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.

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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Running title: Functional traits in harsh environments

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Abstract.

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

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

Introduction

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

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

Ground beetles (Coleoptera: Carabidae) and spiders (Arachnida: Araneae) can be considered among the most important meso- and macro-fauna living on recently deglaciated terrains in terms of species richness and abundance (Hagvar, 2012). Carabid beetle and spider life-history traits along environmental gradients (see Schirmel *et al.,* 2012; Pizzolotto *et al.*, 2016) are quite well known in terms of response traits (*sensu* Díaz *et al.,* (2013), i.e. traits that impact on individuals' capacity to colonise and persist in a habitat). On the other hand, there are no studies involving both spider and ground beetle life-history traits that describe, by means of a functional approach, the ground-dwelling arthropod functional diversity and the turnover of life-history traits along a primary succession on glacier forelands and on the glacier surfaces. The functional trait approach would ensure a better characterization of the arthropod colonisation strategies on the glaciers and on terrain left free by retreating glaciers.

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

Material and Methods

Study area

The study was carried out on the glacier foreland of Vedretta d'Amola glacier (Adamello-Presanella Group, Central-Eastern Italian Alps, 46°13'12''-10°41'02'') (Fig. 1), and on the glacier surface. Vedretta d'Amola glacier is a debris-covered glacier of c. 82.1 hectares (area recorded by one of the authors, RS, in summer 2012), covered approximately for 70% by stony debris with variable depth, from a few centimeters to about one meter. The glacier tongue is located above the treeline.

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

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

On the supraglacial debris (mean elevation: 2642 m asl) the pioneer plant community (total plant cover <10%) is dominated by *Cerastium uniflorum*, *C. pedunculatum*, and *Saxifraga oppositifolia*. On the glacier foreland (mean elevation: 2520 m asl) the plant community (plant cover ranging from 5% to 70% along the foreland) is dominated by *Poa alpina*, *P. laxa*, *Saxifraga bryoides*, *Geum reptans*, and *Luzula alpino-pilosa*. Outside the glacier foreland (mean elevation: 2426 m asl), Late Glacial sites are occupied by *Carex curvula*-dominated communities with >80% ground cover.

Sampling design

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

Sampling method

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

2012. Given that no important variation in air temperature was found, we can assume that it did not affect the carabid beetle assemblage richness and composition in the two sampling seasons. Carabids were identified to the species level following Pesarini & Monzini (2010, 2011), while spiders were identified to the species level following Netwing *et al.*, (2017). Nomenclature refers to the checklist of the European Carabid beetles Fauna (Vigna Taglianti, 2013) and to The World Spider Catalogue (WSCA, 2017). For spiders, juveniles were excluded from the analysis.

Environmental variables

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

Functional traits

Carabids. We considered the following well-established response traits of primary succession (Gobbi *et al.,* 2010; Schirmel *et al.,* 2012): dispersal ability (high dispersal power = winged species; low dispersal power = short-winged species); diet (omnivorous, carnivorous), and mean body length (millimeters) of the pool of species in each trap. We analyzed for the first time along primary succession the following traits: larval hunting strategy (surface runner, surface walker, soil pore explorer) and adult hunting strategy (zoospermophagous, olphactory-tactil predator, visual predator). Data about species traits were obtained on the base of specialized literature (Hůrka, 1996; Brandmayr *et al.,* 2005; Homburg *et al.,* 2014) (Table 1).

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

Data analysis

Environmental variables. Due to the high number of environmental variables recorded in the field, we performed a preliminary correlation analysis in order to minimize multicollinearity-related problems on the estimate of the regression model parameters (Legendre & Legendre, 2012) and to test if they are function of the time since deglaciation (class of deglaciation). Time since deglaciation, vegetation cover, plant species richness, soil gravel percentage, pH and organic matter resulted highly correlated (Spearman's rho > 0.9 in all cases except one – time since deglaciation and pH - where it is > 0.7; Table S2 – Supporting Information). Thus, on the basis of all previous information suggesting the importance of time since deglaciation, the latter was entered as the sole explanatory variable in statistical models. This choice was further motivated by the fact that time since deglaciation is the only variable that may influence the others, with a positive influence on plant species richness, percentage of vegetation cover, organic matter content and a negative influence on pH and gravel percentage. Furthermore, we described time since deglaciation as the main variable influencing carabid and spider primary succession along glacier forelands (see Hagvar, 2012).

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

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

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

The proportion of adult carabid hunting strategies with each class of deglaciation were not tested by the GLS since all the species except two (*Amara erratica* (Duftschmid 1812) and *Notiophilus biguttatus* (Fabricius 1779)) are olphactory-tactil predators, in the same way that adult feeding guilds were not tested since all species except one (*Amara erratica*) are carnivorous (see. Tab. 1). The proportion of carabid species with spermophagous larvae was not tested by the GLS since all specie except one are carnivorous, thus we tested only the proportion of spermophagous individuals in each site. The spider hunting guild "other hunter" proportion was not tested by the GLS because belonging only to three species, and eight individuals.

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

Results

Diversity trends

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

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

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

Life-history traits proportion

Among carabids, the proportion of surface walkers gradually increased along the chronosequence of glacier retreat as described by the four classes of age of deglaciation ($R^2 = 0.78$) (Table 2, Fig. 4). Conversely, the proportion of surface runners ($R^2 = 0.73$) gradually decreased in relation to the time since deglaciation. Instead, the proportion of soil explorers did not change along the chronosequence. The proportion of high dispersal species reached the highest values in the early successional stages (Class 1), then gradually decreased along the chronosequence of glacier retreat ($R^2 = 0.70$) (Table 2, Fig. 4). The community weighted mean body length of the species in each trap did not change along the chronosequence.

Among spiders, the proportion of ballooners species reached the highest value on the glacier surface, then it decreased along the chronosequence of glacier retreat as described by the four classes of age of deglaciation ($R^2 = 0.56$) (Table 2, Fig. 3). The proportion of each hunting strategy did not change along the chronosequence. The mean body length of the species pool in each trap increased along the chronosequence of glacier retreat (R^2 = 0.67) until the class 3, then it slightly decreased (Table 2, Fig. 3).

Life-history traits distribution

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

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

Discussion

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

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

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

Diversity

With respect to species richness values, differences among the five classes of deglaciation were found both on carabid beetles and spiders. The species richness pattern is in accordance with previous studies on invertebrate primary successions along glacier forelands (see Hagvar, 2012) confirming the increasing of number of species with the time since deglaciation.

In contrast, the functional diversity along the chronosequence of glacier retreat revealed different patterns in carabids when compared to spiders. Concerning carabids, no detectable trend was found, neither for functional richness, nor for functional dispersion. According to Mason *et al*. (2013) this result highlights that there is no change in influence of niche complementarity on either species occurrences or abundances, with increasing time since deglaciation. This result indicate that in our study system there are not habitat filtering processes (*sensu* HilleRisLambers *et al.,* 2012), thus there are no environmental factors limiting the occurrence of species without certain traits. Interestingly, habitat filtering processes in carabid beetles distribution were found along glacier forelands located below the treeline due to a more complex habitat and community structure (Brambilla & Gobbi, 2014; Vater & Matthews, 2015). Probably, above the treeline the variation of complexity of habitat and community structure, in relation to the time since deglaciation, is not high enough to be able to filter the species/traits occurrence.

On the contrary, for spiders time since deglaciation affected positively the functional richness, but not functional dispersion. According to Mason *et al.* (2013), this result highlights an increasing influence of niche complementarity on species occurrences, but not abundances, with increasing of time since deglaciation.

Life-history trait types and distribution

Traits distribution analysis revealed that on the glacier (Class 0) and during the first stage of deglaciation (Class 1) the early successional carabid assemblages were characterized by species with the following features: surface running larvae, mainly short-winged species, olphactory-tactil predators. Surface running larvae are probably mainly linked to the gravelly soils of the early successional stages, as they are effective at capturing their preys running between the stones or at the edge of the stones. Accordingly to this hypothesis, species with soil exploring larvae (i.e. small larvae living into the soil (Brandmayr *et al.,* 2005)) appeared in the mid- and late-successional stages, where the habitat maturity should sustain several prey species living in the soil and with a low ability to escape (e.g. earthworms, fly larvae). After 20 years since glacier retreat (Class 1) until the late successional stages (Class 3-4), all larval hunting strategies (surface walkers, surface runners, soil pore explorers, spermophagous), adult diet types (carnivorous, omnivorous) and wing statuses (short-winged and winged) were represented and persisted along the glacier foreland. Therefore, this result supports the general pattern found in other glacier forelands where the number of low dispersal species increase in stable and mature environments (Gobbi *et al.,* 2007; Gobbi *et al.,* 2010). Most of the sampled carabid species are olphactory-tactil hunters (Brandmayr *et al.,* 2005). This hunting strategy is considered to be the most primitive hunting strategy, performed by unspecialized nocturnal predators with small eyes (Brandmayr *et al.,* 2005; Fountain-Jones *et al.,* 2015). Since the olphactory-tactil hunting strategy is related to nocturnal predation (Brandmayr *et al.,* 2005), we can hypothesize that this strategy is particularly frequent in the species living in this kind of harsh habitats in order to partially avoid niche competition with spiders, and opiliones, which are also top-predators (Hagvar, 2012), but with diurnal habits. Visual predators appeared only in late successional stages (Classes 3-4). Visual hunting is typical of diurnal predators (e.g. *Notiophilus* spp.) with large eyes (Brandmayr *et al.,* 2005; Fountain-Jones *et al.,* 2015). Most carabids specialized in feeding on springtails occurring in late successional stages, where high vegetation cover favors high springtail abundance (Schirmel *et al.,* 2012).

The analysis of spider trait distribution revealed that most of the hunting strategies are represented along the primary succession, but without a clear trend. The proportion of ballooners is higher on the glacier and in early successional stages, then decreased along the succession. As a consequence, the dispersal strategy (ballooners vs ground dispersers) influenced spiders' distribution. Ballooning may be initiated by both environmental and physiological factors, and in general overcrowding and food shortage can stimulate aerial dispersal (Duffey, 1998; Weyman *et al.,* 2002), which happens during the snow free period (Coulson *et al.,* 2003). Spider body length increased along the primary succession. Since bigger species are generally not ballooners, this trend can be explained by the correlation between body size and dispersal ability. In addition, our results are consistent with mechanisms invoking metabolic rate and desiccation resistance to predict an increase of body size from cool and moist habitats, such as the glacier surface and early successional stages, to warmer and dryer habitats, as late successional stages (Entling *et al.,* 2010).

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

Conclusions

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

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

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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.

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Tables

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

Oreonebria castanea			14,48	20,49	18,58	low	olphactory tactil predator	surface runner	Carnivorous	8,8
Platynus teriolensis				0,27	2,19	low	olphactory tactil predator	surface walker	Carnivorous	11,25
Princidium bipunctatum			0,14	0,14		high	olphactory tactil predator	soil pore explorer	Carnivorous	4
Pterostichus multipunctatus			0,14	2,32		low	olphactory tactil predator	soil pore explorer	Carnivorous	14
Trechus tristiculus			0,14			low	olphactory tactil predator	soil pore explorer	Carnivorous	4

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

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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 (± 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 again 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±0.43**	**0.92±0.72**	**3.92±0.72*** **	**4.60±0.72*** **	**4.92±0.93*** **
Proportion of surface walkers	**0.00±0.05**	**0.00±0.08**	**0.09±0.07**	**0.28±0.07** **	**0.50±0.09*** **
Proportion of surface runners	**1.00±0.09*** **	**0.00±0.15**	**-0.25±0.13**	**-0.53±0.13**	**-0.59±0.17*** **
Proportion of soil explorers	0.00±0.04	0.00±0.06	0.09±0.05	0.18±0.06**	0.00±0.07
Proportion of winged species	**0.00±0.06**	**0.38±0.09*** **	**0.20±0.08* **	**0.11±0.08**	**0.11±0.09**
Mean body lenght	10.25±0.84	0.49±1.34	0.43±1.17	2.07±1.17	2.06±1.55
FRic	1.00±0.48	0.78±0.75	1.48±0.65*	2.31±0.67**	2.03±0.87*
FRve	0.30±0.05			0.06±0.06	-0.14±0.07
FDis	0.00±0.04	0.04±0.05	0.07±0.05	0.11±0.05*	0.10±0.06
RaoQ	0.00±0.02	0.01±0.02	0.03±0.02	0.03±0.02	0.02±0.03
SPIDERS	**intercept**	**Class 1**	**Class 2**	**Class 3**	**Class 4**
Species richness	**0.73±0.31* **	**-0.06±0.52**	**1.94±0.52*** **	**1.77±0.53** **	**2.63±0.70*** **

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*

Figures

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).

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.

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.

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.

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

Supplementary File

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 0**	**Class 1**	**Class 2**	**Class 3**	**Class 4**	**Dispersal ability**	**Adult hunting strategies**	**Larval hunting strategies**	**Diet**	**Mean body length (mm)**
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Sitticus longipes				2,20		ground disperser	other hunter	9,15
Tenuiphantes monachus			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 (± 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 again 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±0.43**	**0.92±0.72**	**3.92±0.72*** **	**4.60±0.72*** **	**4.92±0.93*** **
Proportion of surface walkers	**0.00±0.05**	**0.00±0.08**	**0.09±0.07**	**0.28±0.07** **	**0.50±0.09*** **
Proportion of surface runners	**1.00±0.09*** **	**0.00±0.15**	**-0.25±0.13**	**-0.53±0.13**	**-0.59±0.17*** **
Proportion of soil explorers	0.00±0.04	0.00±0.06	0.09±0.05	0.18±0.06**	0.00±0.07
Proportion of winged species	**0.00±0.06**	**0.38±0.09*** **	**0.20±0.08* **	**0.11±0.08**	**0.11±0.09**
Mean body lenght	10.25±0.84	0.49±1.34	0.43±1.17	2.07±1.17	2.06±1.55
FRic	1.00±0.48	0.78±0.75	1.48±0.65*	2.31±0.67**	2.03±0.87*
FRve	0.30±0.05			0.06±0.06	-0.14±0.07
FDis	0.00±0.04	0.04±0.05	0.07±0.05	0.11±0.05*	0.10±0.06
RaoQ	0.00±0.02	0.01±0.02	0.03±0.02	0.03±0.02	0.02±0.03
SPIDERS	**intercept**	**Class 1**	**Class 2**	**Class 3**	**Class 4**
Species richness	**0.73±0.31* **	**-0.06±0.52**	**1.94±0.52*** **	**1.77±0.53** **	**2.63±0.70*** **

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*

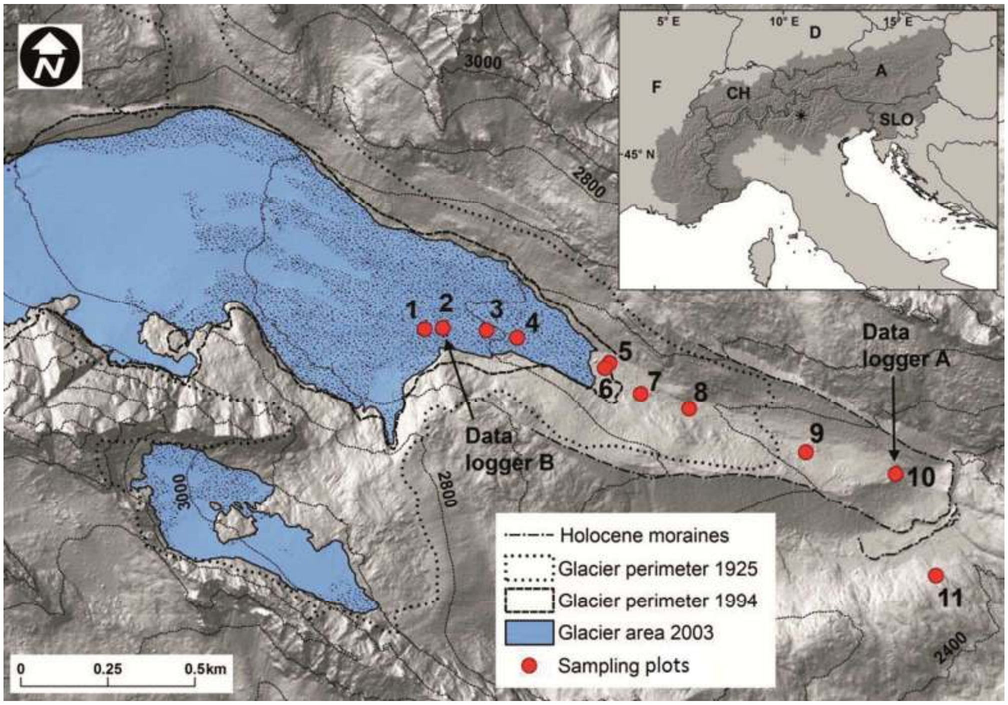

Figure 1 - Geographic location of the sampling plots in relation to the chronosequence of glacier retreat. Plots 1, 2, 3, 4 = Class 0 (not yet deglaciated – glacier surface); plots 5, 6, = Class 1 (areas freed by the glacier in the period 1994-2003); plots 7, 8 = Class 2 (1925-1994); plots 9, 10 = Class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

86x60mm (300 x 300 DPI)

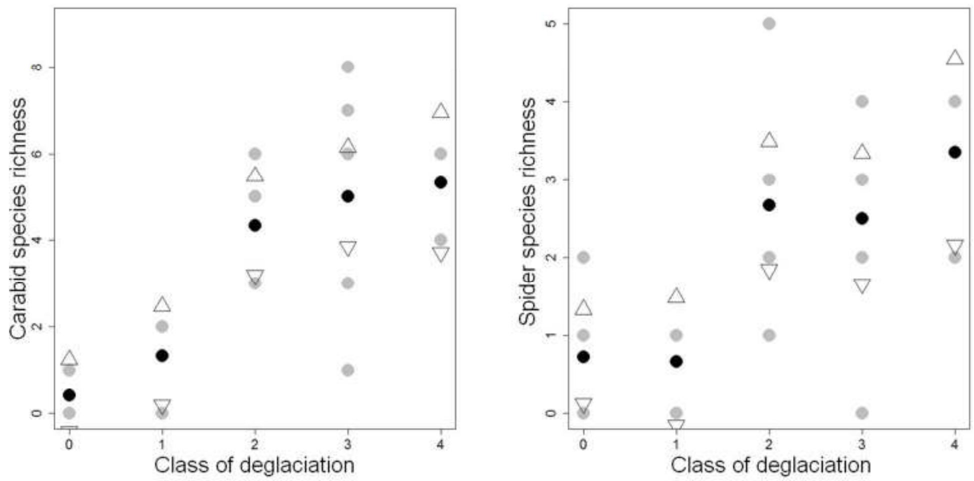

Figure 2 – Observed (grey dots) and expected (black dots) carabid and spider species richness in relation to the class of deglaciation. Triangles represent 95% C.I.

106x56mm (300 x 300 DPI)

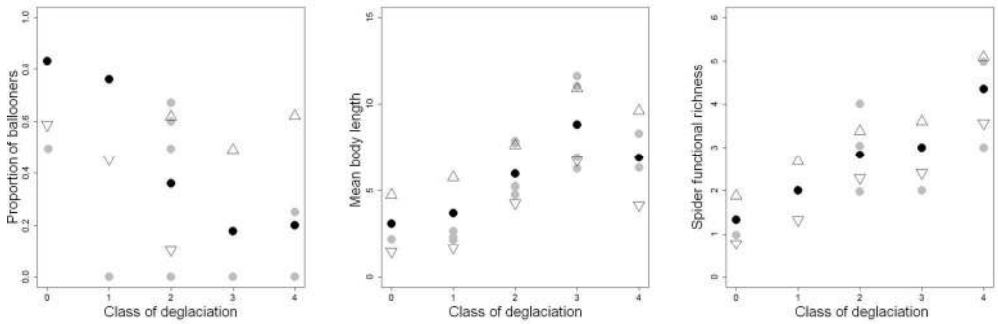

Figure 3 - Observed (grey dots) and expected (black dots) spider life-history traits in relation to the class of deglaciation. Only the cases in which the effect of time since deglaciation was supported (model including the variable most parsimonious than the null model; see text) are displayed. Triangles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

159x57mm (300 x 300 DPI)

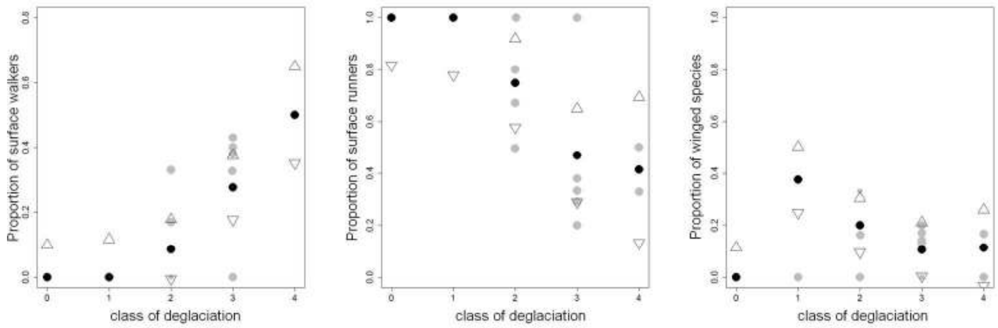

Figure 4 – Observed (grey dots) and expected (black dots) carabid life-history traits in relation to the class of deglaciation. Only the cases in which the effect of time since deglaciation was supported (model including the variable most parsimonious than the null model; see text) are displayed. Triangles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

159x57mm (300 x 300 DPI)

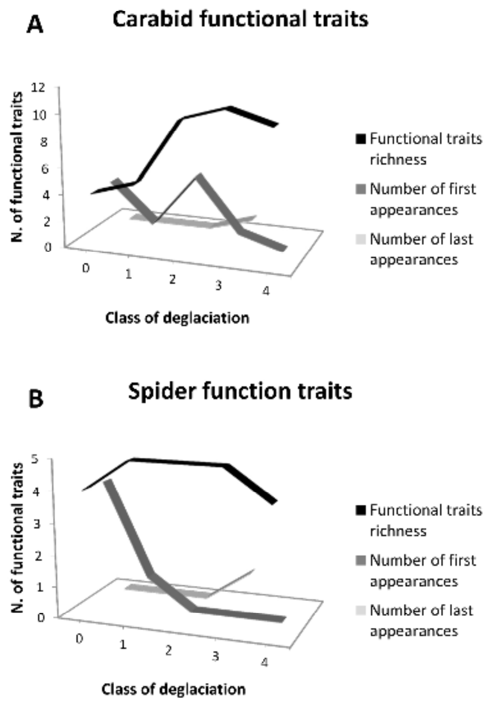

Figure 5 – Functional trait richness and functional trait first and last appearances among the classes of deglaciation; (A) carabids, (B) spiders.

209x297mm (300 x 300 DPI)

Acknowledgments

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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.