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Do carabids (Coleoptera: Carabidae) and chironomids (Diptera: Chironomidae) exhibit similar diversity and distributional patterns along a spatio-temporal gradient on a glacier foreland?

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ABSTRACT

Carabid beetles and chironomid midges are two dominant cold-adapted taxa, respectively on glacier forefiel terrains and in glacial-stream rivers. Although their sensitivity to high altitude climate warming is well known, no studies compare the species assemblages exhibited in glacial systems. Our study compares diversity and distributional patterns of carabids and chironomids in the foreland of the receding Amola glacier in central-eastern Italian Alps. Carabids were sampled by pitfall traps; chironomids by kick sampling in sites located at the same distance from the glacier as the terrestrial ones. The distance from the glacier front was considered as a proxy for time since deglaciation since these variables are positively correlated. We tested if the distance from the glacier front affects: i) the species richness; ii) taxonomic diversity; and iii) species turnover. Carabid species richness and taxonomic diversity increased positively from recently deglaciated sites (those ca. 160 m from the glacier front) to sites deglaciated more than 160 yrs ago (those located >1300 m from glacier front). Species distributions along the glacier foreland were characterized by mutually exclusive species. Conversely, no pattern in chironomid species richness and turnover was observed. Interestingly, taxonomic diversity increased significantly: closely related species were found near the glacier front, while the most taxonomically diverse species assemblages were found distant from the glacier front. Increasing glacial retreat differently affect epigeic and aquatic insect taxa: carabids respond faster to glacier retreat than do chironomids, at least in species richness and species turnover patterns.

Key words: Glacial retreat; species richness; species turnover; taxonomic diversity; Italian Alps.

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INTRODUCTION

Most glaciers are retreating worldwide due to climate change (Pepin *et al.,* 2015), exposing barren ground and new stream bed for biotic colonisation (Robinson *et al*., 2014). Areas located between the current leading edge of the glacier and the moraines of latest maximum (in the Alps it belongs to the end of Little Ice Age, ca. AD 1850), are called glacier forelands (Matthews, 2008). These can be considered a unique field laboratory because the spatial pattern from recently deglaciated areas to the oldest moraines represents temporal change and thus can be regarded as model system for biotic population and community development (Matthews, 2008). Plots located at increasing distance from the glacier front allow description of a space-for-time biotic substitution. Because distance from the glacier front and time since deglaciation are strongly positivelly correlated, both variables represent a temporal sequence (Matthews, 2008; Hågvar, 2012).

Carabid beetles (Coleoptera: Carabidae) and chironomid midges (Diptera: Chironomidae) are important components of the terrestrial and aquatic habitats along the glacier forelands in terms of species richness and population sizes (Kaufmann, 2001; Gobbi *et al.,* 2006a; Lods-Crozet*et al*., 2001). Carabids are early colonisers that typically establish before plants; most are predators, specifically those living near the glacier front and the river banks of the glacial stream. Their diet is mainly represented by springtails (Collembola) and adult chironomids (Raso *et al.,* 2014; Hågvar *et al.,* 2016). Chironomids include early colonizers of glacier-fed streams, and are often the only taxon present within the first hundreds of meters downstream of the glacier front (Lencioni *et al*., 2007a). They are grazers, feeding epilithic algae (mainly diatoms) and allochthonous detritus released by the glacier during melting (Zah *et al.*, 2001). High altitude carabid and chironomid species are affected by climate warming due to their low dispersal ability and low plasticity in relation to perturbation or stressing factors triggered by climate change (Brambilla and Gobbi, 2014; Pizzolotto *et al.,* 2014; Moret *et al.,* 2016; Lencioni and Bernabò, 2017; Brown *et al*., 2018). In addition, several species are endemic (carabids) or restricted to kryal habitats (chironomids) and are particularly threatened by extinction (Pizzolotto *et al.,* 2014; Lencioni *et al*., 2015).

The spatio-temporal distribution of carabids along glacier forelands and of chironomids in glacier-fed streams have been extensively investigated in relation to abiotic and biotic factors (*e.g.* Schirmel *et al.,* 2012; Jacobsen *et al.,* 2012; Tampucci *et al.,* 2015; Lencioni *et al*., 2017a). However, no one comparative study concern spatio-temporal diversity patterns in carabids and chironomids along the same glacier foreland.

Here we make a first attempt to study the diversity and distributional pattern of carabids and chironomids in relation to the distance from the glacier front, thus from the recently deglaciated areas to the oldest moraines. We selected the Vedretta d'Amola glacier foreland in Italian Alps which has been investigated previously from the glaciological, geomophological and ecological point of view (Losapio *et al.,* 2015; Losapio *et al.,* 2016; Tenan *et al.,* 2016; Gobbi *et al.,* 2017; Lencioni, 2018). The general aim was to investigate if global warming affects in the same way terrestrial and aquatic glacial communities trophically related, and to know which species and in which relative proportion colonize aquatic and terrestrial habitats left free under glacier retreating, so describing primary succession patterns.

Specifically, we tested if the distance from the glacier front drives the carabid and chironomid: i) species richness, ii) taxonomic diversity and iii) species turnover.

METHODS

Study area

The study was carried out along the Vedretta d'Amola glacier foreland (Adamello-Presanella Group, central-eastern Italian Alps, 46°13′12″-10°41′02″) (Fig. 1), where the glacier front is at an average altitude of 2566 m above sea level (asl). The glacier foreland is ca. 1.23 km long, covers an altitudinal range of ca. 150 m, and is characterised by a large moraine system dating back to the Little Ice Age (LIA, ca. AD 1850). Field observations and various sources, including maps, reports, aerial photographs, iconography, and records of length change

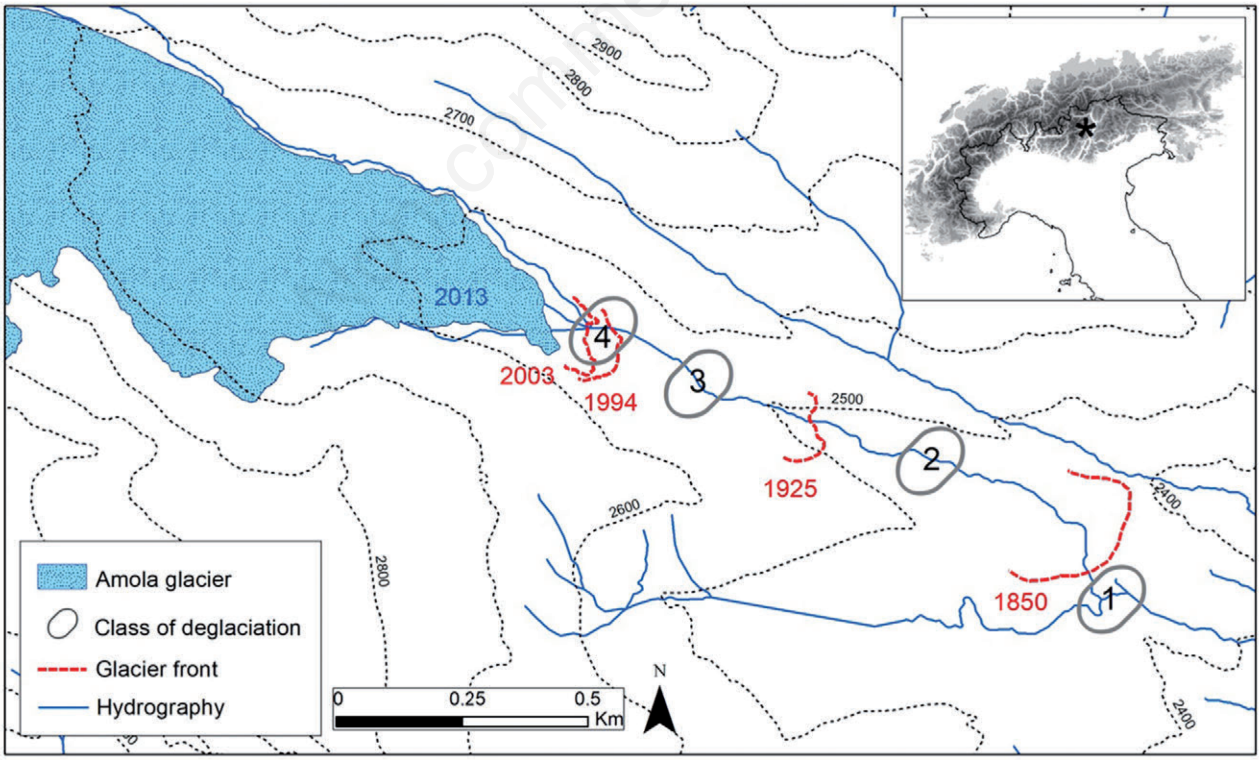


Fig. 1. Amola glacier foreland. The dashed red line represents the chronosequence of glacier retreat (glacier front position and year). The blue line represents the streams. The numbers indicate the class of deglaciation: Class 1, areas freed by the glacier in the period 1994-2003; Class 2, 1925-1994; Class 3, 1850-1925; Class 4; Late Glacial Period.

collected over the last 100 years, allowed us to reconstruct the glacier tongue position during the LIA, in 1925, 1994, 2003 (Gobbi *et al.,* 2017) and 2013 (Casarotto and Bertoni, 2015) (Fig. 1). Sampling was performed during the snow-free period, between late June and late September, in 2011-2012 for carabids and in 2014 for chironomids. Annual mean below-ground temperature on the glacier foreland, recorded during the period 5 August 2011 to 5 August 2012, was 1.7°C, while mean below-ground relative air humidity was 96% (Gobbi *et al.,* 2017). On the glacier foreland (mean elevation 2520 m asl) plant cover ranged from 5% to 70%, dominated by *Poa alpina*, *Poa 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 (Gobbi *et al.,* 2017). Time since deglaciation, thus the distance from the glacier front, was the main variable influencing positively plant species richness, vegetation cover, and soil organic matter (Gobbi *et al.,* 2017).

The stream reach investigated on the Amola glacier-fed stream was rather homogeneous for physical and chemical features during summer 2014 (from late June to late September) (*i.e.*, low silica content=1.1±0.1 mg L^{-1}, low pH= 6.6±0.2 and low conductivity= 13.4±1.5 µS cm^{-1}, high channel stability (Bottom Pfankuch Index)=40±4) (Lencioni, 2018). Only water temperature (r=0.92; P=0.02; T_mean=1.1±0.5°C) and discharge (r=0.88; P=0.04; Q_mean= 0.26±0.13 m^3 sec^{-1}) increased significantly with distance from the glacier front.

Sampling

Carabids

Adults were sampled by 21 pitfall traps located at increasing distance from the glacier front to Late Glacial substrata outside the LIA moraines (Fig. 1; Tab. 1) using plastic vessels (diameter 7 cm, height 10 cm) baited with wine-vinegar and salt. Traps were active over the entire snow-free seasons, from early July to late September

Tab. 1. Sampling points of carabids and chironomids on the Amola glacier foreland.

Carabids				Chironomids			
Class of deglaciation	Time since deglaciation (yrs)	Sampling points	Distance from the glaciet front (m)	Class of deglaciation	Time since deglaciation (yrs)	Sampling points	Distance from the glacier front (m)
1	11-20	1	151.2	1	11-20	1	144.13
1	11-20	2	161.2	1	11-20	2	151.13
1	11-20	3	171.2	1	11-20	3	158.13
1	11-20	4	170.5	1	11-20	4	165.13
1	11-20	5	180.53	1	11-20	5	172.13
1	11-20	6	190.5	2	20-89	6	277.89
2	20-89	7	290.2	2	20-89	7	284.89
2	20-89	8	300.2	2	20-89	8	291.89
2	20-89	9	310.2	2	20-89	9	298.89
2	20-89	10	426.9	2	20-89	10	305.89
2	20-89	11	436.9	3	89-164	11	720.82
2	20-89	12	446.9	3	89-164	12	727.82
3	89-164	13	757.2	3	89-164	13	734.82
3	89-164	14	767.2	3	89-164	14	741.82
3	89-164	15	777.2	3	89-164	15	748.82
3	89-164	16	1016.9	3	89-164	16	946.79
3	89-164	17	1026.9	3	89-164	17	953.79
3	89-164	18	1036.9	3	89-164	18	960.79
4	>164	19	1316.6	3	89-164	19	967.79
4	>164	20	1326.6	3	89-164	20	974.79
4	>164	21	1336.6	4	>164	21	1198.49
			4	>164	22	1205.49	
			4	>164	23	1212.49	
			4	>164	24	1219.49	
			4	>164	25	1226.49	

2011-2012, and emptied at 25-day intervals. Carabids were identified to the species level following Pesarini and Monzini (2010, 2011). Nomenclature refers to the checklist of the European Carabid Beetles Fauna (Vigna Taglianti, 2013).

Chironomids

Larvae were sampled by kick sampling in 25 sampling plots located at increasing distance from the glacier front to stream portion crossing the Late Glacial substrata outside the LIA moraines, within 1.3 km from the front (Fig. 1; Tab. 1). Sampling was carried out in early summer, mid-summer and early autumn 2014 by kick sampling a 0.1 m^2 area using a 33 x 33 cm pond net with 250 µm mesh. Samples were preserved in 75% ethanol. Specimens were sorted and identified to species/group of species level according to Wiederholm (1983), Schmid (1993), Janecek (1998), Lencioni *et al*. (2007b). *Diamesa cinerella*, *D. zernyi* and *D. latitarsis* are identifiable as larvae at species group level, including more than one species (Rossaro and Lencioni, 2015).

All specimens, preserved in 75% ethanol and on microscope slides, have been deposited in the MUSE-Museo delle Scienze in Trento (Italy), archived in the collection cINV0017.

Data analysis

Distance of each sampling plot from the glacier front was used as proxy of the time since deglaciation (Matthews, 2008), with those near the glacier front recently deglaciated (between 10 and 20 yrs ago, Class of deglaciation n. 1; Fig.1 and Tab. 1), and those more distant deglaciated for more than 160 yrs (Class of deglaciation n. 4; Fig. 1 and Tab. 1).

For each terrestrial and aquatic plot, we calculated the distance from the glacier front, the species richness and the taxonomic diversity. Species richness was calculated as sum of the number of species (count data). Taxonomic diversity index was calculated according to Hammer *et al*. (2001), on the presence-absence matrix and including taxonomic information also above the species level, entered for each species. Taxonomic diversity index is able to incorporate, for each species assemblage, other taxonomic information like, for instance, the number of different genera or families. A higher taxonomic index value identifies a species assemblage comprising species "taxonomically distantly related" thus belonging to different genera. On the contrary, a lower index value identifies the species assemblage composed by species taxonomically closely related because belonging to the same genus. Therefore, respect to species richness, taxonomic diversity emphasizes the taxonomic relatedness between species in a community (Clarke and Warwick, 1998). A major benefit of this index over species richness is its virtual independence of sampling effort. Furthermore, taxonomic diversity is closely related to ecological diversity and functionality, it is evident that evaluating this parameter may be crucial to evaluating the ecological complexity and degree of disturbance of a certain ecosystem (Heino, 2008; Paschetta *et al*., 2013).

The effect of distance from the glacier front (explanatory variable) on carabid and chironomid species richness and taxonomic diversity (response variables) was tested using Linear Regression Analysis (Gotelli and Hellison, 2004; Hammer, 2001).

Species turnover with increasing distance from the glacier front was tested using Seriation analysis, an incidence-based reciprocal averaging analytic technique to arrange comparable units (species and sites) linearly such that the position of each unit reflects its similarity to other units (Liiv, 2010). The probability of obtaining the observed spatial turnover between species was calculated using a Monte Carlo simulation (30 random matrices, Hammer *et al.,* 2001). This analysis was performed removing the rare species (frequency <0.5%) and sampling plots where no species were found.

The Linear Regression and Seriation analyses were performed using PAST 3.18 (Hammer *et al.,* 2001). The other analyses were performed using Microsoft Excel©.

RESULTS

Carabids

Thirteen species were collected along the glacier foreland with *Oreonebria castanea* (occurrence=67%) commonest followed by *Nebria germari* (occurrence =62%). Distance from the glacier front affected positively species richness (ANOVA test: $F_{1,20}$=10.33, P=0.005) and taxonomic diversity (ANOVA test: $F_{1,20}$=8.32, P=0.01) (Tab. 2; Fig 2 a,b).

The spatial turnover in species distribution was significantly higher than expected by random chance (P=0.013), with an anti-nested pattern of the analysed meta-community. Therefore, there are species whose presences are mutually exclusive (Fig. 3a).

Chironomids

Thirteen species were collected along the glacier foreland, with *Diamesa steinboecki* (occurrence: 100%) commonest followed by *Diamesa zernyi* (occurrence =92%).

The distance from the glacier front did not affect species richness (ANOVA test: $F_{1,24}$=1.169, P=0.291), but positively affected the taxonomic diversity (ANOVA test: $F_{1,24}$=9.877, P=0.005) (Tab. 2; Fig 2 a,b).

The spatial turnover in species distribution in plots was not significantly higher than expected by random chance (P=0.777), with a nested pattern of the analysed meta-community. Therefore, there are not species whose presences are mutually exclusive (Fig. 3b).

DISCUSSION

The comparison between the spatio-temporal distribution of carabid and chironomid assemblages along the Amola glacier foreland emphasised some similarities and dissimilarities. As regards the similarities, first of all the carabid and chironomid communities living respectivelly above-ground and in the glacial stream include the same total number of species (=gamma-diversity). Furthermore, the most common carabid (*O. castanea* and *N. germari*) and chironomid species (*D. steinboecki* and *D. zernyi*) belong to genera typical of high altitude habitats, including cold-adapted species (Kavanaugh, 1979; Lencioni *et al*., 2015).

A similar pattern was observed for the taxonomic diversity. It changed significantly, both in carabids and chironomids, increasing along the glacier foreland gradually in chironomids and with a strong increase at ca. 300 m from the glacial front, thus in plots deglaciated by an average of 50 yrs in carabids. Thus, species assemblages living near the glacier front are characterised by closely related species respect to those in more distant plots. Taxonomic diversity is closely related to ecological diversity and functionality (Warwick and Clarke, 1998; Paschetta *et al.,* 2013), thus higher value of taxonomic diversity indicates higher habitat functionality. Therefore, we can assume that lower values of taxonomic diversity reflect the absence of a variety of ecological niches to support complex biological assemblages. According to Heino *et al.* (2005) the environmental preferences of species may be directly related to increased habitat heterogeneity and availability of resources, with heterogeneous environmental conditions allowing

Tab. 2. Model coefficients of linear regression analysis with species richness and taxonomic diversity as dependent variables.

	t	P
Carabid species richness		
(constant)	2.585	0.180
Distance	3.214	0.005
Carabid taxonomic diversity		
(constant)	2.877	0.010
Distance	2.884	0.010
Chironomid species richness		
(constant)	6.338	<0.000
Distance	1.081	0.291
Chironomid taxonomic diversity		
(constant)	10.528	<0.000
Distance	3.143	0.005

Distance, distance from the glacier front.

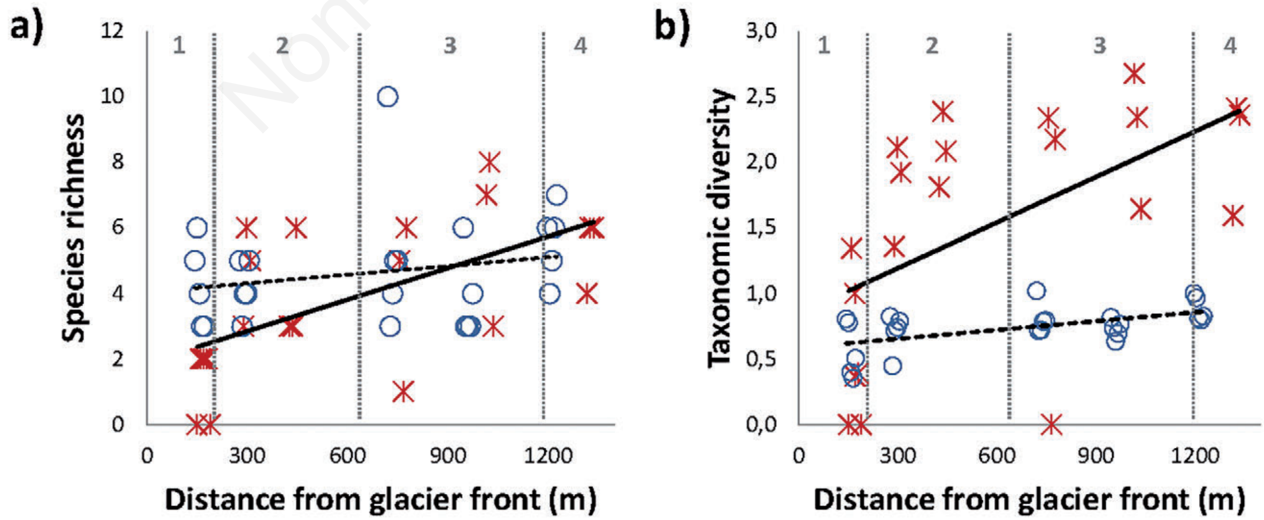
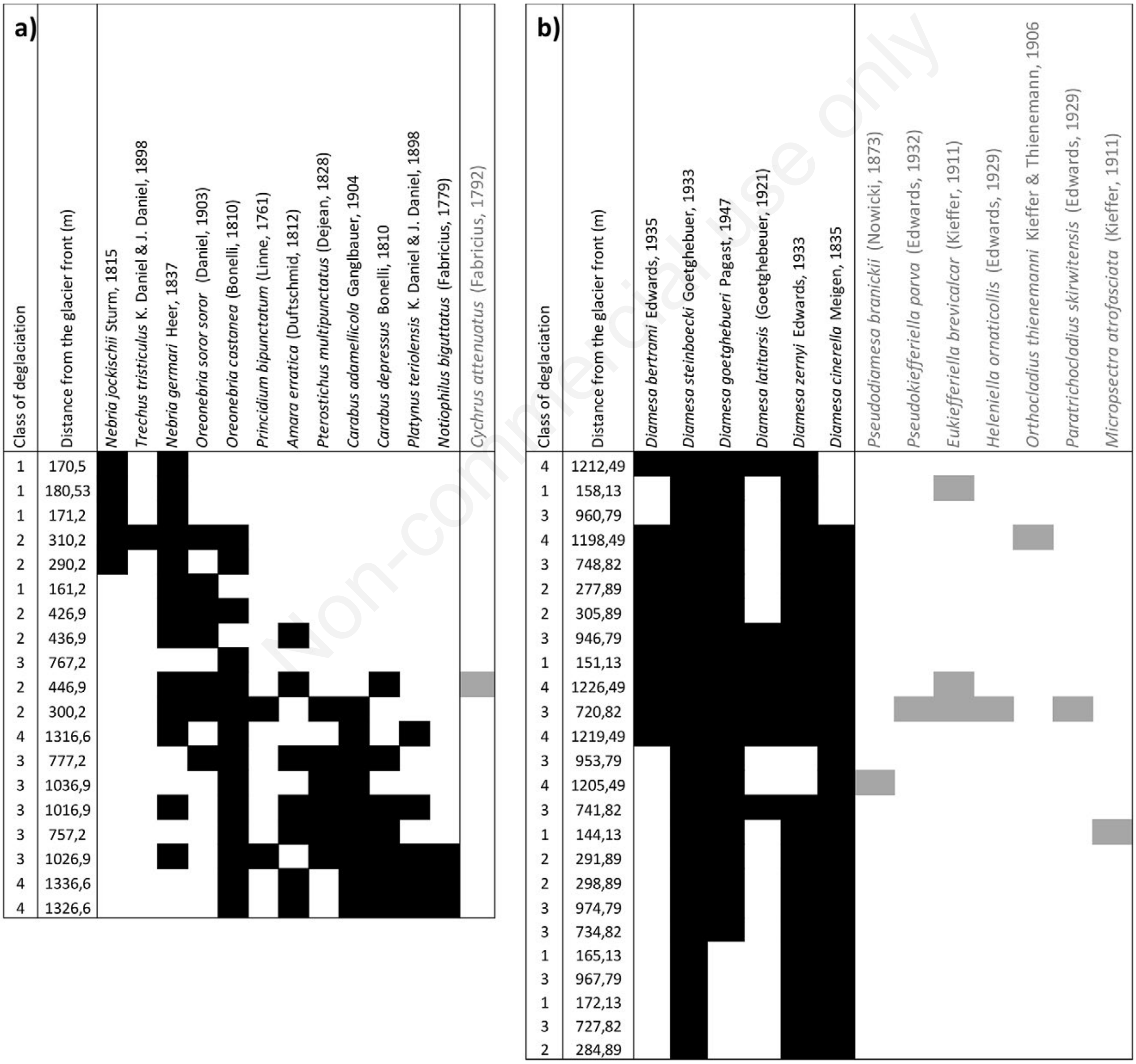


Fig. 2. Carabid (stars) and chironomid (circles) species richness (a) and taxonomic diversity (b) in relation to distance from the glacier front (metres). The bold and dashed black lines represent respectively the regressions line for carabid species richness/taxonomic diversity and chironomid species richness/taxonomic diversity. The vertical dashed grey lines, and the grey numbers put within them, represent the limit of the classes of deglaciation (see Tab. 1).

taxonomically diverse species, thus species from highly differing taxonomic levels, to coexist.

This result agrees with the general ecological patterns highlighted along glacier forelands: plots located near the glacier fronts are those recently deglaciated and represent the early successional stages. Plots further apart, specifically those deglaciated by more than 100-150 years, are more mature, near the climax, and represent the older successional stages. Early successional stages support only few species well adapted to harsh conditions (*e.g.*, lack of nutrients) thus the higher survival probability is linked to species taxonomically closely related. The variety of ecological niches in the late successional stages support species belonging to different genera, assumed to include species with different functional traits (*e.g.*, foraging habits).

As regards dissimilarities, the first regards the species richness pattern, increasing significantly with distance from the glacier front, therefore with the time since deglaciation, only in carabids. This is in accordance with



a)

Class of deglaciation	Distance from the glacier front (m)	*Nebria jockischii* Sturm, 1815	*Trechus tristiculus* K. Daniel & J. Daniel, 1898	*Nebria germari* Heer, 1837	*Oreonebria soror soror* (Daniel, 1903)	*Oreonebria castanea* (Bonelli, 1810)	*Princidium bipunctatum* (Linne, 1761)	*Amara erratica* (Duftschmid, 1812)	*Pterostichus multipunctatus* (Dejean, 1828)	*Carabus adamellicola* Ganglbauer, 1904	*Carabus depressus* Bonelli, 1810	*Platynus teriolensis* K. Daniel & J. Daniel, 1898	*Notiophilus biguttatus* (Fabricius, 1779)	*Cychrus attenuatus* (Fabricius, 1792)
1	170,5	■		■										
1	180,53	■		■										
1	171,2	■		■										
2	310,2	■	■	■	■	■								
2	290,2	■		■		■								
1	161,2			■	■									
2	426,9			■	■	■								
2	436,9			■	■			■						
3	767,2					■								
2	446,9			■	■	■		■			■			▨
2	300,2			■	■	■	■		■	■				
4	1316,6			■		■				■		■		
3	777,2				■	■		■	■	■	■			
3	1036,9					■			■	■				
3	1016,9			■		■		■	■	■	■	■		
3	757,2					■		■	■	■	■			
3	1026,9			■		■	■		■	■	■	■	■	
4	1336,6					■		■		■	■	■	■	
4	1326,6					■		■		■	■	■	■	

b)

Class of deglaciation	Distance from the glacier front (m)	*Diamesa bertrami* Edwards, 1935	*Diamesa steinboecki* Goetghebuer, 1933	*Diamesa goetghebueri* Pagast, 1947	*Diamesa latitarsis* (Goetghebeuer, 1921)	*Diamesa zernyi* Edwards, 1933	*Diamesa cinerella* Meigen, 1835	*Pseudodiamesa branickii* (Nowicki, 1873)	*Pseudokiefferiella parva* (Edwards, 1932)	*Eukiefferiella brevicalcar* (Kieffer, 1911)	*Heleniella ornaticollis* (Edwards, 1929)	*Orthocladius thienemanni* Kieffer & Thienemann, 1906	*Paratrichocladius skirwitensis* (Edwards, 1929)	*Micropsectra atrofasciata* (Kieffer, 1911)
4	1212,49	■	■	■	■	■								
1	158,13		■	■		■				▨				
3	960,79		■	■		■								
4	1198,49	■	■	■		■	■					▨		
3	748,82	■	■	■		■	■							
2	277,89	■	■	■		■	■							
2	305,89	■	■	■		■	■							
3	946,79	■	■	■	■	■	■							
1	151,13	■	■	■	■	■	■							
4	1226,49	■	■	■	■	■	■			▨				
3	720,82	■	■	■	■	■	■		▨	▨	▨		▨	
4	1219,49	■	■	■	■	■	■							
3	953,79		■	■			■							
4	1205,49		■	■			■	▨						
3	741,82		■	■	■	■	■							
1	144,13		■	■		■	■							▨
2	291,89		■	■		■	■							
2	298,89		■	■		■	■							
3	974,79		■	■		■	■							
3	734,82		■	■		■	■							
1	165,13		■			■	■							
3	967,79		■			■	■							
1	172,13		■			■	■							
3	727,82		■			■	■							
2	284,89		■			■	■							

Fig. 3. Carabid (a) and chironomid (b) species distribution in relation to the distance from the glacier front (metres). Species are ordered according to the first axis obtained from the seriation analysis. The species excluded by the analysis because rare (frequency <0.5%) are indicated in grey.

previous studies on terrestrial invertebrate primary successions along glacier forelands (Hågvar, 2012). The same trend was expected for chironomids (Milner *et al.,* 2001), known to be represented species other than *Diamesa* spp. with increasing distance from the glacier front. Perhaps the stream reach studied was too homogeneous in physical and chemical features to support different zoobenthic communities.

The second one dissimilarity was found in the species turnover. This was evident for the carabid community, with a major change in species composition ca. 700 m from the glacial front, therefore in the transition from sites deglaciated at least since 100 yrs ago. This result is in agreement with similar studies on other alpine glacier forelands and on different taxa (*e.g*., spiders), confirming that around one-hundred years since deglaciation significant changes in species assemblages composition occur (Brambilla and Gobbi, 2013; Gobbi *et al.,* 2006b). This ecological threshold probably marks the boundary between immature and mature habitats (Huggett, 2005; Gobbi *et al.,* 2010). On the contrary, we did not observe a spatially structured distribution of chironomid species, meaning distance from the glacier front did not affect the species distribution within 1.3 km of stream. Most species are ubiquitous (all belonging to *Diamesa* genus), thus there are not species exclusive to a specific site apart from some rare species found only in one site. Their catch must be considered accidental, for example *Micropsectra atrofasciata* at c 100 m from the front. This species is not typical of kryal habitat, it colonises lowland waters or alpine non-glacial streams. The adult females of chironomids typically fly upstream to lay eggs, but young larvae drift downstream within few days after hatching (Maiolini and Lencioni, 2002). A stream reach at just over 1 km was too homogeneous in abiotic conditions to support different macroinvertebrate communities (Lods-Crozet *et al*., 2001), so restricting species turnover in chironomids.

CONCLUSIONS

This work highlighted how the increasing areas of barren ground and stream bed due to melting glaciers could differently affect epigeic and aquatic insect taxa. Carabids seemed to be more sensitive, with respect to chironomids, to the distance from glacier front. We can affirm that c 1.3 kilometres from the glacier front, thus more than 150 years since the glacier retreat, constitute a time span sufficient to determine changes in carabid assemblages. Conversely, 1.3 km of stream length seemed insufficient to change the environmental conditions and to affect the chironomid species assemblages, being, the longitudinal pattern of taxa richness and diversity, predictable in glacier-fed streams (Castella *et al*., 2001). Distance at which the macroinvertebrate community changes depends also by the surface of glacier feeding the stream and its state of retreating. So, it is possible that in the future, if the Amola glacier will be reduced due to global warming, within 1 km of the Amola stream significant species turnover might occur (Brown and Milner, 2012). This suggests that long-term studies may describe better the biodiversity trend of trophically related invertebrates, such as carabids and chironomids, along glacial forelands.

Within this study we investigated the diversity as richness and taxonomical diversity of carabids (which are mainly predators) and chironomids (which are mainly grazer/detritivorous). However, the glacier forelands are colonised by other predators (*e.g*., spiders on the ground and nematods and water mites in the water) and grazer/detritivorous taxa (*e.g*., collembolans, diplopods and orthopterans on the ground, and oligochaetes and mayflies in the water), besides other representative of feeding groups (*e.g*., the simulid filtrators) *etc*.. Future studies might consider this other component of biodiversity, the functional diversity, in relation to the distance from the glacier front. It could help to better understand the effects of climate change on glacier foreland communities.

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