K., Mair V., Nickus U., Reidl D., Thies H., Tonidandel D. 2015. A 10,300-year-old permafrost core from the active rock glacier Lazaun, southern Ötztal Alps (South Tyrol, northern Italy). Quaternary Research, 83(2): 324–335. Doi: 10.1016/j.yqres.2014.12.005

Ledoux G., Roux P. 2005. *Nebria* (Coleoptera: Nebriidae). Faune Mondiale. Muséum and Société Linneénné de Lyon, Lyon. 976 pp

Marshall J., Miller M., Lelito J., Storer A. 2013. Latitudinal variation in body size of *Agrilus planipennis* and relationship with fecundity. Agricultural and Forest Entomology, 15: 294–300. Doi: 10.1111/afe.12017

Nylin S., Gotthard K. 1998. Plasticity in life-history traits, Annual Review of Entomology, 43: 63–83

Paje F., Mossakowski D. 1984. pH-preferences and habitat selection in carabid beetles. Oecologia, 64(1): 41-46. Doi: 10.1007/BF00377541. PMID: 28311636

Panza R., Gobbi M., 2022. Areal contraction, upward shift and habitat fragmentation in the cold-adapted ground beetle *Nebria germarii* Heer, 1837 in the Brenta Dolomites, Italy. Rendiconti Lincei. Scienze Fisiche e Naturali, 33: 923–931. Doi: https://doi.org/10.1007/s12210-022-01112-6

Pesarini C., Monzini V. 2010. Insetti della fauna italiana: Coleotteri Carabidi. 1, Volume 1, Parte 2 di Natura – Società Italiana di Scienze Naturali, ISSN 0369-6243, 152 pp.

Pesarini C., Monzini V. 2011. Insetti della fauna italiana: Coleotteri Carabidi. 2, Volume 2, Parte 2 di Natura – Società Italiana di Scienze Naturali, ISSN 0369-6243, 144 pp.

Pizzolotto R., Gobbi M., Brandmayr P. 2014. Changes in ground beetle assemblages above and below the treeline of the Dolomites after almost 30 years (1980/2009), Ecology and Evolution, 4(8): 1284–1294. Doi: https://doi.org/10.1002/ece3.927

Pizzolotto R., Albertini A., Gobbi M., Brandmayr P. 2016. Habitat diversity analysis along an altitudinal sequence of alpine habitats: the Carabid beetle assemblages as a study model. Periodicum Biologorum, 118: 241–254. Doi: https://doi.org/10.18054/pb.2016.118.3.3924

Poore M.E.D. 1955. The Use of Phytosociological Methods in Ecological Investigations: I. The Braun-Blanquet System. Journal of Ecology, 43(1): 226–244. Doi: https://doi.org/10.2307/2257132

R Development Core Team. 2020. R: A language and environment for statistical computing. R Foundation For Statistical Computing, Vienna, Austria https://www.r-project.org/ (2019).

Raso L., Sint D., Mayer R., Plangg S., Recheis T., Brunner S., Kaufmann R., Traugott M. 2014. Intraguild predation in pioneer predator communities of alpine glacier forelands. Molecular Ecology, 23(15): 3744–3754. Doi: 10.1111/mec.12649

Sint D., Kaufmann R., Mayer R., Traugott M. 2019. Resolving the predator first paradox: Arthropod predator food webs in pioneer sites of glacier forelands. Molecular Ecology, 28: 336–347. Doi: https://doi.org/10.1111/mec.14839

Sukhodolskaya R. 2016. Intra-specific Body Size Variation of Ground Beetles (Coleoptera: Carabidae) in Latitudinal Gradient. Periodicum Biologorum, 118: 273–280. 10.18054/pb.2016.118.3.3918

Sukhodolskaya R. & Ananina T. 2017. Elevation Changes of Morphometric Traits Structure in *Pterostichus montanus* Motch. (Coleoptera, Carabidae). Asian Journal of Biology, 2: 1–9. Doi: 10.9734/AJOB/2017/32748

Sukhodolskaya R., Saveliev A., Ukhova N., Vorobyova I., Solodovnikov I., Anciferov A., Gordienko T., Shagidullin R., Vavilov D. 2020. Modeling sexual differences of body size variation in ground beetles in geographical gradient (The case study in *Pterostichus oblongpunctatus* Fabricius, 1787). GSC Biological and Pharmaceutical Sciences, 13: 149–161. Doi: 10.30574/gscbps.2020.13.3.0388

Sukhodolskaya R.A., Ananina T.L., Saveliev A.A. 2021. Variation in Body Size and Sexual Size Dimorphism of Ground Beetle *Pterostichus montanus* Motsch. (Coleoptera, Carabidae) in Altitude Gradient. Contemporary Problems of Ecology, 14: 62–70. Doi: 10.1134/S199542552101008X

Talarico F., Mazzei A., Gangale C., Scrivano G., Brandmayr P. 2020. Morphometric differences in populations of *Nebria kratteri* Dejean and Boisduval, 1830 from two old forests in Calabria (Coleoptera, Carabidae). Fragmenta entomologica, 52: 57–62. Doi: 10.4081/fe.2020.408

Tampucci D., Gobbi M., Marano G., Boracchi P., Boffa G., Ballarin F., Pantini P., Seppi R., Compostella C., Caccianiga M. 2017. Ecology of active rock glaciers and surrounding landforms: climate, soil, plants and arthropods. Boreas, 46(2): 185–198. Doi: 10.1111/bor.12219.

Tenan S., Maffioletti C., Caccianiga M., Compostella C., Seppi R., Gobbi M. 2016. Hierarchical models for describing space-for-time variations in insect population size and sex-ratio along a primary succession. Ecological Modelling, 329: 18–28. Doi: 10.1016/j.ecolmodel.2016.02.006

Valle B., Ambrosini R., Caccianiga M., Gobbi M. 2020. Ecology of the cold-adapted species *Nebria germari* (Coleoptera: Carabidae): the role of supraglacial stony debris as refugium during the current interglacial period. Acta Zoologica Academiae Scientiarum Hungaricae, 66: 199–220. Doi:10.17109/azh.66.suppl.199.2020

Valle B., Cucini C., Nardi F., Caccianiga M., Gobbi M., Di Musciano M., Carapelli A., Ficetola G. F., Guerrieri A., Fanciulli P. P. 2021. *Desoria calderonis* sp. nov., a new species of alpine cryophilic springtail (Collembola: Isotomidae) from the Apennines (Italy), with phylogenetic and ecological considerations. European Journal of Taxonomy, 787: 32–52. Doi: https://doi.org/10.5852/ejt.2021.787.1599

Whalley B., Martin H. 1987. Rock glacier: Part 1: Rock glacier morphology: Classification and distribution. Progress in Physical Geography, 11: 260–282. Doi: 10.1177/030913338701100205

Supplementary material

Supplementary Table 1: Lazaunkar trap station data and trap sampling activity

Plot	Trap code	Landform type	Altitude [m a.s.l.]	Coordinates UTM WGS84 (32T) Lat	Coordi-nates UTM WGS84 (32T) Long	Sampling period	Days of activity
Laz1	A	Active rock glacier	2547	5178609	634169	from 14.VII.2020 to 04.IX.2020	52
Laz1	B	Active rock glacier	2544	5178615	634173	from 14.VII.2020 to 04.IX.2020	52
Laz1	C	Active rock glacier	2541	5178624	634171	from 14.VII.2020 to 04.IX.2020	52
Laz2	A	Active rock glacier	2539	5178602	634112	from 14.VII.2020 to 04.IX.2020	52
Laz2	B	Active rock glacier	2540	5178597	634116	from 14.VII.2020 to 04.IX.2020	52
Laz2	C	Active rock glacier	2540	5178591	634111	from 14.VII.2020 to 04.IX.2020	52
Laz3	A	Active rock glacier	2562	5178540	633983	from 14.VII.2020 to 04.IX.2020	52
Laz3	B	Active rock glacier	2565	5178536	633980	from 14.VII.2020 to 04.IX.2020	52
Laz3	C	Active rock glacier	2571	5178529	633985	from 14.VII.2020 to 04.IX.2020	52
Laz4	A	Active rock glacier	2546	5178588	634079	from 14.VII.2020 to 04.IX.2020	52
Laz4	B	Active rock glacier	2546	5178594	634071	from 14.VII.2020 to 04.IX.2020	52
Laz4	C	Active rock glacier	2548	5178587	634074	from 14.VII.2020 to 04.IX.2020	52
Laz5	A	Active rock glacier	2550	5178581	634163	from 14.VII.2020 to 04.IX.2020	52
Laz5	B	Active rock glacier	2549	5178583	634157	from 14.VII.2020 to 04.IX.2020	52
Laz5	C	Active rock glacier	2551	5178574	634165	from 14.VII.2020 to 04.IX.2020	52
Laz6	A	Active rock glacier	2563	5178409	633998	from 14.VII.2020 to 04.IX.2020	52
Laz6	B	Active rock glacier	2566	5178405	633993	from 14.VII.2020 to 04.IX.2020	52
Laz6	C	Active rock glacier	2573	5178400	633998	from 14.VII.2020 to 04.IX.2020	52
Laz7	A	Fossil rock glacier	2506	5179155	634061	from 15.VII.2020 to 04.IX.2020	51
Laz7	B	Fossil rock glacier	2504	5179150	634069	from 15.VII.2020 to 04.IX.2020	51
Laz7	C	Fossil rock glacier	2505	5179159	634068	from 15.VII.2020 to 04.IX.2020	51
Laz8	A	Fossil rock glacier	2509	5179174	634083	from 15.VII.2020 to 04.IX.2020	51
Laz8	B	Fossil rock glacier	2509	5179180	634078	from 15.VII.2020 to 04.IX.2020	51
Laz8	C	Fossil rock glacier	2510	5179178	634066	from 15.VII.2020 to 04.IX.2020	51
Laz9	A	Scree slope	2538	5179204	633923	from 15.VII.2020 to 04.IX.2020	51
Laz9	B	Scree slope	2539	5179211	633928	from 15.VII.2020 to 04.IX.2020	51
Laz9	C	Scree slope	2541	5179221	633935	from 15.VII.2020 to 04.IX.2020	51
Laz10	A	Scree slope	2541	5179238	633973	from 15.VII.2020 to 04.IX.2020	51
Laz10	B	Scree slope	2542	5179248	633978	from 15.VII.2020 to 04.IX.2020	51
Laz10	C	Scree slope	2547	5179247	633961	from 15.VII.2020 to 04.IX.2020	51