



Life in harsh environments: carabid and spider trait types and functional diversity on a debris-covered glacier and along its foreland

Journal:	<i>Ecological Entomology</i>
Manuscript ID	17-0106-EEN.R1
Manuscript Type:	Original Article
Date Submitted by the Author:	25-May-2017
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Keywords:	Araneae, Carabidae, colonisation, dispersal power, hunting strategies, turnover

Life in harsh environments: carabid and spider trait types and functional diversity on a debris-covered glacier and along its foreland

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Life-history trait types and functional diversity in carabid and spider assemblages living on the glaciers surface, or colonising recently deglaciated terrains, are still few known.

We found that dispersal abilities and hunting strategies are two key factors affecting the species survival in harsh landforms quickly changing to global warming.

Our study sheds new light on how functional approach improves our knowledge on the adaptive strategies of ground-dwelling arthropods in colonising glaciers surface and recently deglaciated terrains.

For Review Only

1 **Life in harsh environments: carabid and spider trait types and functional**
2 **diversity on a debris-covered glacier and along its foreland**

3

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25 Running title: Functional traits in harsh environments

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35 **Abstract.**

- 36 1. Patterns of species richness and species assemblage composition of ground-dwelling
37 arthropods in primary successions along glacier forelands are traditionally described using a
38 taxonomic approach. On the other hand, the functional trait approach could ensure a better
39 characterization of their colonisation strategies on these kind of habitats.
- 40 2. We applied the functional trait approach to investigate patterns of functional diversity and
41 life-history traits of ground beetles and spiders on an alpine debris-covered glacier and along
42 its forefield in order to describe their colonization strategies.
- 43 3. We sampled ground beetles and spiders in different successional stages, representing five
44 stages of deglaciation.
- 45 4. Our results showed that the studied glacier hosts ground beetle and spider assemblages
46 mainly characterized by the following traits: walking colonisers, ground hunters and small
47 sized species. These traits are typical of species living in cold, wet and gravelly habitats. The
48 diversity of functional traits in spiders increased along the succession, and both in carabids
49 and spiders, life-history traits follow the “addition and persistence model”. Accordingly,
50 there is no turnover but there is an addition of new traits and a variation in their proportion
51 within each species assemblage along the succession. The distribution of ground beetles and
52 spiders along the glacier foreland and on the glacier seems to be driven by dispersal ability
53 and foraging strategy.
- 54 5. The proposed functional approach improves our knowledge on the adaptive strategies of
55 ground-dwelling arthropods in colonising glaciers surface and recently deglaciated terrains,
56 which represent landforms quickly changing due to global warming.

57

58 **Key-words:** Araneae, Carabidae, colonisation, dispersal power, hunting strategies, turnover.

59

60 Introduction

61 Two of the main visible effects of climate warming on alpine areas are glacier retreat and increasing
62 supraglacial debris on glacier surfaces (e.g. Citterio *et al.*, 2007; Paul *et al.*, 2007).

63 Several studies describe the structural changes (species richness trends and species
64 turnover/persistence) in ground-dwelling arthropod assemblages along the primary succession on
65 recently deglaciated areas (i.e. glacier forelands) (see Hagvar, 2012). Spatial distribution of ground-
66 dwelling arthropods is mainly determined by site age (time since deglaciation), with its related local
67 fine-scale environment conditions, such as soil grain size, vegetation cover and/or soil organic
68 matter (see. Kaufmann, 2001; Brambilla & Gobbi, 2014; Tampucci *et al.*, 2015). More recently,
69 attention has shifted from the glacier forelands to the surface of debris-covered glaciers, because of
70 the emerging interest of debris-covered glaciers as suitable habitats for micro-, meso- and macro-
71 fauna and plant life (Caccianiga *et al.*, 2011; Gobbi *et al.*, 2011; Azzoni *et al.*, 2015). Debris-
72 covered glaciers are formed by frequent slipping and casting of deposits creating large quantities of
73 stony material which covers the glacier surface, in particular on the ablation area (Citterio *et al.*,
74 2007), and they significantly increased during the last decade. Arthropod distribution on debris-
75 covered glaciers is mainly determined by rock grain size, debris thickness, glacier
76 movements/instability, and microclimate conditions (Gobbi *et al.*, 2011).

77 Traditionally, a taxonomic approach was used to describe ground-dwelling arthropod assemblages
78 along primary successions (e.g. Kaufmann, 2001, Gobbi *et al.*, 2006, Vater, 2012), on the other
79 hand the functional trait approach has been rarely applied even if it can be useful to understand
80 ecosystem complexity and dynamics (Diaz & Cabido, 2001; Losapio *et al.*, 2015; Moretti *et al.*
81 2017). A possible reason might be the lack of knowledge about traits of many taxa and whether
82 these traits are related to environmental changes.

83 Ground beetles (Coleoptera: Carabidae) and spiders (Arachnida: Araneae) can be considered among
84 the most important meso- and macro-fauna living on recently deglaciated terrains in terms of
85 species richness and abundance (Hagvar, 2012). Carabid beetle and spider life-history traits along

86 environmental gradients (see Schirmel *et al.*, 2012; Pizzolotto *et al.*, 2016) are quite well known in
87 terms of response traits (*sensu* Díaz *et al.*, (2013), i.e. traits that impact on individuals' capacity to
88 colonise and persist in a habitat). On the other hand, there are no studies involving both spider and
89 ground beetle life-history traits that describe, by means of a functional approach, the ground-
90 dwelling arthropod functional diversity and the turnover of life-history traits along a primary
91 succession on glacier forelands and on the glacier surfaces. The functional trait approach would
92 ensure a better characterization of the arthropod colonisation strategies on the glaciers and on
93 terrain left free by retreating glaciers.

94 The study area selected to shade light on this topic is one of the few known cases in the Italian Alps
95 in which it is possible to investigate, at the same time, the species assemblage colonisation and the
96 survival strategies on a debris-covered glacier surface and along more than one-hundred and sixty
97 year glacier foreland chronosequence. Therefore, firstly, we described the carabid and spider
98 species assemblages and life-history traits on the debris covered glacier, then we analysed the
99 species richness, life-history trait and functional diversity patterns along the chronosequence of
100 Holocene glacier retreat. Specifically we (i) tested whether species richness as well as functional
101 diversity increase with time since deglaciation and (ii) hypothesized that time since deglaciation
102 triggers the turnover of life-history traits.


103

104 **Material and Methods**


105

106 *Study area*

107 The study was carried out on the glacier foreland of Vedretta d'Amola glacier (Adamello-Presanella
108 Group, Central-Eastern Italian Alps, 46°13'12''-10°41'02'') (Fig. 1), and on the glacier surface.

109 Vedretta d'Amola glacier is a debris-covered glacier of c. 82.1 hectares (area recorded by one of the
110 authors, RS, in summer 2012), covered approximately for 70% by stony debris with variable depth,
111 from a few centimeters to about one meter. The glacier tongue is located above the treeline 

112 The glacier foreland is c. 1.23-km long, covers an altitudinal range of c. 150 meters, and is
113 characterized by a large moraine system dating back to the Little Ice Age (LIA, c. AD 1850). Field
114 observations and various sources including maps, reports, aerial photographs, iconography, and
115 records of length change collected over the last 100 years allowed us to reconstruct the glacier
116 tongue position during the LIA, in 1925, in 1994, and in 2003 (Fig. 1).

117 The snow-free period usually lasts from late June to late September. Annual mean ground
118 temperature on the glacier foreland, recorded during the period 5 August 2011 – 5 August 2012,
119 was 1.7 °C, while  an relative air humidity was 96% (datalogger located at about 15 cm depth in
120 the stony debris at plot 10, see Fig. 1 and Figure S1 – Supporting Information). The mean annual
121 temperature, recorded during the period 15 July 2011 – 15 July 2012, on the supraglacial debris was
122 0.5 °C (datalogger located at 10 cm depth in the supraglacial debris at plot 2, see Fig. 1 and Figure
123 S1 – Supporting Information).

124 On the supraglacial debris (mean elevation: 2642 m asl) the pioneer plant community (total plant
125 cover <10%) is dominated by *Cerastium uniflorum*, *C. pedunculatum*, and *Saxifraga oppositifolia*.

126 On the glacier foreland (mean elevation: 2520 m asl) the plant community (plant cover ranging
127 from 5% to 70% along the foreland) is dominated by *Poa alpina*, *P. laxa*, *Saxifraga bryoides*, *Geum*
128 *reptans*, and *Luzula alpino-pilosa*. Outside the glacier foreland (mean elevation: 2426 m asl), Late
129 Glacial sites are occupied by *Carex curvula*-dominated communities with >80% ground cover.

130

131 *Sampling design*

132 We selected eleven sampling plots located along a linear transect starting on the glacier surface and
133 ending on Late Glacial substrata outside the LIA moraines (Fig.1). We assigned to each plot a class
134 of deglaciation: Class 0 (not yet deglaciated – glacier surface; plots 1, 2, 3, 4), Class 1 (areas
135 deglaciated in the period 1994-2003; plots 5, 6), Class 2 (1925-1994; plots 7, 8), Class 3 (1850-
136 1925; plots 9, 10), and Class 4 (Late Glacial Period; plot 11) (Fig. 1). Plots were selected on the
137 base of the following two criteria: (i) areas not subjected to physical disturbance (e.g. rockslides,
138 river flooding), (ii) detection probability of the considered species (e.g. on the glacier surface –
139 class 0 – we located four plots due to the low species detection probability (see Tenan *et al.*, 2016)).

140

141 *Sampling method*

142 We sampled carabid beetles and spiders using pitfall traps (Eymann *et al.*, 2010). In each plot three
143 traps were located about 10 m apart (Kotze *et al.*, 2011), which led to a total of 33 pitfall traps.
144 Traps consisted of plastic vessels (7 cm of diameter and 10 cm of height) baited with a mixture of
145 wine-vinegar and salt. The traps were active over the entire snow free seasons, from early July to
146 late September 2011-2012. Samples were taken at 25-day intervals. Plots 2, 4, 5, 8 and 10 were
147 studied in year 2011, whereas plots 1, 3, 6, 7, 9 and 11 were studied in 2012 in order to optimize the
148 sampling effort in this kind of harsh environments. Since temperature is one of the main factors
149 affecting carabids life cycle, distribution, and species assemblage composition in montane habitats
150 (Kotze *et al.*, 2011), the choice to sample in two different sampling years could be a bias in our
151 dataset. Thus, we compared the annual mean temperature in each of the sampling year (2011 vs
152 2012). We considered air temperatures data from the nearest (c. 6,5 km from our study site)
153 meteorological station (Pinzolo –Italy; lat: 46°09'22''- 10°45'25'', elevation: 760 m slm;
154 www.meteotrentino.it). The mean annual temperature in 2011 was 9.2°C, while it was 9.0°C in

155 2012. Given that no important variation in air temperature was found, we can assume that it did not
156 affect the carabid beetle assemblage richness and composition in the two sampling seasons.

157 Carabids were identified to the species level following Pesarini & Monzini (2010, 2011), while
158 spiders were identified to the species level following Netwing *et al.*, (2017).

159 Nomenclature refers to the checklist of the European Carabid beetles Fauna (Vigna Taglianti, 2013)
160 and to The World Spider Catalogue (WSCA, 2017). For spiders, juveniles were excluded from the
161 analysis.

162

163 *Environmental variables*

164 We recorded abiotic (percentage of gravel, soil pH, and soil organic matter) and biotic (plant
165 species richness and vegetation cover) variables within a buffer of 1 m around each trap.

166 We collected a substrate sample of 1–2 kg at every plot for particle size distribution. Two hundred
167 grams of substrate were sampled at each pitfall trap for organic matter content analysis (Walkley–
168 Black method: Walkley & Black, 1934) and pH measurement. All the soil samples were taken at the
169 surface. We recorded plant cover using a 50 cm diameter metal circle placed at the four opposite
170 sides of the pitfall trap. We recorded vascular plants, bryophytes, and ground lichens occurring
171 within the plot and visually estimate the overall vegetation cover and that of every species, with a
172 resolution of 5%. We calculated the mean values from the four 50 cm samplings to obtain a single
173 value associated with each trap. For each plot, we recorded and averaged environmental variables
174 around the three pitfall traps.

175

176 *Functional traits*

177 *Carabids.* We considered the following well-established response traits of primary succession
178 (Gobbi *et al.*, 2010; Schirmel *et al.*, 2012): dispersal ability (high dispersal power = winged species;
179 low dispersal power = short-winged species); diet (omnivorous, carnivorous), and mean body
180 length (millimeters) of the pool of species in each trap. We analyzed for the first time along primary

181 succession the following traits: larval hunting strategy (surface runner, surface walker, soil pore
182 explorer) and adult hunting strategy (zoophilous, omniphagous, olfactory-tactil predator, visual
183 predator). Data about species traits were obtained on the base of specialized literature (Hůrka, 1996;
184 Brandmayr *et al.*, 2005; Homburg *et al.*, 2014) (Table 1).

185 *Spiders.* We considered the following response traits: adult dispersal ability (flying dispersers =
186 ballooners; ground dispersers = walkers); hunting strategies (ground hunters, sheet web weavers,
187 other hunters) and mean body length (millimeters) of the pool of species in each trap. Traits were
188 gathered on the base of Nentwig *et al.* (2017) and specific information on ballooning was derived,
189 whenever possible from literature (Bell *et al.*, 2005; Blandenier, 2009). We assigned functional
190 groups according to Cardoso *et al.*, (2011). In this respect, the mixed guild “other hunters” — small
191 sheet web weavers and stalkers — includes in our case, Linyphiidae belonging to the subfamily
192 Erigoninae (Salticidae are represented by one single species, and two individuals) (Table 1).
193 For each trap, we calculated the proportion of each trait within the community.

194

195 *Data analysis*

196

197 *Environmental variables.* Due to the high number of environmental variables recorded in the field,
198 we performed a preliminary correlation analysis in order to minimize multicollinearity-related
199 problems on the estimate of the regression model parameters (Legendre & Legendre, 2012) and to
200 test if they are function of the time since deglaciation (class of deglaciation). Time since
201 deglaciation, vegetation cover, plant species richness, soil gravel percentage, pH and organic matter
202 resulted highly correlated (Spearman’s rho > 0.9 in all cases except one – time since deglaciation
203 and pH - where it is > 0.7; Table S2 – Supporting Information). Thus, on the basis of all previous
204 information suggesting the importance of time since deglaciation, the latter was entered as the sole
205 explanatory variable in statistical models. This choice was further motivated by the fact that time
206 since deglaciation is the only variable that may influence the others, with a positive influence on

207 plant species richness, percentage of vegetation cover, organic matter content and a negative
208 influence on pH and gravel percentage. Furthermore, we described time since deglaciation as the
209 main variable influencing carabid and spider primary succession along glacier forelands (see
210 Hagvar, 2012).

211

212 *Diversity.* Species richness was expressed as the number of species per trap (count data). According
213 to Mason *et al.* (2013), we computed the index of functional richness (FRic) and functional
214 dispersion (FDis) as descriptors of the functional diversity of carabid and spider assemblages along
215 the succession. These two functional diversity indexes are indicators of community assembly
216 processes (Mason *et al.*, 2012). Functional richness (FRic) measures how much of the niche space is
217 occupied by the species present. It is usually interpreted as an indicator for potentially used/unused
218 niche space (Schleuter *et al.*, 2010). Functional dispersion (FDis) estimates the dispersion of the
219 species in the multidimensional trait space, calculated as the weighted mean distance of individual
220 species in the traits space to the weighted centroid of all species, accounting for species relative
221 abundance (Laliberté & Legendre, 2010). In plots 1 and 2 of the class 0 no carabids were collected;
222 thus, FDis were excluded when calculating FDis for the carabid community in these plots.



223

224 *Species traits distribution.* We analysed the turnover or ‘persistence’ of carabid and spider traits
225 along the succession according to the descriptive analysis proposed by Vater (2012) and Vater &
226 Matthews (2013, 2015). Specifically, we analysed three community parameters for each class of
227 deglaciation: (1) total functional traits (number of functional traits at plot level), (2) first
228 appearances of functional traits (number of functional traits appearing for the first time along the
229 succession, including first-and-last appearances), (3) last appearances of functional traits (number
230 of functional traits appearing for the last time along the succession, including first-and-last
231 appearances).

232

233 *Statistical analysis.* Given that our data have a clear spatial structure, with three traps within each
234 sampling plot, and that spatial autocorrelation is a key issue for studies investigating invertebrate
235 ecology (and carabid and beetles in particular) along glacier forelands (Gobbi & Brambilla, 2016),
236 we adopted a modelling technique able to deal with spatially autocorrelated data. We worked with
237 generalized least squares (GLS) models, which can incorporate the spatial structure into model's
238 error and are one of the most performing methods for similar spatial analyses (Dormann *et al.*,
239 2007; Beale *et al.*, 2010). We thus used GLS models to estimate the potential effect of time since
240 deglaciation on the selected traits/indexes, and checked for residuals distribution for all models for
241 which the effect of time since deglaciation was not rejected; in all but one (proportion of winged
242 species among ground beetles) of such cases, residual distribution approached a normal distribution.
243 We assessed models' support by means of an information-theoretic approach (Burnham and
244 Anderson, 2002), based on AICc (Akaike's information criterion corrected for small sample size):
245 in all cases when the model including the factor time since deglaciation was more supported than
246 the null model, we considered time since deglaciation as a meaningful predictor of a given
247 trait/index; otherwise, we treated it as uninfluential for such a parameter. We run models using three
248 different correlation structures (Gaussian, spherical and exponential; see e.g. Brambilla & Ficetola,
249 2012) and obtained fully consistent results between the three runs.

250 The proportion of adult carabid hunting strategies with each class of deglaciation were not tested by
251 the GLS since all the species except two (*Amara erraticata* (Duftschmid 1812) and *Notiophilus*
252 *biguttatus* (Fabricius 1779)) are olphactory-tactil predators, in the same way that adult feeding
253 guilds were not tested since all species except one (*Amara erraticata*) are carnivorous (see. Tab. 1).

254 The proportion of carabid species with mophagous larvae was not tested by the GLS since all
255 specie except one are carnivorous, thus we tested only the proportion of mophagous individuals
256 in each site. The spider hunting guild "other hunter" proportion was not tested by the GLS because
257 belonging only to three species, and eight individuals.

258 All statistical analyses were performed with the software R (R Development Core Team, 2016),
259 using FD R package version 1.0-12 (Laliberté *et al.*, 2014) to compute the functional diversity
260 indices and the packages 'MuMIn', 'mass' and 'nlme' (Venables & Ripley, 2002; Pinheiro *et al.*,
261 2017; Bartoń, 2016) for GLS models.

262

263

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265 **Results**

266

267 *Diversity trends*


268 A total of 13 carabid species (732 individuals) and 13 spider species (91 individuals) were sampled
269 (Table 1).

270 Carabid and spider species richness increased along the chronosequence of glacier retreat as
271 described by the four classes of deglaciation ($R^2_{\text{carabids}} = 0.72$; $R^2_{\text{spiders}} = 0.57$). Both for carabids and
272 spiders the species richness value was low on the glacier and during the early successional stage
273 (class 1), then it increased, but not linearly (Table 2, Fig. 2).

274 None of the two used functional diversity indexes of carabid assemblages resulted correlated to the
275 time since deglaciation. Spider FRich gradually increased in relation to the time since deglaciation
276 ($R^2 = 0.71$) and with a similar trend observed for the species richness (Table 2, Fig. 3). On the other
277 hand, spider FDis did not change in relation to the time since deglaciation.

278

279 *Life-history traits proportion*

280 Among carabids, the proportion of surface walkers  gradually increased along the chronosequence of
281 glacier retreat as described by the four classes of age of deglaciation ($R^2 = 0.78$) (Table 2, Fig. 4).

282 Conversely, the proportion of surface runners ($R^2 = 0.73$) gradually decreased in relation to the time
283 since deglaciation. Instead, the proportion of soil explorers did not change along the
284 chronosequence. The proportion of high dispersal species reached the highest values in the early
285 successional stages (Class 1), then gradually decreased along the chronosequence of glacier retreat
286 ($R^2 = 0.70$) (Table 2, Fig. 4). The community weighted mean body length of the species in each trap
287 did not change along the chronosequence.

288 Among spiders, the proportion of ballooners species reached the highest value on the glacier
289 surface, then it decreased along the chronosequence of glacier retreat as described by the four
290 classes of age of deglaciation ($R^2 = 0.56$) (Table 2, Fig. 3). The proportion of each hunting strategy

291 did not change along the chronosequence. The mean body length of the species pool in each trap
292 increased along the chronosequence of glacier retreat ($R^2 = 0.67$) until the class 3, then it slightly
293 decreased (Table 2, Fig. 3).

294

295 *Life-history traits distribution*

296 For carabids, the total number of functional traits increased among classes of deglaciation until the
297 Class 3, and then slightly decreased in class 4. Functional traits first appearances tended to decrease
298 with site age with the exception of Class 2. No last appearances occurred until Class 3, where a
299 single functional trait disappeared (Fig.5A).

300 For spiders, the total number of functional traits followed a concave pattern, with the lower values
301 in Class 0 and 4 and the higher values in Class 1, 2 and 3. Functional trait first appearances occurs
302 only within the first two classes of deglaciation, while the only one last appearance occurred in
303 Class 3 (Fig. 5B).

304 Discussion

305

306 *Species and their life-history traits on the debris-covered glacier*

307 Debris-covered glaciers with their tongue descending below the treeline can host arthropod life on
308 their surface (Gobbi *et al.*, 2011). Our study demonstrated that a debris-covered glacier with its
309 tongue located above the treeline, is also capable of hosting arthropods. Specifically, we collected
310 three different ground-dwelling arthropod species on the glacier: the carabid beetle *Nebria germari*
311 Heer 1837, the wolf spider *Pardosa nigra* (C.L. Koch, 1834) and the linyphiid spider *Agyneta*
312 *rurestris* (C. L. Koch, 1836). The life-history traits of these species are the following: both *N.*
313 *germari* and *P. nigra* are walking colonisers with low dispersal ability, as the former is short-
314 winged and the latter is not a ballooner, at least at the adult stage. Both species are ground hunters;
315 specifically, *N. germari* is an olfactory-tactil predator (Brandmayr *et al.*, 2005), while *P. nigra* is a
316 ground dweller with good eyesight which runs about in search of prey (Roberts, 1985). .
317 Notwithstanding these two species feed on similar preys, mainly collembolan and other insects
318 (Raso *et al.*, 2014) transported as aeroplankton (Hagvar, 2012), the niche competition is reduced as
319 they have different foraging habits: the former is a nocturnal predator (Homburg *et al.*, 2014) while
320 the latter is mainly a diurnal predator (Raso *et al.*, 2014). . Given the collection of juvenile instars
321 on the glacier, it seems likely that both species complete their life cycle on the ice.

322 The spider *Agyneta rurestris* is a widespread spider in Europe and its presence on the glacier is
323 likely to be a result of its ability to quickly colonise pioneer habitats (Meijer, 1977). For this
324 species, however, we have no evidence of its ability to reproduce on the glacier.

325

326 *Diversity*




327 With respect to species richness values, differences among the five classes of deglaciation were
328 found both on carabid beetles and spiders. The species richness pattern is in accordance with

329 previous studies on invertebrate primary successions along glacier forelands (see Hagvar, 2012)
330 confirming the increasing of number of species with the time since deglaciation.
331 In contrast, the functional diversity along the chronosequence of glacier retreat revealed different
332 patterns in carabids when compared to spiders. Concerning carabids, no detectable trend was found,
333 neither for functional richness, nor for functional dispersion. According to Mason *et al.* (2013) this
334 result highlights that there is no change in influence of niche complementarity on either species
335 occurrences or abundances, with increasing time since deglaciation. This result indicate that in our
336 study system there are not habitat filtering processes (*sensu* HilleRisLambers *et al.*, 2012), thus
337 there are no environmental factors limiting the occurrence of species without certain traits.
338 Interestingly, habitat filtering processes in carabid beetles distribution were found along glacier
339 forelands located below the treeline due to a more complex habitat and community structure
340 (Brambilla & Gobbi, 2014; Vater & Matthews, 2015). Probably, above the treeline the variation of
341 complexity of habitat and community structure, in relation to the time since deglaciation, is not high
342 enough to be able to filter the species/traits occurrence.
343 On the contrary, for spiders time since deglaciation affected positively the functional richness, but
344 not functional dispersion. According to Mason *et al.* (2013), this result highlights an increasing
345 influence of niche complementarity on species occurrences, but not abundances, with increasing of
346 time since deglaciation.

347

348 *Life-history trait types and distribution*

349 Traits distribution analysis revealed that on the glacier (Class 0) and during the first stage of
350 deglaciation (Class 1) the early successional carabid assemblages were characterized by species
351 with the following features: surface running larvae, mainly short-winged species, olphactory-tactil
352 predators. Surface running larvae are probably mainly linked to the gravelly soils of the early
353 successional stages, as they are effective at capturing their preys running between the stones or at
354 the edge of the stones. Accordingly to this hypothesis, species with soil exploring larvae (i.e. small

355 larvae living into the soil (Brandmayr *et al.*, 2005)) appeared in the mid- and late-successional
356 stages, where the habitat maturity should sustain several prey species living in the soil and with a
357 low ability to escape (e.g. earthworms, fly larvae). After 20 years since glacier retreat (Class 1) until
358 the late successional stages (Class 3-4), all larval hunting strategies (surface walkers, surface
359 runners, soil pore explorers, phagous), adult diet types (carnivorous, omnivorous) and wing
360 statuses (short-winged and winged) were represented and persisted along the glacier foreland.
361 Therefore, this result supports the general pattern found in other glacier forelands where the number
362 of low dispersal species increas in stable and mature environments (Gobbi *et al.*, 2007; Gobbi *et*
363 *al.*, 2010). Most of the sampled carabid species are olfactory-tactil hunters (Brandmayr *et al.*,
364 2005). This hunting strategy is considered to be the most primitive hunting strategy, performed by
365 unspecialized nocturnal predators with small eyes (Brandmayr *et al.*, 2005; ountain-Jones *et al.*,
366 2015). Since the olfactory-tactil hunting strategy is related to nocturnal predation (Brandmayr *et*
367 *al.*, 2005), we can hypothesize that this strategy is particularly frequent in the species living in this
368 kind of harsh habitats in order to partially avoid niche competition with spiders, and opiliones,
369 which are also top-predators (Hagvar, 2012), but with diurnal habits. Visual predators appeared
370 only in late successional stages (Classes 3-4). Visual hunting is typical of diurnal predators (e.g.
371 *Notiophilus* spp.) with large eyes (Brandmayr *et al.*, 2005; Fountain-Jones *et al.*, 2015). Most
372 carabids specialized in feeding on springtails occurring in late successional stages, where high
373 vegetation cover favors high springtail abundance (Schirmel *et al.*, 2012).

374 The analysis of spider trait distribution revealed that most of the hunting strategies are represented
375 along the primary succession, but without a clear trend. The proportion of ballooners is higher on
376 the glacier and in early successional stages, then decreased along the succession. As a consequence,
377 the dispersal strategy (ballooners vs ground dispersers) influenced spiders' distribution. Ballooning
378 may be initiated by both environmental and physiological factors, and in general overcrowding and
379 food shortage can stimulate aerial dispersal (Duffey, 1998; Weyman *et al.*, 2002), which happens
380 during the snow free period (Coulson *et al.*, 2003). Spider body length increased along the primary

381 succession. Since bigger species are generally not ballooning, this trend can be explained by the
382 correlation between body size and dispersal ability. In addition, our results are consistent with
383 mechanisms invoking metabolic rate and desiccation resistance to predict an increase of body size
384 from cool and moist habitats, such as the glacier surface and early successional stages, to warmer
385 and dryer habitats, as late successional stages (Entling *et al.*, 2010).

386 In contrast to our expectations, we did not observe a true turnover of carabid and spider functional
387 traits along the primary succession. Therefore, the presence of filtering process on life-history traits
388 can be excluded. Indeed, most of the traits were added and persisted, according to the “addition and
389 persistence model” (Vater, 2012; Vater & Matthews, 2013, 2015). Our results bring to advance the
390 hypothesis that, in our study system, ground beetles and spiders occurrence on the glacier and
391 distribution along the glacier foreland seems to be driven by dispersal ability and foraging strategies
392 of each species.

393

394

395 **Conclusions**

396 Our results highlighted that carabid and spider primary successions along a glacier foreland can be
397 described not only by considering species diversity and turnover, as traditionally performed, but
398 also via the functional diversity and traits distribution approach, as already applied to plant
399 assemblages (e.g. Caccianiga *et al.*, 2006; Erschbamer & Mayer, 2012). However, unlike plant
400 assemblages, in our study system carabid and spider species assemblages cannot be discriminated
401 from their life-history trait types, as the traits are not mutually exclusive, but they mainly follow the
402 “addition and persistence model” and not the “replacement change model” (Vater & Matthews,
403 2012). On the other hand, the proportion of most of the considered life-history traits within each
404 species assemblage clearly changes in relation to the successional gradient; the species assemblages
405 can thus be discriminated on the base of the proportion of each trait. The use of life-history traits
406 proved a useful tool to describe in more detail, the ecological and behavioral features of the ground-
407 dwelling arthropods involved in a primary succession triggered by glacier retreat.

408 To our knowledge, this is the first study to measure different components of functional diversity of
409 ground-dwelling arthropods in response to glacier retreat and, in general, in harsh high-altitude
410 environments. Using the trait-based approach and including functional diversity components, we
411 contribute to the description of the adaptive strategies adopted by carabids and spiders colonising
412 glaciers surfaces and recently deglaciated terrains, landforms which are rapidly changing in
413 response to the current global warming.

414

415

416 **Acknowledgments**

417 We thank the Adamello-Brenta Natural Park for issuing the research permit. We are thankful to
418 Silvia Bussolati for her fieldwork assistance. The research project was co-financed by Autonomous
419 Province of Trento (Italy). GL was supported by the Swiss National Science Foundation

420 (PZ00P3_148261). A. E. Vater provided English revision and useful suggestions. The Associate
421 Editor and the three referees provided very helpful comments on a first draft of the manuscript.

422

423 **Contribution of authors**

424 Mauro Gobbi designed the experiment, coordinated the research project, wrote the manuscript,
425 participated to the field work, and supervised carabids identification. Francesco Ballarin identified
426 the spiders. Mattia Brambilla performed the statistical analysis in R. Chiara Compostella helped in
427 the fieldwork and performed the soil analysis. Marco Isaia gave a substantial contribution to the
428 writings, especially in the discussion of spiders. Gianalberto Losapio performed the functional
429 diversity analysis adding important insights about the functional diversity trends. Chiara Maffioletti
430 helped on the field work, sorted the arthropods and identified the carabids. Roberto Seppi
431 reconstructed the chronosequence of glacier retreat and gave important information about the
432 glacier features. Duccio Tampucci performed the analysis of species turnover and contributed in
433 writing the paper. Marco Caccianiga helped in the experiment design, participated to the field work,
434 identified the plant species and supervised the final version of the manuscript.

435

436

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641 **Tables**

642

643 Table 1 – Carabid and spider species assemblages and life-history traits in each class of deglaciation (Class 0 = not yet deglaciated – glacier surface,
 644 Class 1 = areas deglaciated in the period 1994-2003, Class 2 = areas deglaciated in the period 1925-1994, Class 3 = areas deglaciated in the period
 645 1850-1925, and Class 4 = Late Glacial Period). Species abundance is indicated as percentage on total captures of each taxon. Data about carabid and
 646 spider life-history traits were obtained on the base of specialized literature (Bell *et al.*, 2005; Blandenier, 2009; Hürka, 1996; Brandmayr *et al.*,
 647 2005; Homburg *et al.*, 2014; Nentwig *et al.*, 2017).

648


Carabids	Class	Class	Class	Class	Class	Dispersal ability	Adult hunting strategies	Larval hunting strategies	Diet	Mean body length (mm)
	0	1	2	3	4					
<i>Amara erratica</i>			0,41	0,55	0,27	high	zoospermophagous	spermophagous	Omnivorous	7,2
<i>Carabus adamellicola</i>			0,14	3,14	1,37	low	olfactory tactil predator	surface walker	Carnivorous	19
<i>Carabus depressus</i>			0,27	3,69	1,50	low	olfactory tactil predator	surface walker	Carnivorous	22,5
<i>Cychrus attenuatus</i>			0,14			low	olfactory tactil predator	surface walker	Carnivorous	15
<i>Nebria germari</i>	3,28	6,83	13,11	0,68	0,14	low	olfactory tactil predator	surface runner	Carnivorous	10,25
<i>Nebria jockischii</i>		0,41	0,27			high	olfactory tactil predator	surface runner	Carnivorous	12,2
<i>Notiophilus biguttatus</i>				0,14	0,41	low	visual predator	surface runner	Carnivorous	5
<i>Oreonebria angustata</i>		0,14	4,10	0,14		low	olfactory tactil predator	surface runner	Carnivorous	8

<i>Oreonebria castanea</i>			14,48	20,49	18,58	low	olfactory tactil predator	surface runner	Carnivorous	8,8
<i>Platynus teriolensis</i>				0,27	2,19	low	olfactory tactil predator	surface walker	Carnivorous	11,25
<i>Princidium bipunctatum</i>			0,14	0,14		high	olfactory tactil predator	soil pore explorer	Carnivorous	4
<i>Pterostichus multipunctatus</i>			0,14	2,32		low	olfactory tactil predator	soil pore explorer	Carnivorous	14
<i>Trechus tristiculus</i>			0,14			low	olfactory tactil predator	soil pore explorer	Carnivorous	4
Spiders	Class	Class	Class	Class	Class	Dispersal strategies	Hunting strategies	Mean body		
	0	1	2	3	4	of the adult		length (mm)		
<i>Acantholycosa pedestris</i>			1,10			ground disperser	ground hunter	9,25		
<i>Agyneta rurestris</i>	7,69				2,20	ballooner	sheet web weaver	2,18		
<i>Arctosa alpigena</i>					2,20	ground disperser	ground hunter	6,80		
<i>Coelotes pickardi tirolensis</i>			8,79	19,78	10,99	ground disperser	sheet web weaver	8,85		
<i>Diplocephalus helleri</i>		1,10	1,10	2,20		ballooner	other hunter	2,18		
<i>Drassodex heeri</i>				7,69		ground disperser	ground hunter	18,15		
<i>Erigone dentipalpis</i>		1,10	1,10			ballooner	other hunter	2,33		
<i>Mughiphantes handschini</i>			4,40	1,10		ballooner	sheet web weaver	2,75		
<i>Oreonetides glacialis</i>		1,10	1,10			ballooner	sheet web weaver	2,68		
<i>Pardosa nigra</i>	2,20	1,10	7,69	4,40	4,40	ground disperser	ground hunter	7,75		
<i>Pardosa oreophila</i>			2,20			ground disperser	ground hunter	5,55		
<i>Sitticus longipes</i>				2,20		ground disperser	other hunter	9,15		
<i>Tenuiphantes monachus</i>			1,10			ballooner	sheet web weaver	2,60		

649

For Review Only

650 Table 2 – Summary of the effect of time since deglaciation (class) on the response variables
 651 (species richness, species traits and functional indices). The cases for which the effect of time since
 652 deglaciation was supported (model including the variable most parsimonious than the null model;
 653 see text) are reported in bold; for all other variables, the model with time since deglaciation was less
 654 supported than the null model. Values are estimated coefficients (\pm relative standard error) for the
 655 effect of time since deglaciation in relation to class of deglaciation 0 (glacier surface); also the
 656 significance of effect is tested against class 0 (legend: * $P < 0.05$; ** $P < 0.01$; *** < 0.001).

CARABIDS	intercept	Class 1	Class 2	Class 3	Class 4
Species richness	0.41\pm0.43	0.92\pm0.72	3.92\pm0.72***	4.60\pm0.72***	4.92\pm0.93***
Proportion of surface walkers	0.00\pm0.05	0.00\pm0.08	0.09\pm0.07	0.28\pm0.07**	0.50\pm0.09***
Proportion of surface runners	1.00\pm0.09***	0.00\pm0.15	-0.25\pm0.13	-0.53\pm0.13	-0.59\pm0.17***
Proportion of soil explorers	0.00 \pm 0.04	0.00 \pm 0.06	0.09 \pm 0.05	0.18 \pm 0.06**	0.00 \pm 0.07
Proportion of winged species	0.00\pm0.06	0.38\pm0.09***	0.20\pm0.08*	0.11\pm0.08	0.11\pm0.09
Mean body length	10.25 \pm 0.84	0.49 \pm 1.34	0.43 \pm 1.17	2.07 \pm 1.17	2.06 \pm 1.55
FRic	1.00 \pm 0.48	0.78 \pm 0.75	1.48 \pm 0.65*	2.31 \pm 0.67**	2.03 \pm 0.87*
FRve	0.30 \pm 0.05			0.06 \pm 0.06	-0.14 \pm 0.07
FDis	0.00 \pm 0.04	0.04 \pm 0.05	0.07 \pm 0.05	0.11 \pm 0.05*	0.10 \pm 0.06
RaoQ 	0.00 \pm 0.02	0.01 \pm 0.02	0.03 \pm 0.02	0.03 \pm 0.02	0.02 \pm 0.03
SPIDERS	intercept	Class 1	Class 2	Class 3	Class 4
Species richness	0.73\pm0.31*	-0.06\pm0.52	1.94\pm0.52***	1.77\pm0.53**	2.63\pm0.70***

Proportion of ground hunters	0.17±0.13	0.08±0.21	0.32±0.19	0.20±0.22	0.33±0.26
Proportion of sheet web weavers	0.83±0.12	-0.58±0.20**	-0.38±0.18*	-0.42±0.20*	-0.33±0.24
Proportion of ballooners	0.83±0.13***	-0.07±0.20	-0.47±0.18*	-0.66±0.20***	-0.63±0.25*
Mean body length	3.11±0.84***	0.61±1.33	2.86±1.20*	5.70±1.35***	3.80±1.62*
Fric	1.33±0.28***	0.66±0.44	1.50±0.39**	1.67±0.41***	3.00±0.48***
FRve	0.66±0.07			-0.14±0.10	-0.02±0.11
FDis	0.16±0.06	0.16±0.10	0.23±0.09*	0.32±0.09*	0.31±0.11*
RaoQ	0.08±0.04	0.03±0.06	0.09±0.05	0.17±0.05**	0.15±0.06*

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660 **Figures**

661 Figure 1 - Geographic location of the sampling plots in relation to the chronosequence of glacier
662 retreat. Plots 1, 2, 3, 4 = Class 0 (not yet deglaciated – glacier surface); plots 5, 6, = Class 1 (areas
663 freed by the glacier in the period 1994-2003); plots 7, 8 = Class 2 (1925-1994); plots 9, 10 = Class 3
664 (1850-1925); and plot 11 = Class 4 (Late Glacial Period).

665

666 Figure 2 – Observed (grey dots) and expected (black dots) carabid and spider species richness in
667 relation to the class of deglaciation. Triangles represent 95% C.I.

668

669 Figure 3 - Observed (grey dots) and expected (black dots) spider life-history traits in relation to the
670 class of deglaciation. Only the cases in which the effect of time since deglaciation was supported
671 (model including the variable most parsimonious than the null model; see text) are displayed.

672 Triangles represent 95% C.I.

673

674 Figure 4 – Observed (grey dots) and expected (black dots) carabid life-history traits in relation to
675 the class of deglaciation. Only the cases in which the effect of time since deglaciation was
676 supported (model including the variable most parsimonious than the null model; see text) are
677 displayed. Triangles represent 95% C.I.

678

679 Figure 5 – Functional trait richness and functional trait first and last appearances among the classes
680 of deglaciation; (A) carabids, (B) spiders.

681

682

683 **Supplementary File**

684 Appendix S1 and S2

Table 1 – Carabid and spider species assemblages and life-history traits in each class of deglaciation (Class 0 = not yet deglaciated – glacier surface, Class 1 = areas deglaciated in the period 1994-2003, Class 2 = areas deglaciated in the period 1925-1994, Class 3 = areas deglaciated in the period 1850-1925, and Class 4 = Late Glacial Period). Species abundance is indicated as percentage on total captures of each taxon. Data about carabid and spider life-history traits were obtained on the base of specialized literature (Bell *et al.*, 2005; Blandenier, 2009; Hůrka, 1996; Brandmayr *et al.*, 2005; Homburg *et al.*, 2014; Nentwig *et al.*, 2017).

Carabids	Class	Class	Class	Class	Class	Dispersal ability	Adult hunting strategies	Larval hunting strategies	Diet	Mean body length (mm)
	0	1	2	3	4					
<i>Amara erratica</i>			0,41	0,55	0,27	high	zoospermophagous	spermophagous	Omnivorous	7,2
<i>Carabus adamellicola</i>			0,14	3,14	1,37	low	olfactory tactil predator	surface walker	Carnivorous	19
<i>Carabus depressus</i>			0,27	3,69	1,50	low	olfactory tactil predator	surface walker	Carnivorous	22,5
<i>Cychrus attenuatus</i>			0,14			low	olfactory tactil predator	surface walker	Carnivorous	15
<i>Nebria germari</i>	3,28	6,83	13,11	0,68	0,14	low	olfactory tactil predator	surface runner	Carnivorous	10,25
<i>Nebria jockischii</i>		0,41	0,27			high	olfactory tactil predator	surface runner	Carnivorous	12,2
<i>Notiophilus biguttatus</i>				0,14	0,41	low	visual predator	surface runner	Carnivorous	5
<i>Oreonebria angustata</i>		0,14	4,10	0,14		low	olfactory tactil predator	surface runner	Carnivorous	8
<i>Oreonebria castanea</i>			14,48	20,49	18,58	low	olfactory tactil predator	surface runner	Carnivorous	8,8
<i>Platynus teriolensis</i>				0,27	2,19	low	olfactory tactil predator	surface walker	Carnivorous	11,25
<i>Princidium bipunctatum</i>			0,14	0,14		high	olfactory tactil predator	soil pore explorer	Carnivorous	4

<i>Pterostichus multipunctatus</i>			0,14	2,32		low	olfactory tactil predator	soil pore explorer	Carnivorous	14
<i>Trechus tristiculus</i>			0,14			low	olfactory tactil predator	soil pore explorer	Carnivorous	4
Spiders	Class	Class	Class	Class	Class	Dispersal strategies	Hunting strategies	Mean body		
	0	1	2	3	4	of the adult		length (mm)		
<i>Acantholycosa pedestris</i>			1,10			ground disperser	ground hunter	9,25		
<i>Agyneta rurestris</i>	7,69				2,20	ballooner	sheet web weaver	2,18		
<i>Arctosa alpigena</i>					2,20	ground disperser	ground hunter	6,80		
<i>Coelotes pickardi tirolensis</i>			8,79	19,78	10,99	ground disperser	sheet web weaver	8,85		
<i>Diplocephalus helleri</i>		1,10	1,10	2,20		ballooner	other hunter	2,18		
<i>Drassodex heeri</i>				7,69		ground disperser	ground hunter	18,15		
<i>Erigone dentipalpis</i>		1,10	1,10			ballooner	other hunter	2,33		
<i>Mughiphantes handschini</i>			4,40	1,10		ballooner	sheet web weaver	2,75		
<i>Oreonetides glacialis</i>		1,10	1,10			ballooner	sheet web weaver	2,68		
<i>Pardosa nigra</i>	2,20	1,10	7,69	4,40	4,40	ground disperser	ground hunter	7,75		
<i>Pardosa oreophila</i>			2,20			ground disperser	ground hunter	5,55		
<i>Sitticus longipes</i>				2,20		ground disperser	other hunter	9,15		
<i>Tenuiphantes monachus</i>			1,10			ballooner	sheet web weaver	2,60		

Table 2 – Summary of the effect of time since deglaciation (class) on the response variables (species richness, species traits and functional indices). The cases for which the effect of time since deglaciation was supported (model including the variable most parsimonious than the null model; see text) are reported in bold; for all other variables, the model with time since deglaciation was less supported than the null model. Values are estimated coefficients (\pm relative standard error) for the effect of time since deglaciation in relation to class of deglaciation 0 (glacier surface); also the significance of effect is tested against class 0 (legend: * $P < 0.05$; ** $P < 0.01$; *** < 0.001).

CARABIDS	intercept	Class 1	Class 2	Class 3	Class 4
Species richness	0.41\pm0.43	0.92\pm0.72	3.92\pm0.72***	4.60\pm0.72***	4.92\pm0.93***
Proportion of surface walkers	0.00\pm0.05	0.00\pm0.08	0.09\pm0.07	0.28\pm0.07**	0.50\pm0.09***
Proportion of surface runners	1.00\pm0.09***	0.00\pm0.15	-0.25\pm0.13	-0.53\pm0.13	-0.59\pm0.17***
Proportion of soil explorers	0.00 \pm 0.04	0.00 \pm 0.06	0.09 \pm 0.05	0.18 \pm 0.06**	0.00 \pm 0.07
Proportion of winged species	0.00\pm0.06	0.38\pm0.09***	0.20\pm0.08*	0.11\pm0.08	0.11\pm0.09
Mean body length	10.25 \pm 0.84	0.49 \pm 1.34	0.43 \pm 1.17	2.07 \pm 1.17	2.06 \pm 1.55
FRic	1.00 \pm 0.48	0.78 \pm 0.75	1.48 \pm 0.65*	2.31 \pm 0.67**	2.03 \pm 0.87*
FRve	0.30 \pm 0.05			0.06 \pm 0.06	-0.14 \pm 0.07
FDis	0.00 \pm 0.04	0.04 \pm 0.05	0.07 \pm 0.05	0.11 \pm 0.05*	0.10 \pm 0.06
RaoQ	0.00 \pm 0.02	0.01 \pm 0.02	0.03 \pm 0.02	0.03 \pm 0.02	0.02 \pm 0.03
SPIDERS	intercept	Class 1	Class 2	Class 3	Class 4
Species richness	0.73\pm0.31*	-0.06\pm0.52	1.94\pm0.52***	1.77\pm0.53**	2.63\pm0.70***

Proportion of ground hunters	0.17±0.13	0.08±0.21	0.32±0.19	0.20±0.22	0.33±0.26
Proportion of sheet web weavers	0.83±0.12	-0.58±0.20**	-0.38±0.18*	-0.42±0.20*	-0.33±0.24
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Review Only

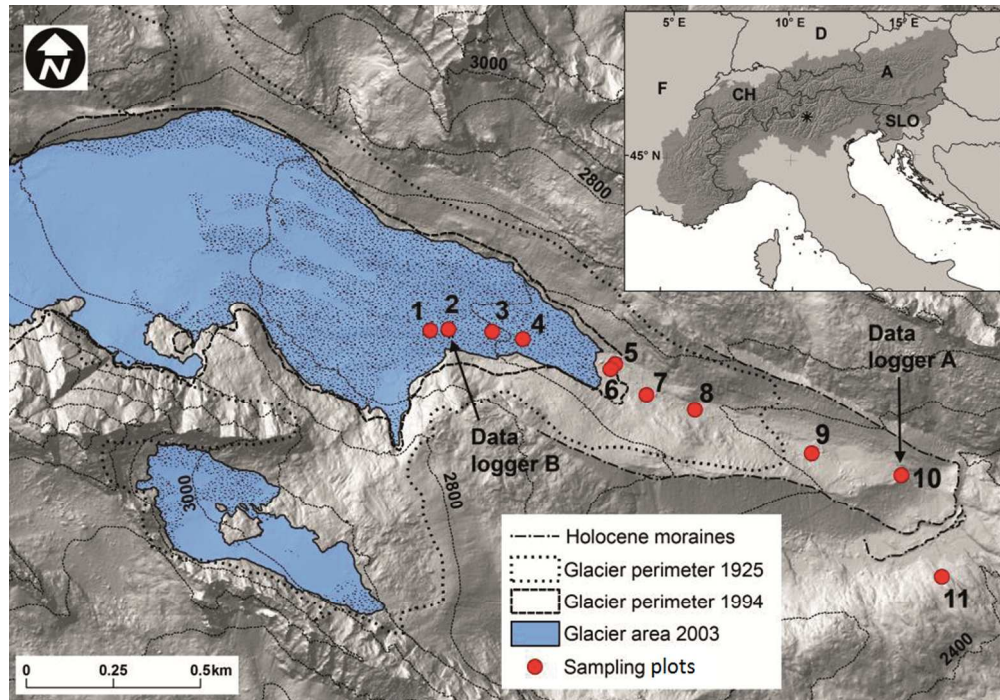


Figure 1 - Geographic location of the sampling plots in relation to the chronosequence of glacier retreat. Plots 1, 2, 3, 4 = Class 0 (not yet deglaciated – glacier surface); plots 5, 6, = Class 1 (areas freed by the glacier in the period 1994-2003); plots 7, 8 = Class 2 (1925-1994); plots 9, 10 = Class 3 (1850-1925); and plot 11 = Class 4 (Late Glacial Period).

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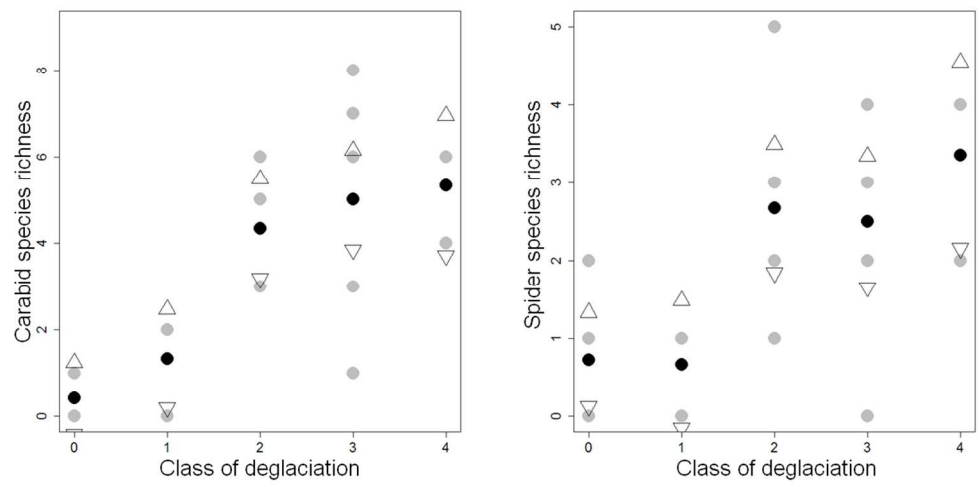


Figure 2 – Observed (grey dots) and expected (black dots) carabid and spider species richness in relation to the class of deglaciation. Triangles represent 95% C.I.

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View Only

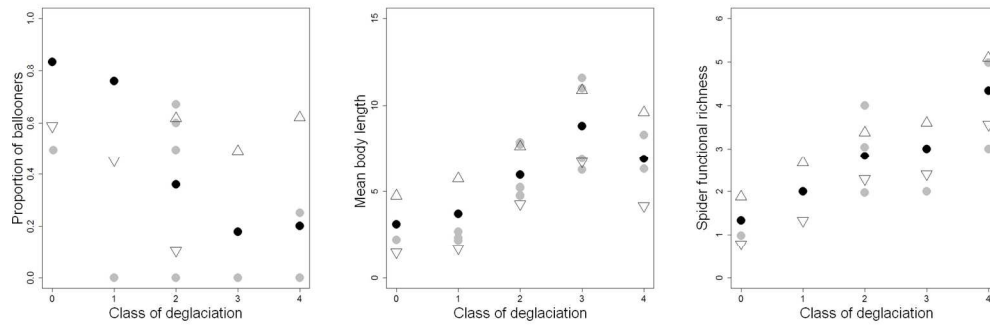


Figure 3 - Observed (grey dots) and expected (black dots) spider life-history traits in relation to the class of deglaciation. Only the cases in which the effect of time since deglaciation was supported (model including the variable most parsimonious than the null model; see text) are displayed. Triangles represent 95% C.I.

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Review Only

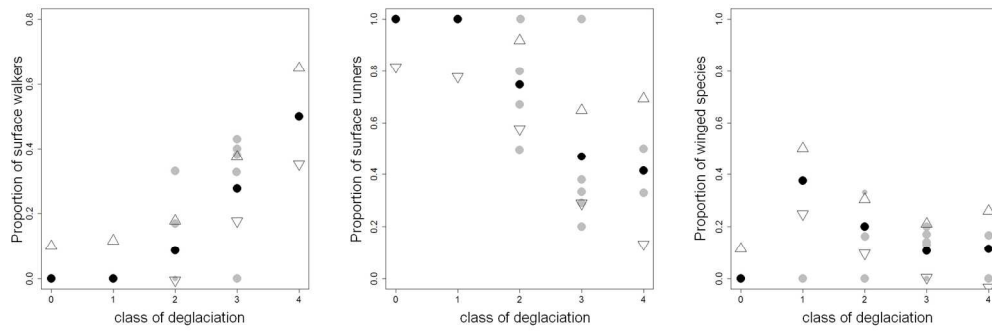


Figure 4 – Observed (grey dots) and expected (black dots) carabid life-history traits in relation to the class of deglaciation. Only the cases in which the effect of time since deglaciation was supported (model including the variable most parsimonious than the null model; see text) are displayed. Triangles represent 95% C.I.

159x57mm (300 x 300 DPI)

Review Only

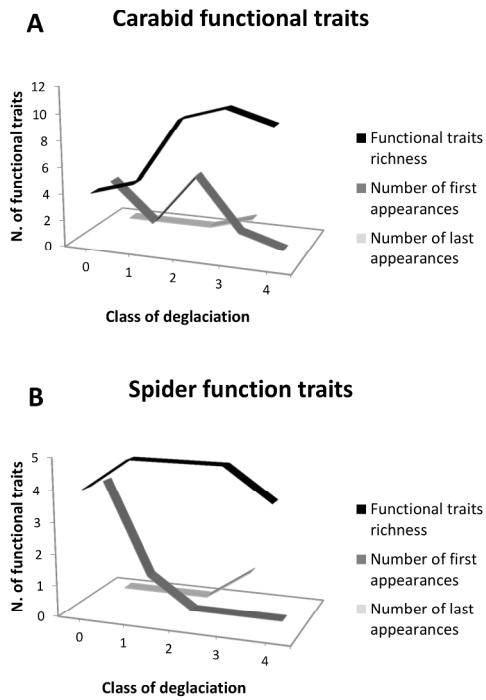


Figure 5 – Functional trait richness and functional trait first and last appearances among the classes of deglaciation; (A) carabids, (B) spiders.

209x297mm (300 x 300 DPI)

Acknowledgments

We thank the Adamello-Brenta Natural Park for issuing the research permit. We are thankful to Silvia Bussolati for her fieldwork assistance. The research project was co-financed by Autonomous Province of Trento (Italy). GL was supported by the Swiss National Science Foundation (PZ00P3_148261). A. E. Vater provided English revision and useful suggestions. The Associate Editor and the three referees provided very helpful comments on a first draft of the manuscript.

Contribution of authors

Mauro Gobbi designed the experiment, coordinated the research project, wrote the manuscript, participated to the field work, and supervised carabids identification. Francesco Ballarin identified the spiders. Mattia Brambilla performed the statistical analysis in R. Chiara Compostella helped in the fieldwork and performed the soil analysis. Marco Isaia gave a substantial contribution to the writings, especially in the discussion of spiders. Gianalberto Losapio performed the functional diversity analysis adding important insights about the functional diversity trends. Chiara Maffioletti helped on the field work, sorted the arthropods and identified the carabids. Roberto Seppi reconstructed the chronosequence of glacier retreat and gave important information about the glacier features. Duccio Tampucci performed the analysis of species turnover and contributed in writing the paper. Marco Caccianiga helped in the experiment design, participated to the field work, identified the plant species and supervised the final version of the manuscript.