

Environmental gradients and succession patterns of carabid beetles (Coleoptera: Carabidae) in an Alpine glacier retreat zone

Jürg Schlegel · Matthias Riesen

Received: 28 June 2011 / Accepted: 10 November 2011 / Published online: 30 November 2011
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Abstract Accelerated by global warming, retreating glaciers leave behind spatially ordered moraines with underlying primary succession and disturbance. Current knowledge of primary succession comes mainly from studies of vegetation dynamics. Information about above-ground macroinvertebrates is still scarce. We used carabid beetles (Coleoptera; Carabidae) as indicator taxon to assess the effects of (1) terrain age (species turnover along the proglacial chronosequence) and (2) small-scale habitat architecture (vegetation cover, surface texture) on the carabid assembly. For this purpose, 33 sampling sites with pitfall traps were installed throughout the glacier foreland Morteratsch (Engadine, Switzerland), adjacent sparse forests serving as reference sites. With a total of 33 carabid species on the foreland and another 2 on the reference sites, the study area yielded a very high carabid species diversity compared to other glacier forelands. In general, the age of deglaciation proved to be a highly significant predictor for the carabid distribution, especially for particularly discriminant species. Observed species richness and activity densities showed bimodal patterns with a steep increase within the first ca. 40 years, a decline between around 40–90 years, and a further increase towards the terminal moraine. There was no evidence of dispersal-stochasticity: distinct clusters of sites with similar species composition were found. Microhabitat suitability proved to be a secondary effect, embedded in a temporal framework of primary succession. Surface cover with litter, herbs and dwarf-shrubs turned out to be the crucial habitat factors.

Habitat loss as a result of climate warming will primarily affect cold-stenotopic carabids, but may potentially be absorbed by active selection for cooler microhabitats.

Keywords Glacier foreland · Invertebrate fauna · Primary succession · Habitat factors · Climate change · Swiss Alps

Introduction

Retreating glaciers are considered to be key indicators of global warming (IPCC 2007; Oerlemans 2005; Paul et al. 2004). It is estimated that glaciers in the European Alps lost about half of their total volume between around 1850 (“little ice age”) and 1975, another 25% of the remaining amount between 1975 and 2000, and an additional 10–15% in the first 5 years of this century (Haeberli et al. 2007). Based on extrapolations of the “Swiss Glacier Inventory 2000”, a total of more than 600 km² has become ice-free since 1850 (Zemp et al. 2007).

Retreating glaciers leave behind barren moraines with various textures, stability and fertility, consisting of fine rock flour particles up to larger boulders. Secondary disturbances following deglaciation include landslides from the side moraines, floodplains, wind-blown loess and winds that desiccate and cool the environment (Walker and Del Moral 2003). Dynamic processes such as transportation or rearrangement of till in front of the glacier snout form an unstable habitat (Geo7 and UNA 1998).

Primary succession is ecosystem development in situations where no previously developed soil exists (Dobson et al. 1997). Glacier forelands represent ideal spatio-temporal model systems for studying primary succession and recovery from severe disturbance. As most of our

J. Schlegel (✉) · M. Riesen
Institute of Natural Resource Sciences, ZHAW Zurich
University of Applied Sciences, Grüental,
8820 Wädenswil, Switzerland
e-mail: juerg.schlegel@zhaw.ch

knowledge of primary succession comes from descriptive studies of vegetation development (Wood and Del Moral 1987), information about fauna is scarce and often anecdotal (Mrzljak and Wiegler 2000).

Common understanding of succession implicates photoautotrophic plants as the first colonisers of newly generated substrates. In primary succession, however, a review by Hodkinson et al. (2002) amassed many research projects with heterotrophic organisms as leadoff arrivals. This also seems to hold true for newly exposed glacier moraines where predators were almost exclusively the first colonisers, as observed in the Arctic (Hodkinson et al. 2001) and in central Europe (Kaufmann 2001). The typical sequence in secondary succession, where invertebrate carnivores follow herbivorous invertebrates (Kaufmann 2001), is reversed. The diet of the first arrivals, among those predatory carabids, is organic “fallout” such as springtails and aphids, drifted by wind turbulence. Walker and Del Moral (2003) mention insects on barren sites hastening soil development by introducing carbon and nitrogen.

Soil and vegetation development on glacier forelands in the European Alps are well documented (e.g. Caccianiga and Andreis 2004 in the Italian Alps; Burga 1999, Egli et al. 2006 in the Swiss Alps; Raffl et al. 2006 in the Austrian Alps). Research on soil communities has been conducted by Matthews (1992), Ohtonen et al. (1999), Tschirko et al. (2005) and numerous others. Several studies have analysed the succession of microbes on glacier forelands (e.g. Sigler et al. 2002). Hågvar (2010) analysed the springtail fauna, and Seniczak et al. (2006) determined oribatid mites in Norwegian glacier forelands. Recent research in proglacial areas highlights the potential of invertebrate fauna to help understand the responses of living organisms to environmental and climatic changes (Gobbi et al. 2006b; Kaufmann 2001). Albrecht et al. (2010) studied interactions between insect-pollinated plants and plant-pollinating insects. The zoobenthos of glacier-fed streams has been documented in several studies, e.g. by Milner et al. (2002) and Robinson et al. (2001).

Despite all the research projects mentioned and the need to enhance biological knowledge, very few studies have focussed on the primary succession of above-ground macroinvertebrates on glacier forelands. Matthews (1992) noted the absence of relevant published data in respect of animals in glacier forelands at the time of his study. In Europe, research on epigeic arthropods is primarily restricted to studies by Janetschek (1949, 1958), Franz (1969), Gereben (1995), Paulus and Paulus (1997), Kaufmann (2001, 2002, 2004), and Kaufmann and Raffl (2002) in the Austrian Alps. Gobbi et al. (2006a, b, 2007, 2010, 2011) studied ground-dwelling arthropods on glacier forelands in the Italian Alps. In northern Europe, Friden (1971) as well as Østbye and Hågvar (1996) carried out

studies on glacier forelands in Scandinavia, while Hodkinson et al. (2004) examined higher latitudes in Spitsbergen. Scattered information about particular alpine invertebrate species is found in many checklists, studies and surveys (e.g. Killias 1894 for the beetle fauna in the Upper Engadine), but it generally does not allow conclusions to be drawn about small-scale habitat colonisation on glacier forelands.

Due to effective passive and active dispersal mechanisms and high reproductive rates, many invertebrates react more quickly to environmental conditions than plant communities: this also seems to be true in the Alpine zone, where all processes slow down with increasing altitude (Kaufmann 2004). At the opposite extreme, microorganisms, with their very rapid responses to changing environmental conditions, tend to fluctuate more wildly and be less stable indicators of longer-term trends (Hodkinson and Jackson 2005). Invertebrates, for example the surface active carabid beetles (=ground beetles; Coleoptera, Carabidae), are therefore considered to have high overall potential to serve as good indicators when studying landscape features and habitat changes (New 2010, but see reservations in Rainio and Niemelä 2003). Literature focusing on the response of carabid beetles to changing environments is diverse (Gobbi et al. 2007), especially for lowland agroecosystems (e.g. Aviron et al. 2005) and forests (e.g. Fuller et al. 2008). Although carabids found in European mountains have been studied by several authors (see review in Brandmayr et al. 2003), little is known about the responses of carabids to climate and ecosystem changes. Carabids are diverse and abundant, occur in all major terrestrial habitats, and are generally well documented taxonomically and autecologically (Lindroth 1986; Marggi 1992). They are mainly epigeic, which allows for easy collection with pitfall traps (Thiele 1977; Samways et al. 2010) and makes large samples of individuals often easy to obtain. Many studies have proved significant correlations to habitat characteristics and habitat modifications (New 2010).

Spatially ordered chronosequences of increasing age might represent, with some care, the history of succession in glacier forelands (Matthews 1992; Kaufmann 2001). Walker and Del Moral (2003) presume a nonlinear process of change in proglacial areas. Burga et al. (2010) also found non-linear microhabitat-controlled (grain size, water supply, microclimate) succession patterns with different pathways for the different ecological niches on the Morteratsch glacier foreland, converging to a common “climax”. Time since deglaciation did not sufficiently contribute to a better understanding of small-scale plant succession.

Taking these different evaluations of proglacial chronosequences for primary succession into account, the

question arises as to whether age of deglaciation might nonetheless be the leading factor controlling carabid assemblage or whether, as with vegetation, small-scale habitat characteristics are more influential. With respect to this core question, the aims of our research project were (1) to analyse spatial patterns of carabid beetle assemblage in terms of the age of deglaciation (chronosequence) and habitat architecture, (2) to assess the key habitat factors which determine carabid coenosis in general and the distribution of certain carabid indicator species in particular, (3) to establish whether carabid coenosis on sites with unequal small-scale plant succession but comparable age of deglaciation are more similar than on sites with equal small-scale plant succession but different age of deglaciation, and (4) to compare the autonomy of carabid coenosis on the glacier foreland with adjacent sparse forests outside the 1857 moraines.

Methods

Study area

The Morteratsch glacier foreland is situated above Pontresina, Upper Engadine, south of the Bernina massif in the eastern part of the Swiss Alps (Fig. 1). It includes the outwash plain of the proglacial area of the Morteratsch glacier (46°26' N; 9°56' E; approximately 2.2 km long with a surface area of around 2 km² and an altitude range from about 1,900–2,100 m a.s.l.), as well as adjoining open forests outside the 1857 terminal moraine.

According to Burga et al. (2010), the first plants appear about 7 years after deglaciation, reaching higher cover-abundance values almost 30 years later. Together they form the long-living *Epilobietum fleischeri* plant community, which dominates the recently deglaciated areas, but can be found in patches almost everywhere on the foreland of the Morteratsch glacier. The first species of the *Oxyrietum digynae* plant community appear approximately 10 years after deglaciation, disappearing around 30 years later. Lichens need about 15–20 years to establish their first populations. The first small trees (*Larix decidua*), tall shrubs and dwarf-shrubs (e.g. *Salix spp.*, *Alnus viridis*, *Rhododendron ferrugineum*) are found on 12–15 year old terrain. The *Alnetum viridis* grows continuously in importance until it overtakes the *Epilobietum fleischeri* after about 100 years of deglaciation. Until about 55 years after deglaciation, pioneer grass communities develop in the same way as *Alnetum viridis*, later decreasing due to higher shrub cover. Even around 150 years later, no near-to-mature larch-Swiss stone pine forest (*Larici-Pinetum cembrae*) can be found on the glacier foreland (Burga et al. 2010). The timber line is above the glacier foreland and

reaches about 2,350 m a.s.l. The mean annual temperature for the glacier foreland is approximately 0.5° C and the mean annual precipitation about 1,000–1,300 mm (Egli et al. 2006). The retreat of the glacier Morteratsch, at an average of 17.5 m per year (ETH Zurich 2010), has been well documented since recordings started in 1878.

The tectonic units are the Bernina- and Stretta-crystalline, mainly constituted of granitoid rocks. Consequently, the glacial till has an acid character (Mavris et al. 2010). Soils in the proglacial area are weakly developed. Mature forests outside the glacier foreland are characterised by podzols and have been ice-free since the Würm glaciation over 10,000 BP (Burga et al. 2010).

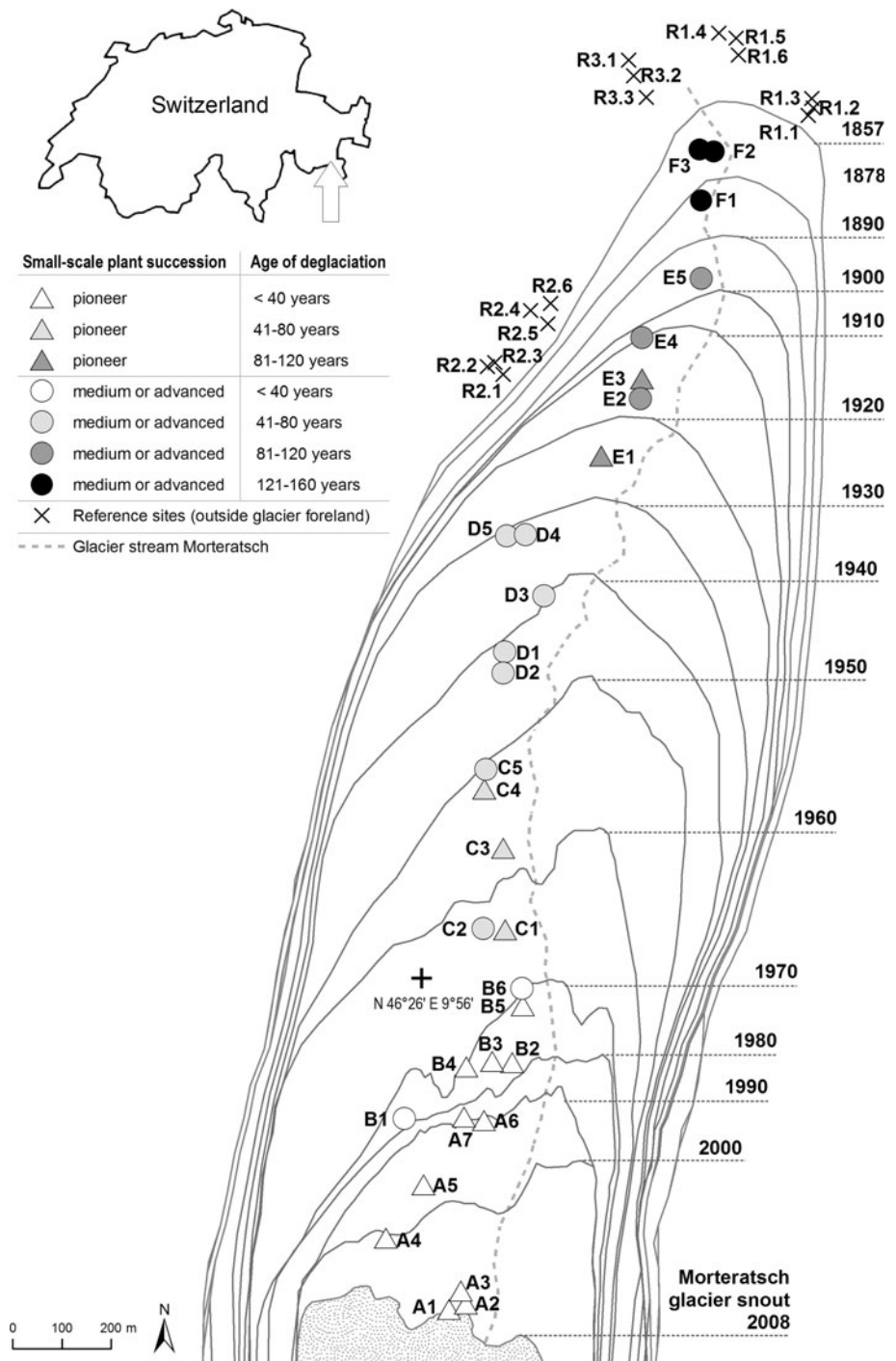
Carabid sampling

Carabids were collected using pitfall traps (Southwood 1978). The traps consisted of plastic cups with a 7.3 cm mouth diameter and 8 cm depth. They were inserted into the ground so that the rim was as flush to the surface as possible. They were partly filled (~75 ml) with a mixture of 40% ethanol, 30% water, 20% glycerol and 10% acetic acid, subsequently diluted to 70% in water, to kill and preserve the trapped invertebrates. Plexiglas lids, kept firmly in place 3–4 cm above the ground surface by two aluminium wires, protected the traps from precipitations and larger animals.

Sampling on the glacier foreland: 18 sampling sites with 3 pitfall traps each (1 m spacing) were established in 2007 (2007: overall 54 traps). In 2008, the same sampling sites were, because of only few drop outs, rerun with 2 pitfall traps each. A further 12 new sites were added to obtain a uniform distribution over the glacier foreland and a better association with age of deglaciation categories (2008: overall 60 traps). In 2009, the 30 sampling sites were reset with 60 pitfall traps and an additional site near the glacier tongue was set up (2009: overall 62 traps; Fig. 1, Table 1). All the traps were placed orographically left of the glacier stream on the outwash plain at adequate distance from the side moraine to prevent disturbance. Because initial colonization was a focus of this study, glacier-near sites were trapped more densely than sites near the terminal moraine, leading to partly unequal numbers of traps per age category. This was taken into account in data analysis and interpretation.

Sampling outside the glacier foreland: reference sampling sites with 3 pitfall traps each were set directly outside the terminal moraine of 1857 in or along near-mature open forests. In 2007, 6 sites on the orographically right side of the glacier foreland were established, in 2008, 6 sites on the orographically left side, and in 2009, 3 sites along an open forest on the orographically left side (2007 and 2008: overall 18 reference traps per year; 2009: overall 9 reference traps). Different reference sampling sites were

Fig. 1 Study area of the Morteratsch glacier foreland (Engadine, Switzerland) with indication of deglaciation and small-scale plant succession (isochrones after Burga 1999; Elsener 2006 and Albrecht et al. 2010). Small-scale plant succession (% plant cover): pioneer <25%, medium 25–74%, advanced \geq 75%



selected from year to year to cover the main habitat types next to the glacier foreland.

The single traps were pooled for each sampling site. The traps were emptied biweekly from 2007 to 2009 between mid-May and the end of September. The invertebrates were stored in 70% ethanol. Subsequently, we identified the carabid beetles to species level using standard keys (Müller-Motzfeld 2006; Hurka 1996). The nomenclature is in accordance with Luka et al. (2009).

Habitat factors

Habitat factors in an area of roughly 100 m² around each active sampling site on the glacier foreland were specified on 6th September 2007, 27th August 2008 and 24th August 2009. The percentages of cover in respect of the following parameters were estimated: boulders/stones (diameter > 60 mm), gravel (diameter 2–60 mm), sand (diameter < 2 mm), humous soil, lichens/mosses, small herbs/grasses (height \leq 30 cm), tall

herbs (height > 30 cm), dwarf-shrubs (height ≤ 50 cm), tall shrubs/trees (height > 50 cm) and litter. The average covers, which hardly differed between the years, were used for analysis. The categories of small-scale plant succession (for locations see Fig. 1) were determined by the total cover of plant vegetation (lichens/mosses, small herbs/grasses, tall herbs, dwarf-shrubs, tall shrubs/trees). If plant vegetation cover exceeded 75%, the successional state of the sampling site was defined as *advanced*, with 25–74% as *medium*, and lower than 25% as *pioneer*. *Medium* and *advanced* sites were pooled for further analysis to get a consistent arrangement (16 *pioneer* sites, 15 *medium* or *advanced* sites).

Data analysis

Carabid species richness

The dominance structure of the carabid species assemblage (Table 1) was assessed using the classification of Engelmann (1978). The total number of species was estimated by the non-parametric estimator Chao 1 (Chao 1984; Colwell and Coddington 1994): $S_{\text{Chao1}} = S_{\text{obs}} + (a^2/2b)$, where S_{Chao1} is the estimated number of species, S_{obs} the observed number of species, a the number of species registered only once (singletons), and b the number of species recorded twice (doubletons).

In imbalanced designs where the total number of traps is unequal across the sampling years, observed species richness might be biased in favour of sites with more traps. To determine whether the observed species richness *per sampling site* was close to species saturation, we calculated non-parametric abundance-based coverage estimators (ACE) for each site (Chao and Lee 1992; Magurran 2004): $S_{\text{ACE}} = S_{\text{abund}} + (S_{\text{rare}}/C_{\text{ACE}}) + (a/C_{\text{ACE}})\gamma_{\text{ACE}}^2$, where S_{ACE} is the estimated number of species, S_{abund} the number of abundant species with > 10 individuals, S_{rare} the number of rare species with ≤ 10 individuals, a the number of singletons and $C_{\text{ACE}} = 1 - (a/N_{\text{rare}})$, where N_{rare} is the total number of individuals in rare species. γ_{ACE}^2 is the estimated coefficient of variation (details see Magurran 2004). The ACE values were calculated using EstimateS software (Colwell 2005). For lack of doubletons Chao 1 values could not be performed on sampling site level.

Carabid species abundance

The mean weekly activity densities of all carabid species were calculated at each sampling site by taking the site-abundance of each species 2007–2009 divided by the site-related total number of sampling weeks 2007–2009, adjusted to the number of intact traps per sampling week. The adjustment to sampling weeks and intact traps was required because, as explained above, only 18 of the total

of 31 sites on the glacier foreland were steadily trapped during the whole sampling period 2007–2009. The trapping periods 2007, 2008 and 2009 were slightly different because of different snow-melt in spring (19–20 weeks per year). A few traps were damaged and were therefore completely out of use for a short time (0.9–1.3% of traps per year).

Statistics and ordination

The pooled mean activities (density per week) of carabid species for 2007–2009 were 4th-root-transformed to approach a normal distribution (Shapiro–Wilk $P = 0.53$ for dataset without reference sites, $P = 0.50$ for whole dataset), while the pooled observed and estimated species richness data for 2007–2009 remained untransformed (Shapiro–Wilk $P_{\text{obs}} = 0.41$ and $P_{\text{est}} = 0.91$ for dataset without reference sites, $P_{\text{obs}} = 0.18$ and $P_{\text{est}} = 0.58$ for whole dataset). In order to diminish the influence of species with high abundance, the mean activity densities for 2007–2009 of *each* species were $\log(n + 1)$ -transformed for further analysis at species level. Spearman rank correlation was performed to obtain an estimate for the relationship between individual species abundance and age of deglaciation.

To evaluate the impact of site-related habitat factors and the age of deglaciation on species richness and activities, separate sigma-restricted one-way Analysis of variance (ANOVA/MANOVA) were performed with the following dependent variables: (1) observed and estimated carabid species richness pooled for 2007–2009 (ANOVA), (2) carabid species abundance with pooled and averaged mean activity densities of *all* carabid species for 2007–2009 (ANOVA), and (3) pooled and averaged mean activity densities of *each* carabid species for 2007–2009 (MANOVA). Analyses (3) were followed by a Tukey post hoc test to assess significant differences between categories of deglaciation.

The age of deglaciation category, used as the predictor variable for (1), (2) and (3), was subdivided into the categories 0–20, 21–40, 41–80, 81–120, 121–160 years with supplementary category “reference” for sites outside the foreland. Parameter estimates β for categories of deglaciation were performed applying a General linear model (GLM). Variance homogeneity between groups complied with (1) and (2) (Brown-Forsythe $P_s = \text{n.s.}$), but not with species level (3) (Brown-Forsythe $P < 0.05$ for 9 of 35 carabid species), taking into account that tests of homogeneity are not necessarily very robust and assumptions of group homogeneity are not always crucial for ANOVA-analysis (Hill and Lewicki 2006). Since differences in species composition due to different sampling periods were not a focus of this study, sampling periods were defined as random factors (mixed-effects model).

Principal coordinate analysis (PCoA), also known as Metric multidimensional scaling (MMS), served to compare the carabid assemblage along the proglacial chronosequence. Bray-Curtis distances were applied as distance measures. Bray-Curtis coefficients are considered as an appropriate quantitative approach to compare the compositional similarity of assemblages between different sites, based on the number of species and individuals collected (Leyer and Wesche 2006, but see Clarke et al. 2006 for critical discussion).

Detrended correspondence analysis (DCA), based on $(\log + 1)$ -transformed pooled mean carabid activity densities for 2007–2009, was performed to identify gradient length for subsequent constrained ordination of the carabid dataset. Thereafter, the dataset was analysed with Canonical correspondence analysis (CCA), applying the default options “biplot scaling” and “interspecies distances”. The CCA method is a constrained ordination technique (=direct gradient analysis) for gradient lengths larger than 3–4 standard deviation units (SD), representing unimodal species responses to the underlying environmental gradients (Ter Braak and Šmilauer 2002). The aim of constrained ordination is to find the variability in species composition that can be explained by the environmental variables measured (Lepš and Šmilauer 2003). The position of a species in the resulting diagram indicates the degree of dependence on the closest environmental parameters (arrows). The distance between the sampling points approximates the dissimilarity of their carabid species composition. The distance between a sampling point and a species point approximates the (predicted) probability of occurrence of a species in the particular sample. The statistical significance of the contribution of each habitat factor in CCA was assessed using a Monte Carlo permutation test under a reduced model (499 permutations) with forward selection of the variables. Additionally, Spearman rank correlations between carabid species ($\log + 1$ -transformed) and habitat factors were performed and compared with the outcomes of the CCA model.

All statistical analyses were performed using Statistica 9.1 (StatSoft Inc. 2010) and Canoco for Windows 4.51 (Ter Braak and Šmilauer 2002). Species with less than 5 individuals pooled for 2007–2009 were excluded from statistical analysis on species level.

Results

Carabid species richness and distribution

A total of 9,952 individuals of carabid beetles belonging to 35 species were recorded during the sampling periods 2007–2009 (Table 1). On the glacier foreland (sites A to F)

9,282 individuals and 33 species were found (2007: 2,458/26; 2008: 4,163/25; 2009: 2,661/26), while on the reference sites outside the glacier foreland (sites R) 670 individuals and 13 species (2007: 25/4; 2008: 293/10; 2009: 352/12) were counted.

The estimated number of carabid species 2007–2009 was 39.0 ± 5.2 for the glacier foreland and 43.2 ± 6.5 for the whole study area with reference sites included (Chao 1 \pm SD). Calculating Chao 1-value *separately* for the reference sites did not yield a value, because the reference sites did not contain any doubletons. The estimated species richness *per sampling site* is given below (Fig. 2b).

Accounting for 48.4% of the mean carabid activity density in 2007–2009, *Calathus erratus* proved to be particularly numerous and the only eudominant species. *Calathus micropterus* (11.1%), *Calathus melanocephalus* (9.3%), *Amara quenseli* (5.8%), *Cymindis vaporariorum* (3.6%) and *Carabus depressus* (3.4%) were subdominant.

Age of deglaciation as predictor for carabid species assemblage

With 16 observed carabid species each, the species-richest sites were A6 (small-scale plant succession = pioneer, age of deglaciation = 18 years), B6 (medium, 39 years) and F1 (advanced, 128 years), thus sites with variable terrain age and small-scale succession (Fig. 2a). In contrast, only 1–5 species were present on the youngest sampling sites A1 to A4 (pioneer, 2–7 years) situated near the glacier snout on barren moraine grounds, and more surprisingly there were also only 5 species on the much older sampling site E1 (still pioneer, 84 years). Reference sites were relatively species-poor except for the sampling sites R3.1, R3.2 and R3.3 with 8 species each. On site R1.2 no carabids were found. However, it should be noted that the 3 reference sites R1, R2 and R3 were each sampled during one season only.

Observed species richness distinctly increased over the first 40 years, then slowly declined and formed a minimum at about 80 years of deglaciation, followed by a further increase up to 140 years. The minima within the categories 1–20 years and 61–80 years were significant (parameter estimates $\beta = -7.00$, $P = 0.023$ and $\beta = -7.90$, $P = 0.024$ respectively; Table 2a).

Estimated species richness on the basis of ACE calculations revealed a more balanced distribution over time than observed species richness (Fig. 2b). Age category of deglaciation did not prove to be a significant predictor there (Table 2b).

The mean yearly activity densities of carabids show similar trends as for the observed species richness (Fig. 3). Near the glacier, the activities were low, increasing distinctly after 20 years of deglaciation to a maximum at

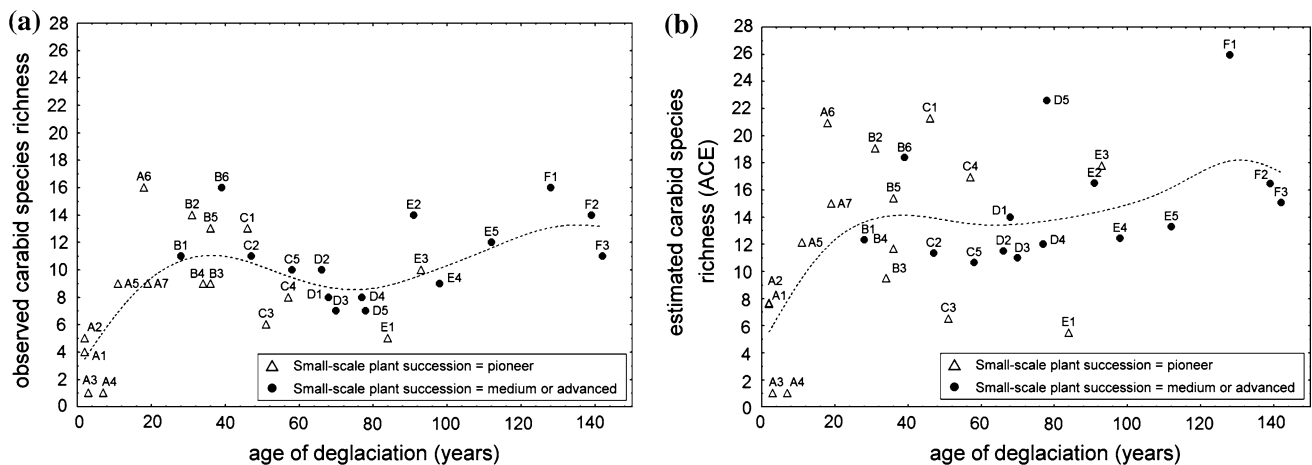


Fig. 2 (a) Observed carabid species richness 2007–2009 and (b) estimated carabid species richness 2007–2009 (ACE) on the glacier foreland Morteratsch relative to age of site-deglaciation. The curves

are fitted to the site data with distance-weighted least squares smoothing procedure. The reference sites outside the foreland are not shown (ice-free > 10,000 years)

about 40 years, followed by a decline reaching the lowest point after 80 years, and then a slight re-increase. Mean activity densities of the age categories 1–20 and 61–80 years were significantly lower, or almost significantly lower respectively, when compared with the remaining age categories (parameter estimates $\beta = -0.78$, $P = 0.027$ and $\beta = -0.76$, $P = 0.057$; Table 3).

Species richness and mean activity of carabids on pioneer sites and on sites with medium or advanced succession are not directly comparable: on young sites (<25 years) there are no medium or advanced plant succession sites while on old sites near the terminal moraine (>100 years) pioneer sites are absent. In parts of the foreland with pioneer and medium or advanced small-scale plant succession side by side, and thus being about the same age, a tendency towards higher activity densities was found for sites with medium or advanced small-scale plant succession. However, Wilcoxon pair-wise comparisons yielded only a significant difference between the sites E2 (medium, 91 years) and E3 (pioneer, 93 years; $Z = 2.27$, $P = 0.023$) and an almost significant difference between the sites B5 (pioneer, 36 years) and B6 (medium, 39 years; $Z = 1.89$, $P = 0.058$).

Age of deglaciation as predictor for carabid assemblage at species level

As seen above, the distribution of the carabid coenosis along the chronosequence reveals a characteristic spatio-temporal pattern. To test the significance *at species level*, a General linear model (GLM) was applied with all species >4 individuals as dependent variables and age of deglaciation (7 categories) as predictor variable (Table 4). For species with significant interactions, a subsequent

Tukey post hoc test was calculated with outcoming significant pair-wise interactions between activity densities and the age category of deglaciation. *Bembidion bualei ssp. baenningeri*¹ manifested maximal activity in the youngest sites (ice-free for 1–20 years). *Amara quenseli* and notably *Carabus depressus* showed a highly significant peak in 21–40 year old sites, with both species also being present in lower numbers in other parts of the foreland. *Cymindis vaporariorum* was also found to prefer this age category, but was also active in many older habitats in the foreland. *Calathus erratus* and *Calathus melanocephalus* favoured 41–60 year old sites, the former also showing high activity on younger terrain. *Amara praetermissa* and *Notiophilus aquaticus* were mainly active in 81–120 year old sites, while *Calathus micropterus* was present on the reference sites as well. *Pterostichus unctulatus* favoured reference sites, but was also found in lower numbers in older parts of the foreland.

Similarity of sites

An ordination plot, based on Principal coordinate analysis (PCoA) with Bray Curtis-dissimilarities as distance measure, revealed patterns of site-clustering based on carabid species distribution (Fig. 4). The model suggests groupings of sites with different progressions of small-scale plant succession. Reference sites seem to have a rather distinctive carabid composition, even though only two species did exclusively occur on these sites (*Notiophilus biguttatus* and *Dromius agilis*, see Table 1). The separation of the reference sites in the plot may be explained by the fact that

¹ syn. *Bembidion cruciatum ssp. baenningeri* in Müller-Motzfeld (2006)

Table 2 Age category of deglaciation as predictor variable for pooled carabid species richness 2007–2009

Analysis of variance table	Sum Sq	df	Mean Sq	F-value	P
(a) Observed carabid species richness ^a					
Intercept	66.06	1	66.06	5.96	0.027*
Sampling period (random)	180.34	4	45.08	6.98	0.000***
Age category of deglaciation (fix)	152.91	6	25.48	3.94	0.000***
Residuals	226.18	35	6.46		
(b) Estimated carabid species richness (ACE) ^b					
Intercept	160.61	1	160.61	5.21	0.031
Sampling period (random)	329.49	4	82.37	3.46	0.017*
Age category of deglaciation (fix)	156.44	6	26.07	1.10	0.384
Residuals	832.73	35	23.79		
General linear model table	Estimate β	P	95% confidence interval		
(a) Observed carabid species richness					
Intercept	4.33	0.000***			
1–20 years	–7.00	0.023*	–12.96		–1.04
21–40 years	–3.45	0.303	–10.15		3.25
41–60 years	–6.30	0.068	–13.10		0.50
61–80 years	–7.90	0.024*	–14.70		–1.10
81–120 years	–4.56	0.178	–11.29		2.17
121–160 years	–1.79	0.609	–8.81		5.24
(b) Estimated carabid species richness (ACE)					
Intercept	8.21	0.000***			
1–20 years	–8.15	0.157	–19.59		3.28
21–40 years	–6.16	0.338	–19.01		6.70
41–60 years	–7.86	0.229	–20.91		5.18
61–80 years	–6.98	0.285	–20.03		6.06
81–120 years	–6.12	0.343	–19.03		6.80
121–160 years	–1.38	0.836	–14.86		12.09

One-way ANOVA with parameter estimates β of a General linear model (GLM), without transformation of species richness data and sampling period as random factor (mixed-effects model). Reference sites outside the glacier foreland served as reference category for the estimates ($\beta = 0$)
 *** $P < 0.001$; * $P < 0.05$
^a $r^2 = 0.74$; $r^2_{adj} = 0.67$
^b $r^2 = 0.55$; $r^2_{adj} = 0.42$

some species hardly ever crossed the foreland boundaries as noticed with the only eudominant species in this research, *Calathus erratus*, and the subdominant species *Cymindis vaporariorum* (even though both were present in the oldest parts of the foreland). The R1 reference sites represent habitats with very low carabid diversity, which explains their proximity to the similarly species-poor glacier-near A sites, however not sharing any common species. Particular older sites, e.g. F3, F2 and D2, with advanced small-scale plant succession, show a rather similar carabid composition, comparable with some R2 and R3 sites. The model predominantly shows clusters of medium or advanced sites in the middle of the ordination plot, whereas pioneer site-clusters tend to congregate around higher axis values (PCoA Axis 1: all pioneer B sites; Axis 2: youngest A sites). Scattered sites do not fit into this classification: the oldest sites in the foreland, which still show small-scale pioneer characteristics (sites E1 and E3), are more similar to sites with more advanced plant succession and to sites with approximately the same age of deglaciation (sites D4, D5 and E4) than to younger

pioneer-sites. On the other hand, carabid assemblages of particular sites with middle (above all: E5, to a lesser extent: D3) to advanced (above all: C2, to a lesser extent: C3) small-scale plant succession have a low species turnover compared to many B and C pioneer sites. The sites B1, E2 and F1 (to a lesser extent: D1) have quite a similar carabid composition despite their considerable range of time elapsed since deglaciation, which varies between approximately 28 years for site B1 and approximately 128 years for site F1.

Habitat factors as predictors for carabid species composition

A preliminarily performed Detrended correspondence analysis (DCA) yielded a maximal gradient length of 5.6 SD for axis 1, indicating unimodal distribution. Accordingly, a Canonical correspondence analysis (CCA) was selected for constrained ordination. CCA-computing with a subsequent Monte Carlo permutation test allowed the impact of the particular habitat factors on the carabid

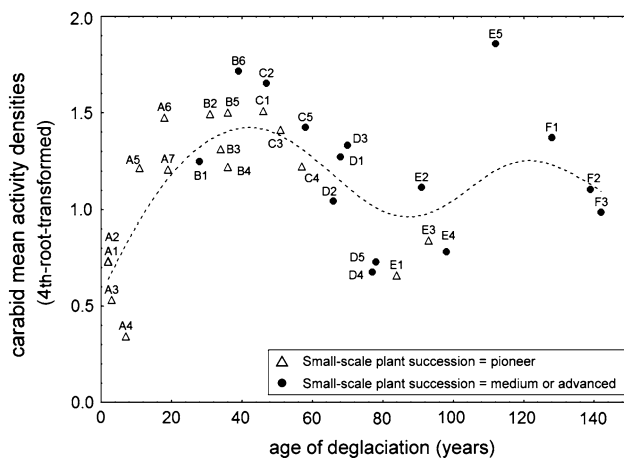


Fig. 3 Mean yearly activity densities of carabid species on the glacier foreland Morteratsch (abundance per intact trap and sampling week), pooled for each site and adjusted to different exposure periods of traps during the sampling periods 2007, 2008 and 2009 (see Table 1). The activity density data are 4th-root-transformed and shown in relation to age of site-deglaciation. The curve is fitted to the site data with distance-weighted least squares smoothing procedure. The reference sites outside the foreland are not shown (ice-free > 10,000 years)

assemblage to be assessed. The first two axes of the resulting ordination biplot in Fig. 5 account for 33.1% of the overall variance in the carabid dataset (axis 1: 17.8%, axis 2: 15.3%; sum of all axes: 53.8%). Percentages between 20 and 50% are usual for constrained ordination (Økland 1999). Axis 1 and the sum of the axes proved to be highly significant in the Monte Carlo permutation test ($P < 0.01$). Cover of “dwarf-shrubs” was found to have a

highly significant impact and cover of “small herbs/grasses”, “tall herbs” and “litter” each had a significant impact on the carabid coenosis (Table 5).

With respect to the CCA model, the carabid species *Notiophilus aquaticus* (*No.aq.*), *Pterostichus multipunctatus* (*Pt.mu*) and *Pterostichus unctulatus* (*Pt.un*) clearly prefer sites with vegetation or/and litter (Fig. 5). Positive Spearman rank correlations to litter for *N. aquaticus* ($r = 0.42$, $P < 0.05$), *P. multipunctatus* ($r = 0.55$, $P < 0.01$) and *P. unctulatus* ($r = 0.48$, $P < 0.01$) affirm this as well as the extremely high correlation to tall herbs for *P. unctulatus* ($r = 0.84$, $P < 0.001$). Thus, these species are generally found at the oldest sites in the foreland (highest densities in sites F, ca. 130–140 years old) and only sporadically in somewhat younger sites. Species around the 0-values of the canonical axis should, according to the model, not show explicit preferences for any habitat factors and should therefore be found on pioneer sites as well as on sites with advanced plant succession throughout the foreland. Indeed, this applies to the species *Amara bifrons* (*Am.bi*), *Amara erratica* (*Am.er*), *Cymindis vaporariorum* (*Cy.va*) and *Calathus erratus* (*Ca.er*), which are widely spread, only being absent in newly exposed terrain which was ice-free for less than 10 years (Table 1). The CCA model, however, does not fully reflect the strong correlations of *C. vaporariorum* and *C. erratus* to sites with high cover of mosses/lichens ($r = 0.61$ and $r = 0.71$, $P_s < 0.001$) and of *A. erratica* to high cover of small herbs/grasses ($r = 0.42$, $P < 0.05$). *Nebria jockischii* (*Ne.jo*), *Nebria picicornis* (*Ne.pi*) and *Bembidion bualei ssp. baenningeri* (*Be.bu*) were mainly restricted to younger pioneer habitats, as

Table 3 Age category of deglaciation as predictor variable for summarised mean yearly activity densities of carabid species 2007–2009

Analysis of variance table ^a	Sum Sq	df	Mean Sq	F-value	P
Intercept	1.85	1	1.85	14.12	0.001**
Sampling period (random)	1.85	4	0.46	5.40	0.002**
Age category of deglaciation (fix)	1.54	6	0.26	2.98	0.019*
Residuals	3.00	35	0.09		
General linear model table	Estimate β	P	95% confidence interval		
Intercept	0.91	0.000***			
1–20 years	−0.78	0.027*	−1.47	−0.10	
21–40 years	−0.35	0.369	−1.12	0.43	
41–60 years	−0.33	0.402	−1.11	0.46	
61–80 years	−0.76	0.057	−1.54	0.02	
81–120 years	−0.69	0.080	−1.46	0.09	
121–160 years	−0.61	0.137	−1.42	0.20	

One-way ANOVA with parameter estimates β of a General linear model (GLM), 4th-root-transformation of activity densities and sampling period as random factor (mixed-effects model). Reference sites outside the glacier foreland served as reference category for the estimates ($\beta = 0$)

^a $r^2 = 0.60$; $r_{adj}^2 = 0.49$

*** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$

Table 4 Age of deglaciation as predictor variable for carabid assemblage at species level on all sites 2007–2009 (categories 1–20, 21–40, 41–60, 61–80, 81–120, 121–160 years and reference)

	F-value	P	Tukey post hoc test (effect: age category of deglaciation)
Intercept	8.69	0.000***	
Age category of deglaciation	3.32	0.000***	
Carabid species (sampling period = random factor)			
<i>Amara quenseli</i>	11.98	0.000***	1–20 vs. reference** 21–40 vs. 1–20***, 41–60***, 61–80***, 81–120***, 121–160***, reference***
<i>Pterostichus unctulatus</i>	9.00	0.000***	reference vs. 1–20***, 21–40***, 41–60***, 61–80***, 81–120**
<i>Amara praetermissa</i>	7.56	0.000***	61–80 vs. reference* 81–120 vs. 1–20***, 21–40***, 41–60***, 61–80**, reference***
<i>Cymindis vaporariorum</i>	7.44	0.000***	21–40 vs. 1–20**, 61–80**, 81–120**, 121–160***, reference*** 41–60 vs. 121–160*, reference***
<i>Calathus micropterus</i>	7.24	0.000***	121–160 vs. 1–20**, 21–40*, 41–60* reference vs. 1–20***, 21–40**, 41–60*
<i>Calathus melanocephalus</i>	4.85	0.000***	41–60 vs. 1–20**, 61–80*, 81–120*, reference*** 121–160 vs. 1–20*, reference**
<i>Calathus erratus</i>	4.60	0.000***	21–40 vs. reference*** 41–60 vs. 1–20**, 61–80*, 81–120*, 121–160**, reference***
<i>Notiophilus aquaticus</i>	4.59	0.000***	121–160 vs. 1–20***, 21–40***, 41–60***, 61–80***, 81–120***, reference***
<i>Pterostichus jurinei</i>	3.62	0.001**	
<i>Amara lunicollis</i>	3.40	0.002**	
<i>Carabus depressus</i>	3.25	0.003**	21–40 vs. 1–20**, 41–60**, 61–80**, 81–120**, 121–160*, reference***
<i>Bembidion bualei ssp. baenn.</i>	3.12	0.004**	1–20 vs. 41–60*, 61–80*, reference**
<i>Trichotichnus laevicollis</i>	2.07	0.044*	
<i>Amara bifrons</i>	2.04	0.047*	
<i>Amara erratica</i>	1.89	0.067	
<i>Nebria picicornis</i>	1.35	0.234	
<i>Cicindela gallica</i>	1.29	0.265	
<i>Amara nigricornis</i>	1.09	0.406	
<i>Nebria jokischii</i>	0.95	0.528	
<i>Cicindela hybrida</i>	0.91	0.563	
<i>Nebria gyllenhali</i>	0.86	0.606	
<i>Leistus nitidus</i>	0.84	0.632	
<i>Pterostichus multipunctatus</i>	0.63	0.831	
<i>Notiophilus biguttatus</i>	0.52	0.910	

ANOVA table of a General linear model (GLM) with all species >4 individuals as dependent variables and sampling period as random factor (mixed-effects model). Activity densities of each species pooled for 2007–2009 and log (n + 1)-transformed. Tukey post hoc test with indication of significant pair-wise interactions between categories

***P < 0.001; **P < 0.01; *P < 0.05

affirmed by negative correlations to small herbs/grasses for *N. jokischii* (r = -0.38, P < 0.05), *N. picicornis* (r = -0.60, P < 0.001) and *B. bualei ssp. baenningeri* (r = -0.33, P = 0.07). These were primarily found on bare or only sparsely vegetation-covered moraines with a high cover of stones and/or gravel in the outwash plain. *Cicindela hybrida* (*Ci.hy*) was concentrated on sand-rich or

gravel-rich habitats in middle-aged (ca. 36–58 years, sites B5, B6, C1, C4 and C5) as well as on considerably older parts of the foreland (ca. 112 years, site E5 having by far the highest sand cover of all sites), which are still characterised by pioneer plant succession but with less stone cover (negative correlation of *C. hybrida* to stone cover r = -0.50, P < 0.01).

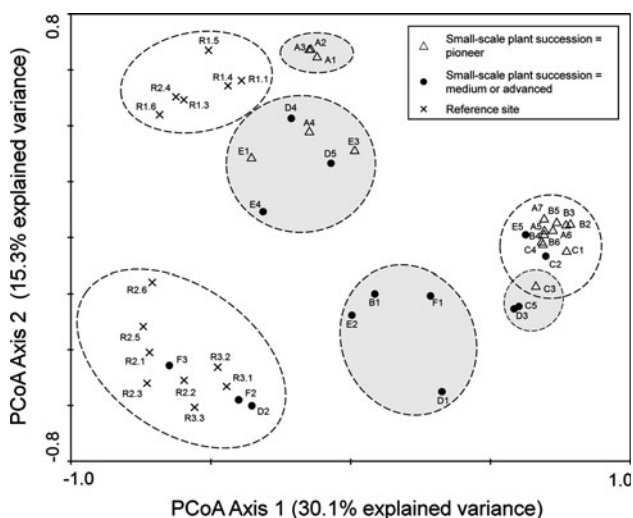


Fig. 4 Principal coordinate analysis PCoA, based on mean yearly activity densities of all carabid species on the glacier foreland Morteratsch with >4 individuals, each species pooled for 2007–2009. The PCoA-plot represents Bray-Curtis dissimilarities of $\log(n + 1)$ -transformed species data

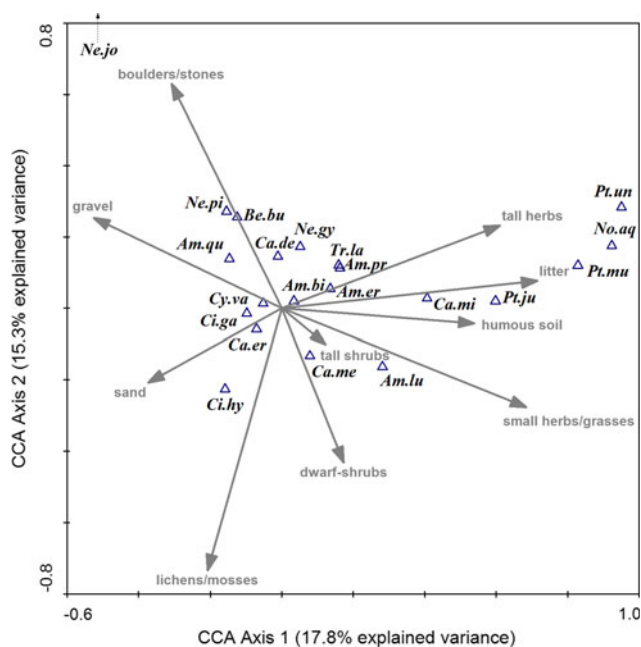


Fig. 5 Constrained ordination biplot of habitat factors and carabid species on the glacier foreland Morteratsch, using Canonical correspondence analysis (CCA). All constraining habitat factors and carabid species with >4 individuals, each species being pooled for 2007–2009 and subsequently $\log(n + 1)$ -transformed, are included in the model. Species names are abbreviated to the first two letters of their genus and their species names. *Nebria jockischii* (*Ne.jo*) proved to be an extreme outlier and was passively inserted into the figure a posteriori. Significance of canonical axis 1, $F = 4.13$ ($P < 0.01$); of all axes, $F = 2.21$ ($P < 0.01$)

Performing CCA with the same habitat factors (but here z-transformed) supplemented with “age of deglaciation” as environmental variable (also z-transformed), a Monte Carlo

permutation test yielded “age of deglaciation” as the main predictor for carabid assemblage. 21.8% of the canonical variance in the carabid dataset can be attributed to this variable ($F = 4.09$, $P < 0.01$), which is followed in the permutation ranking by tall herbs (additional variance explained = 12.9%, $F = 2.67$, $P < 0.05$), small herbs/grasses (additional variance explained = 10.2%, $F = 2.30$, $P < 0.05$), and tall shrubs (additional variance explained = 15.7%, $F = 4.12$, $P < 0.01$) as significant factors. Together the constrained factors explain 58.9% of the total variance in the data set (not displayed).

Discussion

Carabid species richness and pitfall sampling method

With a total of 33 observed carabid species (additional two species on the reference sites in the adjacent open forests), the Morteratsch study area is, to our knowledge, by far the most species-rich glacier foreland to have been investigated in the alpine region. Estimations of potential species richness, considering singletons and doubletons, even give values of up to 39 (± 5.2) species. In two sampling seasons (using 42 and 108 pitfall traps respectively), Gobbi et al. (2006a, 2007) detected a total of 23 carabid species on the Forni glacier foreland in the Ortles-Cevedale group (Italy; 2,150–2,500 m a.s.l.). In the same mountain massif, Gobbi et al. (2010) trapped 9 carabid species in one season on the high-altitude Cedec glacier foreland (2,634–2,726 m a.s.l.). Kaufmann (2001) found 9 carabid species on the Rotmoos glacier foreland in the Oetztal Alps (Austria; 2,280–2,450 m a.s.l.) in one season (70 pitfall traps), and Gereben (1995) 20 species on the Hornkees glacier foreland in the Zillertal Alps (Austria; ca. 1,875–2,150 m a.s.l., status altitude from 1988 according to Paulus and Paulus 1997) in two seasons (both 109 pitfall traps). Janetschek (1958) also collected carabid beetles on the Hornkees glacier foreland (1946 and 1949) and described 17 species. Samplings by Janetschek (1949) from 1937 and 1939 on the Hintereisferner glacier foreland in the Oetztal Alps (Austria; ca. 2,250–2,350 m a.s.l.) revealed 15 carabid species. Possible explanations of the high species richness in the study area are given below.

More than half of the carabid species found in our study were restricted to the glacier foreland. Only two species with a small number of individuals were present exclusively on the reference sites outside the foreland. As all the reference sites were situated in open forests and along forest edges, it cannot be ruled out that some of our foreland species might have migrated into nearby open grassland. Nevertheless, the assumption of distinct clusters separating “inside” from “outside”-carabid coenosis

Table 5 Canonical correspondence analysis (CCA) with contributions of habitat factors to the total of the explained variance (single and cumulative, ranking according to Monte Carlo permutation test)

Explained variance					
Habitat factor	Single	Cumulative	F-ratio	<i>P</i>	
Small herbs/grasses	0.26	0.26	3.23	0.010*	
Litter	0.19	0.45	2.54	0.044*	
Tall herbs	0.16	0.61	2.26	0.040*	
Lichens/mosses	0.14	0.75	1.92	0.078	
Sand	0.08	0.83	1.14	0.328	
Boulders/stones	0.07	0.90	1.01	0.416	
Gravel	0.09	0.99	1.30	0.226	
Tall shrubs	0.04	1.03	0.61	0.672	
Dwarf-shrubs	0.25	1.28	4.18	0.004**	
Humous soil	0.06	1.34	0.97	0.442	
Canonical axis			1	2	3
Canonical eigenvalues (sum of all axis = 1.342)			0.45	0.38	0.17
Explained variance of species data (%) (sum of all axis = 53.8%)			17.8	15.3	6.6
Eigenvalues (=‘total inertia’ = 2.496)			–	–	–

Only species >4 individuals are included and species data log ($n + 1$)-transformed. The canonical eigenvalues express the amount of variability of the species data-set explained by the corresponding CCA-axis. The constrained model explains 53.8% of the total variance in the data set

** $P < 0.01$; * $P < 0.05$

seems to be justified, especially as an ordination of Bray-Curtis site-dissimilarities in a Principal coordinate analysis confirmed these findings.

Pitfall-trapping is an effective, well established method of sampling ground-dwelling invertebrates (Southwood 1978), especially to compare habitats with different habitat structures (Samways et al. 2010). Anyway, it should be borne in mind that there will always be a bias towards actively moving species, e.g. hunting predators (Kaufmann 2004). Ottesen (1996) assumes excessive locomotory activity of carabid species in suboptimal habitats, stressing to find a way out for better surroundings. The sites predominantly visited by carabids in this study, however, seem to correspond well with the environmental requirements mentioned by Marggi (1992) and Luka et al. (2009). Only *Amara ingenua*, from which a single specimen was found on the glacier foreland, would not have been expected to occur. It is a rare species and has not been observed for 30 years in the eastern part of Switzerland (Luka et al. 2009), preferring to live in small areas with poriferous soil below 1,500 m a.s.l. (Marggi 1992). Lindroth (1974) describes *A. ingenua* as a synanthropic species.

Spatio-temporal analysis

By substituting space for time, increasing distance from the margin of a retreating glacier can be interpreted as a temporal sequence in ecosystem development (Matthews 1992). Such proglacial chronosequences are most appropriate for studying communities that follow convergent successional trajectories with low biodiversity, rapid species turnover and low disturbance (Walker et al. 2010). The chronosequence approach seems to be most suitable for

measuring relatively predictive characteristics such as plant cover and plant species richness. Gobbi et al. (2007) considered time since deglaciation to be the main force in determining habitat architecture on the Forni glacier foreland in Italy (primary effect). The strong relation between carabid assemblages and habitat type was interpreted as an indirect impact of site age (secondary effect). But carabid beetle species richness was not found to be influenced by environmental traits and habitat architecture (Gobbi et al. 2007). Many observers suggest, however, that an interpretation of the ecology of recently deglaciated terrain merely in terms of chronosequences is an oversimplification (Walker and Del Moral 2003; Johnson and Miyanishi 2008). Conditions along the foreland vary and colonisation from lateral vegetated areas could confound the succession process (Hodkinson et al. 2004). Moreover, vegetation maps of glacier forelands do not affirm time-dependent zonation but display a complex mosaic of communities, whereby the role of local ecological micro-niches seems to be crucial. This also applies to the vegetation on the Morteratsch glacier foreland (Burga 1999; Elsener 2006), on which Ziefle (2006) found a microhabitat-controlled plant succession scheme with different pathways, each starting with a different pioneer community but converging to a common mature vegetation type. The age of deglaciation did not prove to be a crucial factor for vegetation development. The water supply also appeared to determine plant succession on the Morteratsch glacier foreland, together with substrate porosity (Ziefle 2006).

In this study, a temporal approach was primarily used to demonstrate time-dependent patterns of variability in carabid species richness and activity densities. A steep increase in observed species richness and activity within

the first ca. 40 years of deglaciation was followed by a pronounced decline between ca. 40–80 years (observed species richness) and 40–90 years (species activity), showing a rebound towards the oldest parts of the foreland. The bimodal pattern proved to be significant in both cases, whereas the estimated species richness (ACE) stagnated between ca. 40–80 years. According to Matthews (1992), several investigations on deglaciated terrain have detected a peak in plant species richness early in succession followed by a decline. On the Rotmoos glacier foreland in Austria, species richness and abundance of surface-active invertebrates and, somewhat less conspicuously, vascular plants was characterised by an initial colonisation with a rapid increase over the first 50 years and subsequent development with only little increase. In line with our findings, the invertebrates on the Rotmoos glacier showed a distinct decrease in abundance in the period between 50 and 80 years, followed by a second increase towards the terminal moraine (Kaufmann and Raffl 2002). Sites which were ice-free between 61 and 78 years on the Forni glacier foreland did not show a substantial increase in carabid species richness, considered to be a result of the onset of species turnover (Gobbi et al. 2006a). A two-phase succession pattern with a steep increase over the first ca. 50 years, followed by a stagnation or temporal decrease in diversity, seems to be generally valid for vegetation developing towards both alpine grasslands and coniferous forests on glacier forelands (Kaufmann and Raffl 2002). As affirmed by Matthews (1999), glacier-dependent disturbance might be a key-factor in newly deglaciated habitats due to glacier winds, lower air-temperatures during the day (and elevation at night), and glaciofluvial disturbance by meltwater streams near the glacier snout. Such effects seem to be restricted to within 200 m of the snout of small valley glaciers (Matthews 1999). This corresponds with a terrain-belt deglaciated since 2001 on the Morteratsch glacier foreland (mean retreat of 208 m from 2001 to 2009 according to ETH Zurich 2010) to our sampling sites A1–A4. Indeed, these sites turned out to have a distinctive carabid assemblage with only 1–5 observed species and very low mean yearly activity densities (0.01–0.29). Somewhat older sites, e.g. sites A5–A7 at a distance of around 300–450 m from the glacier edge, already showed distinctly higher species richness (A5: 9; A6: 16; A7: 9) and mean yearly activity densities 2007–2009 (A5: 2.17; A6: 4.75; A7: 2.12). Accordingly, in Principal coordinate analysis, sites A1–A3 formed a distinct cluster, whereas sites A5–A7 were joined together with older B and C sites. There is evidence for glacier-dependent disturbance as a driving force because habitat factors (mainly texture of the surface) did not vary significantly among A sites. Two species, *Bembidion complanatum* and *Oreonebria castanea*, occurred exclusively, but only in low numbers, on sites A1–A4.

Both species are hygrophilous (Luka et al. 2009), which is unusual for many carabid species from glacier forelands, but perfectly suited to their glacier-near occurrence. All carabid species found on the youngest sites A1–A4 were predators (genus *Bembidion* and *Oreonebria/Nebria*). The first herbivorous species, *Amara erratica* and *Amara quenseli*, occurred on site A5 (ice-free since 1998). This is in line with the findings of Kaufmann (2001) and Hodkinson et al. (2001), who found almost exclusively predators and detritivores on newly exposed substrate. Interestingly, the obvious threshold between groups A1–A4 and A5–A7 was exactly in accordance with the first appearance of autotrophic pioneer plants (*Epilobietum fleischeri*) after around 7 years of deglaciation (Burga et al. 2010).

The age category of deglaciation proved to be a highly significant predictor for the spatial distribution of 9 carabid species (only species > 4 individuals considered). For instance, *Amara quenseli*, which had the highest discriminating F-value, clearly preferred sites which had been deglaciated for around 20–40 years, and was almost completely absent from other sites with comparable habitat characteristics. *A. quenseli* is described as a mesophilous, eurytopic, and mainly montane to alpine species from grasslands and snow pockets (Luka et al. 2009). Related spatio-temporal niche patterns were also occupied by *A. quenseli* on the Rotmoos glacier foreland, with a peak between ca. 35–45 years and a flattened peak around 25–30 years, even though still sporadically present in older parts (Kaufmann 2001). Older samplings by Janetschek (1949) on the Hintereisferner outwash plain revealed highest densities of *A. quenseli* on about 17–55 year old habitats, but also scattered findings next to the glacier snout and near terminal moraine. On the Forni glacier foreland, *A. quenseli* exclusively appeared on sites which had been ice-free for 24–52 years (Gobbi et al. 2007). *Bembidion bualei* ssp. *baenningeri* showed a similar spatio-temporal pattern as *A. quenseli*, but was also active in higher numbers proximate to the Morteratsch glacier edge. *B. bualei* was not present on the above-mentioned glacier forelands in Austria and Italy. *Carabus depressus*, a further time-dependent representative, also showed a distinct activity peak on 20 to 40 year old moraines, but was additionally scattered on slightly older parts of the Morteratsch glacier foreland. Surprisingly, not a single individual of *C. depressus* was pitfall-trapped in habitats more than 70 years old, not even on sites with comparable habitat architecture. Luka et al. (2009) describe *C. depressus* as a mesophilous and eurytopic, montane to alpine species with a preference for alpine grassland and coniferous forests. Open ground with low vegetation seems to be favoured (Marggi 1992). On the Forni glacier foreland, *C. depressus* was supplementarily present in areas which had been ice-free for 101–154 years (Gobbi et al. 2007), and on the Cedec

foreland (Gobbi et al. 2010) and the Hornkees foreland (Gereben 1995) even in parts older than 150 years.

The three species of the genus *Calathus* found on the Morteratsch glacier foreland also proved to be highly dependent on terrain age. *C. erratus* and *C. melanocephalus* lived almost exclusively on the glacier foreland, generally avoiding the reference sites, whereas *C. micropterus* clearly favoured the reference sites and the older sites within the foreland. On the Forni glacier foreland, *C. melanocephalus* and *C. micropterus* both appeared around 80 years after deglaciation, and *C. erratus* was not present (Gobbi et al. 2007).

Cymindis vaporariorum was found in a similar chronosequence range as *C. erratus* and *C. melanocephalus*, also avoiding the adjacent forests. On the Hintereisferner glacier foreland, this species exclusively occurred on 50–80 year old habitats in the outwash plain (Janetschek 1949), on the Cedec glacier foreland near the terminal moraine (ca. 150 years old) and behind it (Gobbi et al. 2010), and on the Forni glacier foreland on terrain which has been ice-free for between 51 and 155 years (Gobbi et al. 2007). On the Rotmoos glacier foreland, *C. vaporariorum* was already present on ca. 35 years old terrain, persisting towards the terminal moraine (Kaufmann 2001). *Notiophilus aquaticus* occurred on the Morteratsch glacier foreland only in low abundance on two sites near the terminal moraine (139 and 142 years). *Pterostichus unctulatus* favoured the open forests outside the foreland, but was also present in the older parts of the foreland (>90 years). On the Cedec foreland, *N. aquaticus* was present near the terminal moraine (ca. 150 years) and behind it (>150 years), and on the Forni foreland between ca. 50 and 80 years since deglaciation (Gobbi et al. 2007, 2010). On the Rotmoos foreland, *N. aquaticus* was found on sites only ca. 35 years old, but was present in older parts as well. *P. unctulatus* was only located on terrain ice-free for around 80 years on the Forni foreland, but absent in older parts (Gobbi et al. 2007).

Summing up the spatio-temporal impacts on carabid coenosis, terrain age proved to be a highly significant predictor for the distribution in general and for certain discriminant carabid species in particular. Thus, the community assembly can partly be seen as directional and predictable. The outcomes of the above-mentioned studies in further central European glacier forelands largely affirm our findings, also suggesting distinct carabid assemblages with characteristic species turnover along the chronosequence of deglaciation.

Succession and habitat structure with regard to carabid autecological aspects

Compared to many other glacier forelands in the European Alps, the study area is situated rather low (ca.

1,900–2,100 m a.s.l.) and well below the tree line, which at about 2,350 m a.s.l. is exceptionally high in the Upper Engadine valleys. Therefore, newly deglaciated terrain is close to well-vegetated areas and hence to propagules. Nevertheless, 150 years since glacier retreat the vegetation on the Morteratsch glacier foreland is still distinctly different to the close to climax stands just outside the terminal moraine of 1857. This holds true for the composition of the herb layer as well as for the stem numbers of larch trees (*Larix decidua*) and stone pine trees (*Pinus cembra*) (Elsener 2006).

The establishment of different species in primary succession can be determined by chance, by the state of the habitat, and by interactions between new species and those already present (Dobson et al. 1997). These processes are recognized in alternative models for the mechanism of succession of tolerance, facilitation (smoothing the way for certain species by amelioration of initial site conditions created by earlier colonists), and inhibition. Connell and Slatyer (1977) suggested the facilitation model was the most suitable for certain primary successions of plant communities. Mrzljak and Wiegleb (2000) advised against applying facilitation models for animal succession and proposed alternative models instead: (1) time as a decisive variable in explaining the variance of animal communities on sites with different ages (younger sites are expected to have fewer species than older ones), (2) habitat structure as a driving factor, early arriving animal species being replaced by later arriving species with similar habitat requirements (high animal species turnover, low spatial autocorrelation), and (3) habitat structure as a driving factor accompanied by dominant influence of initially arriving species, characterising all later phases of development (low animal species turnover, high spatial autocorrelation). Model (1) and time-related aspects of models (2) and (3) have been discussed above, suggesting chronosequence to be an essential factor. Because habitat age is considered to be a crucial variable in determining ecosystem functionality and processes in general (Bardgett et al. 2005), it can be assumed that temporal aspects may also be decisive for habitat structure in primary succession. Therefore, the time period since deglaciation might be seen as a primary effect, indirectly influencing carabid assemblage along the chronosequence by altering habitat factors (e.g. coverage of vegetation) as a secondary effect (Gobbi et al. 2007). Thus, time since deglaciation and expression of habitat structure cannot be viewed as being independent of one another. Evidence on the Morteratsch glacier foreland suggests that coverage of vegetation (small herbs/grasses, tall herbs) and litter are key habitat factors determining carabid assemblage. But overall, the constrained model in our study revealed only a modest impact of the pooled habitat factors, explaining around one third of the

variance in the carabid species dataset. By including age of deglaciation as a further factor in the model, constrained ordination explained almost 60% of the variance, age of deglaciation itself accounting for more than half of it. Though, among habitat factors small herbs/grasses, tall herbs and litter remained the most influential.

Sites with about the same habitat age of deglaciation but advanced small-scale plant succession tended to show slightly higher observed species richness and activity of carabids, which confirms that a restricted temporal framework approach is inadequate and that habitat structure needs to be considered. Gobbi et al. (2007) found that environmental variables did not affect species richness along the Forni glacier foreland. Analyses at species level, in contrast, revealed strong interactions in part, e.g. for *Amara quenseli* (stony, wet) and *Calathus micropterus*/*Pterostichus multipunctatus* (dry, old soils), which is in accordance with the findings of our study.

Summing up the influence of habitat traits on carabid species responses, there was no evidence of dispersal-stochasticity. Distinct clusters of sites with similar species composition and species-related activity densities were found, indicating a spatially structured distribution. Microhabitat suitability proved to be decisive as a secondary effect, however embedded in a temporal framework of primary succession as the main effect. Surface cover with litter, herbs and dwarf-shrubs were found to be the crucial habitat factors for the carabid colonisation process in general and for niche differentiation between certain species groups in particular.

Climate change, species conservation and biodiversity

The earliest stages of succession, characterised by poverty and openness of the habitat, help generate ecosystems rich in species sensitive to competition which cannot find living space in more developed ecosystems. On a small-scale level, particularly climate warming might trigger primary succession in early colonising assemblages straight in front of the glacier, diminishing bare areas for stenotopic ruderal species and enlarging habitat areas for eurytopic species and species preferring vegetated ground. This assumption also seems justified to Kaufmann (2002): colonisation of recently deglaciated terrain by invertebrates may constitute a process reacting sensitively to rising temperatures. Early colonising stages (<30 years) currently develop faster and intermediate successional stages (30–50 years old) more slowly than would be indicated by the long-term chronosequence pattern. The effects of disturbance in the immediate vicinity of the glacier edge would quickly fade away in front of a rapidly receding glacier, thus favouring the start of plant colonisation.

The reality of climate change with its severe implications for the distribution of many animal and plant species is supported by reports of latitudinal movements or altitudinal shifts of species from lowlands to higher altitudes (New 2010; Wilson et al. 2007). Kaufmann (2002) showed that an increase of 0.6° C in summer temperatures approximately doubled the speed of initial colonisation by invertebrates in an alpine glacier foreland.

Glacier forelands situated at lower altitudes below the timberline, as represented by this study, may feature unique habitats for pioneer species preferring ruderal terrain. Surrounded by grassland and coniferous forests, such barren or sparsely vegetated areas in the subalpine region can widen habitat diversity, which may be assumed to be paralleled by rising species richness. Especially stenotopic and xerophilous ruderal species, which are not (yet) adapted to permafrost or, generally, to very cold conditions in the alpine region, can therefore benefit from such habitats in subalpine glacier forelands. The high species richness found in this study might reflect this assumption, as many species' altitudinal ranges, according to Luka et al. (2009), do not go up to the alpine zone (e.g. *Amara eurynota* and *Amara ingenua*). Others favour subalpine or even lower regions such as the mainly coline species *Amara apricaria*, *Amara lunicollis* and *Cicindela hybrida*. *A. eurynota*, *A. apricaria* and *C. hybrida* are considered to be xerophilous pioneer species, *A. ingenua* a mesophilous pioneer species and *A. lunicollis* a mesophilous species from grasslands, borders and forest-edges (Luka et al. 2009). None of these five species are known from other European glacier forelands. In the long term, an upward shift of the Morteratsch glacier foreland due to climate warming could not only generate an upward shift of the timberline but also, as a probable scenario, be followed by a movement of carabids to higher altitudes. The exact consequences of such range shifts will vary, but community composition is likely to change (Mills 2007). It is not possible to make exact predictions, since the ability to actively change, or to adapt to changed climate parameters in situ, is generally not yet known for beetles. Upward shifts could be accompanied by local extinction of ecological specialists with little adaptive capability or ecological flexibility (New 2010). High-alpine species near the upper end of an altitudinal range, which eventually run out of habitable areas, might especially be affected by immigration pressure from below and may go extinct. As pointed out by Menéndez (2007), we need to be aware that climate warming can affect several aspects of the insect life-cycle, especially those directly controlled by energy variables such as the sum of mean degrees per day (accumulative temperature needed for development). Due to their life-history flexibility, slow-growing species which need low temperatures to induce diapause are believed to

be most susceptible to range contractions (Bale et al. 2002). This is especially valid for European mountains since most temperate insect species diapause during winter. Because range expansions and contractions are happening at different rates, distributional shifts will also affect biodiversity (Menéndez 2007). As stenotopic organisms are likely to be the most vulnerable (Williams et al. 2008), rare species with small adaptive capacities might be particularly threatened by climate change in alpine ecosystems in general, and in proglacial areas in particular. On the other hand, all organisms are expected to have some intrinsic capacity to adapt to changing conditions, and there is evidence that evolutionary adaptation has occurred in a variety of species over relatively short time spans, e.g. 5–30 years (Williams et al. 2008). In this context Gobbi et al. (2010) refer to *Oreonebria castanea* as an example of a eurytopic carabid species (Luka et al. 2009) which may respond to environmental change by variation in life-history traits (e.g. length of larval development) or by changing microhabitats to make use of small-scale microclimatic gradients. According to Samways et al. (2010), insects respond to microhabitat conditions more than to macroclimate changes, and might in this way be able to compensate for larger-scale warming, if available, by changing small-scale habitats. The microclimatic conditions under boulders and large stones are constant, with humidity of the hypolithic air near saturation (Mani 1968). Such pockets, sheltered from desiccating winds and intense insolation, might provide suitable refuge for hygrophilous and cold-stenotopic representatives of the carabid fauna in warming environments. Research of plant diversity affirms possible overestimation of habitat loss from climate warming, as many alpine species will find thermally suitable escape habitats within short distances due to the topographic variability of alpine landscapes (Scherrer and Körner 2010).

Summing up the possible consequences of climate warming on carabid coenosis in glacier forelands, higher population levels and range expansions are considered to be outweighed by negative impacts of habitat loss and altered ecosystem services. Active selection for cooler microhabitats might absorb the loss of some species which would otherwise go extinct locally as a consequence of climate warming. But, in general, this small-scale approach probably only affects the minority of carabid species and epigaic invertebrates, and it would be unwise to relax and rely on such adaptive capacities.

Acknowledgments We are grateful to everyone who helped with this research project. A. Kunz carried out field work in 2007. M. Bertschinger was responsible for fieldwork in 2009. The carabid specialist Dr. W. Marggi verified some uncertain determinations of the genus *Bembidion*, and Dr. F. Hieke some specimens of the genus *Amara*. M. Lussi Bell and N. Bell kindly helped with proofreading.

R. Ruf, M. Wernli, M. Wytttenbach and R. Rechsteiner made valuable comments on the manuscript. Thanks are also due to two anonymous reviewers who contributed substantial input. The study was generously supported by grants from the following private foundations: G. und B. Schwyzer-Winiker-Stiftung, M. und R. Gsell-Stiftung, K. Mayer-Stiftung.

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