Plant adaptive responses during primary succession are associated with functional adaptations in ground beetles on deglaciated terrain

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Abstract: Little is known of how changes in plant function may influence adaptive traits amongst animals further up the food chain. We addressed the hypothesis that shifts in plant functional traits are associated with the adaptive function of animal species which have an indirect trophic link. We compared community characteristics and functional traits of two trophically detached biotic groups (vascular plants and carabid beetles) along a primary succession on terrain at the Cedec glacier in the Alps, where deglaciation events following post-Little Ice Age climate warmings are marked by moraine ridges. Morphofunctional traits were recorded: canopy height (CH), leaf dry matter content (LDMC), leaf dry weight (LDW) and specific leaf area (SLA) (for plants) and the number of brachypterous, autumn-breeding and predator species, and average body length (for carabid beetles). We found that vegetation cover and plant species richness gradually increased throughout early succession, with an abrupt increase between 40 and 150 years after deglaciation. At the early stages of the succession plant traits were typical of ruderal species (high SLA, low CH, LDW) whilst a shift in traits towards stress-tolerance (low SLA) occurred >150 years. Carabid communities and traits changed alongside changes in plant species richness and cover, with late successional vegetation hosting larger, more diverse, less mobile carabid species with longer larval development. Thus, ruderal plant strategies are the main contributors during vegetation development, determining vegetation quantity, and probably have the greatest impact on changes in carabid assemblages by regulating resource availability. Plants then require greater stress-tolerance to survive in stable vegetation, which supports high carabid diversity. This suggests that different plant strategies may affect ground beetle communities via contrasting mechanisms: both quantities (biomass, species richness) and qualities (functional traits, adaptive strategies) should be taken into account during studies of plant-animal interactions within ecosystems.

Abbreviations: CH–Canopy height; LDMC–Leaf dry matter content; LDW–Leaf dry weight; SLA–Specific leaf area.

Introduction

Climate warming is known to have caused shifts in species ranges and distributions, and has enhanced extinction risks and altered the reproductive biology, phenology, fitness and population dynamics of many plant and animal species (McCarty 2001, Hickling et al. 2006, Parmesan 2006). Global change may also influence local species assemblages and species richness (Walther et al. 2002); different organisms appear to be migrating at different rates in response to climate change (Hickling et al. 2006) potentially breaking apart current species assemblages.

The effects of climate change on plant and animal communities may be investigated by studying the distribution of organisms along natural environmental gradients, particu-larly for situations in which climatic changes of low intensity induce the greatest shifts in distribution, such as along altitudinal/temperature gradients (Parmesan and Yohe 2003, Thomas et al. 2004, Ceriani et al. 2009). However, little is known about the various mechanisms of evolutionary and ecological adaptation to climate change (Bradshaw and Holzapfel 2006). Recently deglaciated terrain includes suitable spatial and temporal scales for understanding the nature of the relationships between animals, plants and abiotic components over decades or hundreds of years, with the timing of deglaciation events marked by moraine ridges (Matthews 1992, Ettema and Wardle 2002, Bardgett et al. 2005). Indeed, terrain freed by retreating glaciers, with a well-known chronology of glacial recession, is a relatively artefact-free system for the detailed study of primary succession triggered by climate warming (Matthews 1992, Bardgett et al. 2005).

Studies of the colonization of recently deglaciated alpine valleys have been conducted for plants (e.g., Burga 1999, Caccianiga and Andreis 2004, Caccianiga et al. 2006) and invertebrates (e.g., Hodkinson et al. 2004, Kaufmann 2001, Gobbi et al. 2006a). However, an integrated study of the dynamics of plant and animal communities has not been performed before, despite promising key insights into the mechanisms that govern these ecosystems. The small number of studies dealing with plant-arthropod interactions along glacier forelands that have been undertaken so far focus on direct trophic interactions (the plant-herbivore relationship) rather than effects on animals further up the food chain (Hodkinson et al. 1998, Kaufmann et al. 2002, Coulson et al. 2003).

There is a growing consensus that diversity in the functional traits of individual species is a key consequence of species diversity and species sensitivity to climate change (Williams et al. 2008) that may control ecosystem functioning (Diaz and Cabido 2001, Grime 2001, Moretti and Legg 2009). A functional approach has proved successful for the interpretation of vegetation dynamics on alpine glacier forelands (Caccianiga et al. 2006), as well as for the evaluation of the role of disturbance in augmenting biodiversity in alpine plant communities (Pierce et al. 2007). These studies focused on the identification of plant functional types (the suite of traits that form the adaptive strategy of the species) rather than variation in individual functional traits. On the other hand, arthropods are not categorized into functional types because a scheme of adaptive strategies for these species is not currently available (Kaufmann and Raffl 2002). Thus, if shifts in adaptive function in plants and arthropods are to be compared it must currently be done on the basis of general trends and directional shifts in the variation of individual traits along environmental gradients. Altered morphofunctional adaptation has been recorded for carabid beetles along successions of arthropods on glacier forelands (Gobbi et al. 2007), but it is not known to what extent this reflects changes

in the plant community. Studies investigating the effect of plant function on animal adaptations are extremely rare and, like plant-animal studies on glacier forelands, are restricted to herbivorous animals and not those further along the food chain (Hodgson 1993, Schaffers et al. 2008).

The goal of the present paper is the integrated study of plant and carabid beetle species assemblages along primary succession, following glacier retreat induced by recent climatic change. Our hypothesis is that carabids exhibit adaptive capacity along succession in step with changes in plant functional traits. We chose carabid beetles as study model for their well-known spatial distribution, richness and adaptation to the alpine environment (Brandmayr et al. 2003ab, Gobbi et al. 2007). Carabids exhibit three main feeding habits: predators, seeds eaters and omnivores (Lövei and Sunderland 1996) and thus within a species assemblage we can consider the predators as a meta-assemblage not directly trophically dependent on plants. Our aims were: (1) to compare the successional pathways of plant and carabid communities (in terms of species richness and number of individuals/plant ground cover), and (2) to quantify changes in a number of key functional and life-history traits of these groups throughout the succession, in order to verify whether directional changes in these traits occur from pioneer to late-successional stages, and whether they occur synchronously in plants and carabid beetles higher up the food chain.

Material and methods

Study area

Fieldwork was performed on the Cedec glacier foreland (46°27'N, 10°35'E; Fig. 1). The Cedec glacier is located in the Ortles-Cevedale group (Sondrio, central/eastern Italian Alps) on the western slope of Mount Cevedale (3757 m a.s.l.) with a surface of approximately 2.4 km^2. Its terminus is di-

Figure 1. The study area – the Cedec glacier foreland in the Ortles-Cevedale group (Sondrio, Italian Alps (the location of the study area in northern Italy is shown inset, top left). White dotted circles represent points along the transect; black circles represent the three randomly-assigned replicate plant species sampling quadrats at each point along the transect. Labels indicate the age of the moraines for which either the precise date or "L.I.A" (Little Ice Age; i.e., ca. 150 years old) is shown.
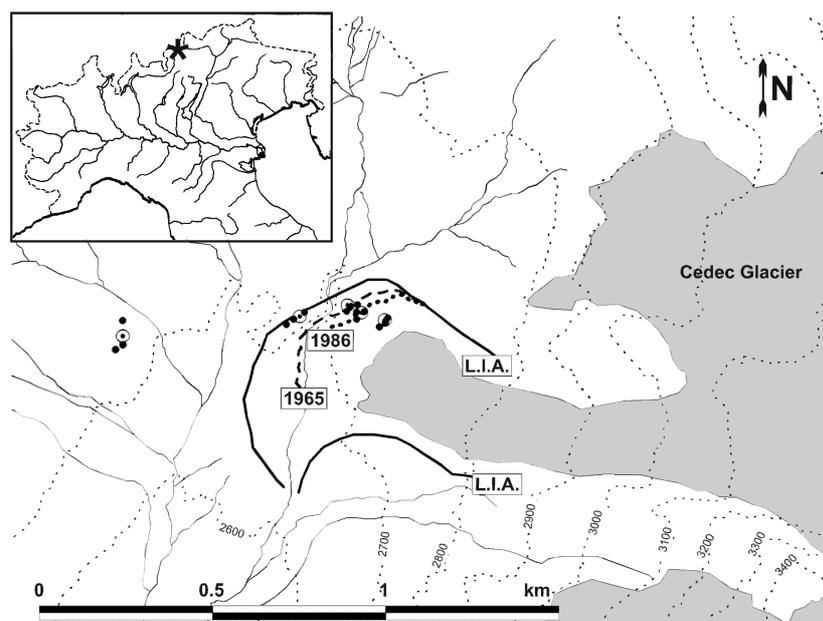
vided into two lobes, the southernmost of which is named Vedretta del Pasquale and extends down to an altitude of 2726 m a.s.l. (Fig. 1). Three main moraines were deposited in front of the southern lobe following Holocene advances: during the Little Ice Age (L.I.A.; ca. 1850), in 1965 and in 1986. Moraines associated with the northern lobe were not taken into account during the present study, as their dating and delimitation are uncertain. The glacier foreland consists of siliceous deposits, but limestone sediments may occur locally, especially near to the glacier meltwater streams originating from the nearby dolomitic Mount Gran Zebrù. The area is characterized by a continental climate with low precipitation concentrated during summer, showing only a slight increase in precipitation with altitude (the nearest weather stations are at Bormio: 802 mm year^{-1} at 1225 m a.s.l.; and at Santa Caterina: 885 mm year^{-1} at 1740 m a.s.l.).

Survey design

Five sampling points were positioned along a transect covering the entire proglacial area from the glacier terminus to the areas untouched by Holocene glacier advances (Late Glacial substrata), between 2694 and 2726 m a.s.l. The transect included terrain adjacent the glacial front, recent and stabilized moraines, and Late Glacial substrata. Each point corresponded with a known substratum age, i.e., <20, 20, 40, 150 years and Late Glacial. To perform the analyses we defined the age of Late Glacial substrata (which are potentially up to 10 000 years old, although the precise date is not available) as >150 years. The age classes of the sampling points are uneven because of the timing of glacial retreats and advances. Vascular plant and carabid beetle sampling was performed at each point. Sampling was replicated at each sampling point as explained under the following subheadings.

Sampling and analysis of vascular plants

At each sampling point the vegetation was recorded for three randomly assigned quadrats of 25 m^2 during the flowering period July-August 2005. The total percentage cover of vegetation was also recorded. Vascular plants were identified following Pignatti (1982) and Aeschimann et al. (2004). Nomenclature follows Pignatti (1982). For each species, canopy height (CH), leaf dry weight (LDW), leaf dry matter content (LDMC) and specific leaf area (SLA) were determined for six replicate, fully developed individuals. These traits were chosen as they represent the fundamental trade-off between rapid acquisition and conservation of resources (Diaz et al. 2004); these traits are also key indicators of the overall adaptive strategy of plants (Hodgson et al. 1999). Canopy height was measured in the field, the other traits on leaf material collected from the field and transported immediately to the laboratory; leaf material was stored at 4°C for transport, and remained chilled overnight over moistened tissue paper, enclosed in aluminium foil. The following day leaves were blotted free of surface water; leaf area was then measured using a digital leaf area meter (Delta-T Image Analysis System; Delta-T Devices Co. Ltd., Burwell, Cambridgeshire, UK),

followed by drying for 24 h at 105°C in a forced-air oven, after which leaf dry weight was determined. The mean value for each trait was calculated for each quadrat.

Sampling and analysis of carabid beetles

Carabid beetles were collected during the snow free period July – September 2007 using 30 pitfall traps located along transects of six traps, 10 m distant from each other, for each sampling point and collected and reset every 20 days. Pitfall trapping is a standard method for sampling ground dwelling arthropods, able to define the species richness and activity density in a habitat (Southwood 1978). Pitfalls used in this study consisted of plastic containers (7 cm diameter) baited with a saturated mixture of wine-vinegar and salt (Brandmayr et al. 2005). Traps were covered with stones to protect them from marmot activity and rain. Carabid beetles were identified to the species level following Porta (1923-1934) and Hürka (1996); nomenclature follows Vigna Taglianti (2007).

Wing morphology, phenology, diet and body length are key adaptive traits for insects that colonize glacier forelands (Brandmayr 1983, Brandmayr and Zetto Brandmayr 1986, Sota 1994, 1996, Gobbi et al. 2007). Wing morphology was determined according to Brandmayr (1991), and included the presence/absence of visible wings and, if visible, the length of functional surfaces (metathoracic alae). This parameter was expressed as the number of brachypterous (short winged) species for each trap. Body length was measured for each individual considering the distance from the margin of labrum to the apex of the elitrae and was expressed as average body length of each species. Diet was expressed as the number of predatory species found in each trap. Phenology was expressed as the number of autumn-breeding species (species with a phenology including overwintering larvae). Information about feeding habits and phenology was taken from Brandmayr and Zetto Brandmayr (1986) and Brandmayr et al. (2005).

Statistical analyses

We aimed to discern directional variation in traits for both plant and carabid assemblages along the chronosequence. Our steps were: (i) to check whether the morphofunctional traits measured (CH, LDMC, LDW and SLA for plants; wing morphology, body length, diet and phenology for carabid beetles) for each assemblage were correlated with each other, (ii) to reduce the number of variables to be analysed by applying a Principal Components Analysis (PCA) to the variables that were found to be highly correlated ($p \leq 0.001$), (iii) to check the correlation between the PCA axis and remaining variables, (iv) to check, using General Linear Model (GLM), the effect of soil deglaciation time (our independent and categorical variable) on assemblage attributes (Gotelli and Ellison 2004), and (v) to evaluate using ANOVA the influence of time since deglaciation on the intra-specific body length of the carabid species sampled. Tukey's Post Hoc test of Honestly Significant Differences

(HSD) (Crawley 2002) was used to disentangle all differences along the chronosequence.

The same steps (i) to (iv) were performed for plant and carabid assemblage traits, i.e., species richness and proportion of ground cover for plants, and number of individuals for carabid beetles. We used the following software packages to perform the analyses: Excel (Microsoft Corporation, Redmond, WA, USA), SPSS (SPSS Inc., Chicago, IL, USA) and MSVP 3.13o (Kovach Computing services, Pentraeth, Anglesey, Wales).

Results

Vascular plants

A total of fifty-five vascular plant species were found along the chronosequence **(Appendix)**. Seven species (*Arabis coerulea, Antennaria carpathica, Deschampsia caespitosa, Potentilla frigida, Pulsatilla vernalis, Salix helvetica,* and *Salix foetida*) were rare and analyses of morphofunctional traits for these species could not be performed, as not enough replicate individuals were available. Both vegetation cover and the number of species were significantly influenced by time since deglaciation (Wilks' Lambda = 0.043, $p < 0.0001$); vegetation cover increased gradually until 150 years after deglaciation, with a steeper increase between 40 and 150 years, and showed a stepwise increase between 150 years and Late Glacial substrata. Species number showed a similar trend, but with a sharper increase between 40 and 150 years and a more gradual increase between 150 years and Late Glacial (Fig. 2, Table 1). Indeed, vegetation cover and the number of species were highly correlated (Spearman's $\rho = 0.884$; $p < 0.0001$).

Canopy height and LDW were highly correlated ($p = 0.001$) (Table 2). These variables were merged using PCA; axis 1 of the PCA accounted for 85% of variability and was highly significantly correlated with both original variables (Spearman's $\rho = 0.986$ and 0.804, respectively; $p < 0.0001$). Its correlation was lower or absent with the remaining variables LDMC and SLA (Spearman's $\rho = 0.618$, $p = 0.014$ and $\rho = 0.004$, $p = 0.990$, respectively).

The influence of time since deglaciation on the three remaining variables (LDMC, SLA and PCA axis 1) was found to be significant (GLM test: Wilks' Lambda = 0.009, $p < 0.0001$) for SLA and LDMC. SLA significantly decreased with increasing age ($p = 0.0016$), LDMC increased ($p < 0.0001$) while PCA axis 1 was not significantly influenced ($p = 0.184$). LDMC increased gradually between 20 and 150 years after deglaciation and a stepwise increase between moraines at 150 years and Late Glacial substrata; SLA decreased significantly only at the last step of the succession (Tukey's HSD test; $p = 0.017$).

Carabid beetles

A total of nine carabid beetle species and 343 specimens were found along the chronosequence (Table 3). The number

Table 1. Homogeneous subsets given by Tukey's HSD test on plant morphofunctional data. The means within a subset are not significantly different from each other. Alpha indicates type I error rate, i.e., the probability of incorrectly rejecting a true statistical null hypothesis.

SLA (mm² mg⁻¹)

Time since deglaciation (years)	N	Subset for alpha=.05	
		1	2
<20	3	16.721	
20	3	16.758	
40	3	16.931	
150	3	17.294	
>150	3		13.804
Significance		0.962	1.000

LDMC (%)

Time since deglaciation (years)	N	Subset for alpha=.05		
		1	2	3
<20	3	19.959		
20	3	20.166		
40	3	21.443	21.443	
150	3		22.944	
>150	3			27.161
Significance		0.085	0.080	1.000

Axis 1 PCA (85%)

Time since deglaciation (years)	N	Subset for alpha=.05
		1
<20	3	-3.123
20	3	-2.265
40	3	-1.297
150	3	1.035
>150	3	5.651
Significance		0.181

Vegetation cover (%)

Time since deglaciation (years)	N	Subset for alpha=.05		
		1	2	3
<20	3	10.000		
20	3	15.000		
40	3	20.000	20.000	
150	3		41.667	
>150	3			90.000
Significance		0.642	0.075	1.000

Number of species

Time since deglaciation (years)	N	Subset for alpha=.05	
		1	2
<20	3	11.000	
20	3	11.000	
40	3	11.667	
150	3	17.333	17.333
>150	3		21.667
Significance		0.066	0.279

Table 2. Correlation coefficients (Spearman's rho) between plant (top) and carabid beetle (bottom) morphofunctional traits. * = $p \leq 0.05$. ** = $p \leq 0.01$. *** = $p \leq 0.001$

Spearman's rho	CH	LDMC	LDW	SLA
CH	1.000	0.629*	0.761***	0.021
LDMC		1.000	0.279	-0.357
LDW			1.000	0.404
SLA				1.000

Spearman's rho	Wing morphology	Phenology	Diet	Body length
Wing morphology	1.000	0.534***	0.876***	0.411*
Phenology		1.000	0.608***	-0.001
Diet			1.000	0.539**
Body length				1.000

of individuals and number of species increased significantly with time since deglaciation (Wilks' Lambda = 0.086, $p < 0.0001$); the number of individuals increased most rapidly between 40 and 150 years and decreased strongly in Late Glacial substrata. Species number exhibited a stepwise increase (with mean values from 1.2 to 4.8 species per site) between 40 and 150 years (Fig. 3, Table 4). The number of individuals and number of species were highly correlated (Spearman's $\rho = 0.718$; $p < 0.0001$).
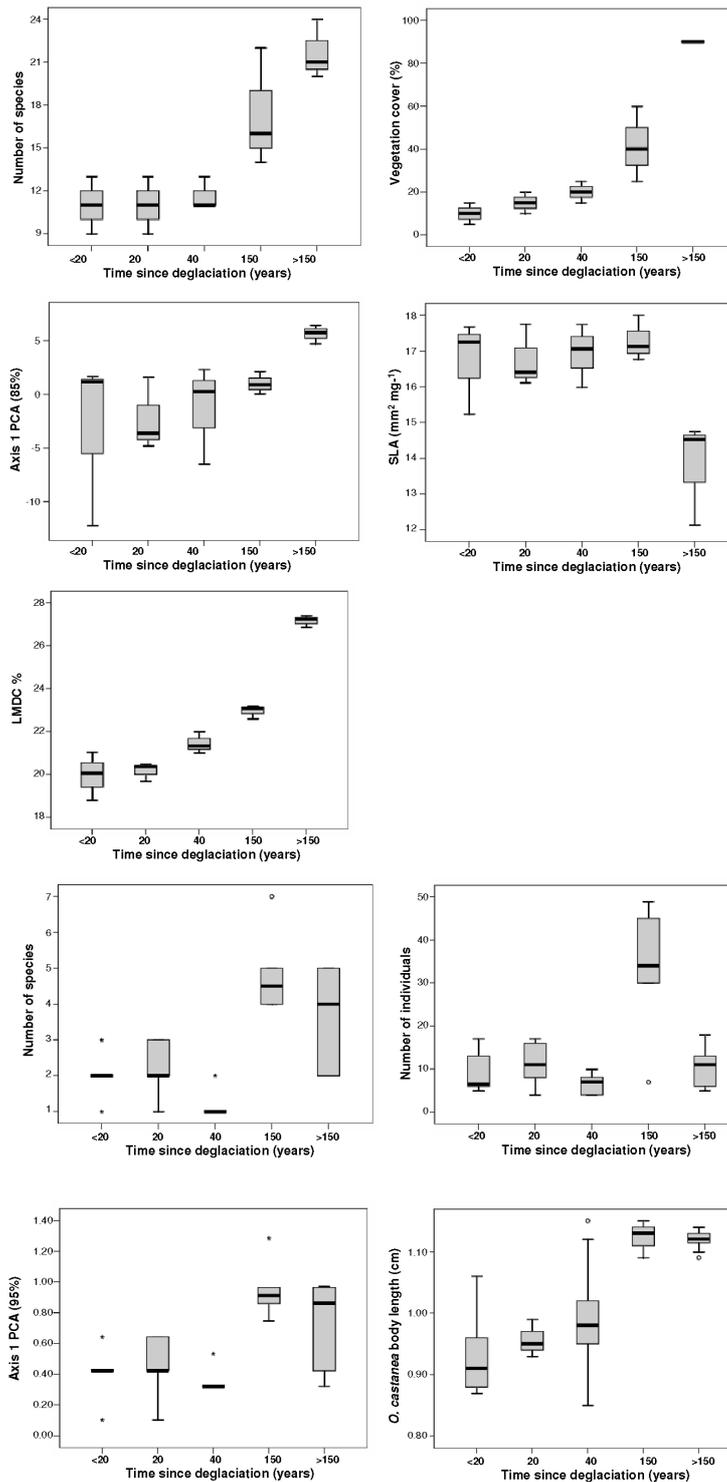
Figure 2. Box plots of the values of the measured traits of vascular plants throughout the succession; axis 1 PCA represents the correlated traits canopy height and leaf dry weight. Boxes represent the interquartile range (Hspread); the median is the horizontal line in the box; the lines extend from the lowest to the highest value within 1.5 Hspread from the end of the box. Circles represent outliers (values between 1.5 and 3 Hspread). Asterisks represent extreme cases (values above 3 Hspread).

Figure 3. Box plots of the values of the measured traits of carabid beetles throughout the succession; axis 1 PCA represents the correlated traits number of brachypterous, number of predators and number of autumn-breeder species. Boxes represent the interquartile range (Hspread); the median is the horizontal line in the box; the lines extend from the lowest to the highest value within 1.5 Hspread from the end of the box. Circles represent outliers (values between 1.5 and 3 Hspread). Asterisks represent extreme cases (values above 3 Hspread).

A number of carabid morphofunctional traits were significantly correlated ($p \leq 0.001$), including the number of brachypterous, predator and autumn-breeding species, although average body length and phenology were not correlated (Table 2). When the data for the number of brachypterous, predator and autumn-breeding species were merged into a single variable, applying PCA, PCA axis 1 explained 95% of the variance, was positively correlated with the original variables and was not correlated with mean body length for each assemblage at each site (Spearman's $\rho = 0.343$, $p = 0.063$).

When the influence of time since deglaciation on these two uncorrelated variables was tested (GLM test: Wilks' Lambda = 0.269, $p < 0.0001$) it was found that the mean body length of each assemblage per site did not change over time ($p = 0.608$), whilst PCA axis 1 (the number of predators,

Table 3. Carabid beetle species recorded at each sampling point.

Species	Time since deglaciation (years)	<20	20	40	150	>150
	Altitude (m a.s.l.)	2700	2700	2704	2710	2634
Amara (Paracelia) quenseli (Schönherr 1806)		+	+	-	+	-
Nebria (Eunebria) jockischii jockischii Sturm 1815		-	-	+	-	-
Amara (Celia) praetermissa (C.R. Sahlberg 1827)		-	-	-	+	-
Notiophilus aquaticus (Linnaeus 1758)		-	-	-	+	+
Amara (Celia) erratica (Duftschmid 1812)		-	-	-	+	+
Cymindis (Tarulus) vaporariorum (Linnaeus 1758)		-	-	-	+	+
Carabus (Platycarabus) depressus Bonelli 1810		-	-	-	-	+
Oreonebria (Oreonebria) castanea (Bonelli 1810)		+	+	+	+	+
Carabus (Orinocarabus) sylvestris Panzer 1793		+	+	-	+	+

Table 4. Homogeneous subsets given by Tukey's HSD test on carabid beetle data. The means within a subset are not significantly different from each other. Alpha indicates type I error rate, i.e., the probability of incorrectly rejecting a true statistical null hypothesis.

Axis 1 PCA (95%)

Time since deglaciation (years)	N	Subset for alpha= .05		
		1	2	3
40	6	0.357		
<20	6	0.409	0.409	
20	6	0.445	0.445	
>150	6		0.735	0.735
150	6			0.948
Significance		0.936	0.056	0.354

Number of species

Time since deglaciation (years)	N	Subset for alpha = .05		
		1	2	3
<20	6	2.000		
40	6	1.167		
20	6	2.167	2.167	
>150	6		3.667	3.667
150	6			4.833
Significance		0.367	0.070	0.227

Number of individuals

Time since deglaciation (years)	N	Subset for alpha = .05	
		1	2
<20	6	9.000	
20	6	11.167	
40	6	6.667	
>150	6	10.667	
150	6		33.167
Significance		0.845	1.000

O. castanea body length (cm)

Time since deglaciation (years)	N	Subset for alpha = .05		
		1	2	3
<20	12			1.119
20	17			1.125
40	21		0.990	
150	9	0.957	0.957	
>150	13	0.928		
Significance		0.584	0.460	0.999

brachypterous and autumn-breeding species) increased with time. The homogeneous subsets displayed by Tukey's HSD test demonstrated that the effect of time since deglaciation on predators, brachypterous and autumn-breeding species exhibited a stepwise increase between 40 and 150 yr since glacier retreat: Tukey's test showed the presence of two groups, the first between 5 and 40 yr since glacier retreat, where there were no changes in the PCA score ($p = 0.936$), and the second after 150yr since glacier retreat ($p = 0.354$) (Fig. 3).

Oreonebria castanea was the only species recorded at every point along the transect, with a total number of 103 specimens. The most numerous specimens were female (n = 72). Body length measured for these individuals exhibited a highly significant positive relationship with time since deglaciation (ANOVA test: $F_{2,71} = 27.54$, $p < 0.0001$). Mean body length increased along the chronosequence between 40

and 150 yr, with a strong variation between 40 and 150 yr, but did not change after 150 yr since deglaciation. Tukey's test confirmed the presence of a strong stepwise increase between 40 and 150 yr ($p < 0.0001$) and of one homogeneous subset in the sites older than 150 yr ($p = 0.998$) (Fig. 3, Table 4).

Discussion

As the primary succession progressed plant species with delicate leaves (high SLA, low LDMC) typical of rapidly growing species were replaced by species with dense leaves, typical of "conservative/retentive" strategies and low relative growth rates (Diaz et al. 2004). Plant above-ground dimensions (considered significant indicators of plant competitive capability: Weiher et al. 1999) and thus ability to monopolise resources and compete did not vary significantly throughout the succession. Indeed, disturbance and stress are more important selection pressures than competition for plants growing on alpine glacier forelands (Caccianiga et al. 2006). These successional changes occurred in two main steps. Between 40 and 150 years after deglaciation the number of species and vegetation cover increased markedly, but average SLA did not change and LDMC increased only slightly. Thus this first step probably coincided with an overall increase in productivity at the community level, rather than changes in plant function. The late-successional assemblage was similar in terms of the number of species and final vegetation cover, but had a significantly different functional profile, being dominated by slow-growing (low SLA and therefore stress-tolerant) species. Although the precise time since deglaciation is unknown for this point (i.e., >150 years), the data reveal that fast-growing ruderal species preside over the process of colonisation and succession *per se*, but when the succession reaches its climax (with stable, well-developed vegetation) plants require greater stress tolerance and less colonising ability in order to survive. This agrees with the predominantly ruderal (early succession) to stress-tolerant (late succession) gradient determined at another glacier foreland site by Caccianiga et al. (2006) (see also Chapin et al. 1994), but suggests that the succession can effectively be considered in two parts dominated by contrasting plant adaptations: the developing succession and the developed (climax) vegetation.

Changes in carabid assemblages and functional attributes followed a similar pattern, with major assemblages and trait differences apparent between developing and climax vegetation. The number of species, the number of specimens, the

frequency of brachypterous, autumn-breeding and predator species increased abruptly between 40 and 150 years after deglaciation. This step coincided with that observed for plant community-level traits (i.e., vegetation cover and plant species number) and probably marks the boundary between different micro-habitats, suggesting the presence of a threshold effect (Hugget 2005). Brachypterous species are characteristic of stable habitats (Gobbi et al. 2007) as species that can only colonize new areas by walking are the first to disappear following disturbance (Brandmayr 1991). As a result these animals are poorly represented in early and mid-successional stages, as they require habitats that have remained suitable for a long period. The greater frequency of autumn breeders in the oldest successional stages confirms that the species with late summer or autumn egg deposition and with winter larval development also require more stable habitats than spring breeders because of their longer developmental times (Sota 1996, Brandmayr et al. 2005). Spring breeders are favoured in the early successional stages due to the short season that induces fast larval development (Sota 1996). The greater frequency of predatory species in sites deglaciated for more than 150 years is probably linked with the higher trophic availability (foraging success) provided by the highest values of vegetation cover, that could support greater prey abundances (e.g., springtails, snails, aphids and worms). Thus, the extent of stability and vegetation determined by ruderal plant species cover play a major role in determining the carabid assemblage.

The body length of *O. castanea* increased with increasing distance from the glacier and showed an abrupt increase between 40 and 150 years since glacier retreat. *O. castanea* is a cold stenotherm, univoltine and brachypterous species adapted to cold and wet habitats such as alpine grasslands, glacier forelands and glacier surfaces (Gereben 1995, Gobbi et al. 2007) and both larvae and adults feed on small insects living within the vegetation or arriving as aeroplankton (Brandmayr and Zetto Brandmayr 1988). Insect body length is negatively correlated with elevation and habitat disturbance (Blake et al. 1994, Magura et al. 2006) but positively with the speed of larval development (Peters 1983, Sustek 1987, Stearns 1992, Blake et al. 1994). The observed change in this trait is probably also linked to prey availability and delayed larval development. In early successional stages, where vegetation cover is scarce or absent, only aeroplankton is available (Antor 1994, Hodkinson et al. 2002); in the late successional stages habitat maturity and stability allow longer larval development (Blake et al., 1994) whilst the higher trophic availability allows greater foraging rates; the action of these two effects can explain the larger specimens recorded in the late succession.

In summary, the hypothesis of a simple, direct link between plant and carabid functional changes is not supported by our data because the functional composition of the vegetation is not the only vegetation characteristic that influences carabid assemblage: beetle survival strategies depend more on the extent of vegetation cover and plant biodiversity during early to mid succession. However, both plant and carabid

beetle traits probably vary throughout the succession following a resource availability and disturbance/stability gradient that can essentially be divided into two stages characterised by contrasting plant functional adaptations: the succession and the climax community. Ruderal plant communities in the developing succession are variable in terms of vegetation cover and biodiversity, and also in the extent to which they can support carabid biodiversity, whereas stable, highly diverse, stress-tolerant vegetation in late succession allows high carabid richness, greater size and longer development. Thus, different plant strategies may ultimately have different ways of affecting carabid assemblages via changes in the quantity and quality of vegetation. For both plants and carabids, the shift in community/assemblage traits is achieved through a change in species composition rather than through species-specific plasticity. However, according to the definition of adaptive capacity reported by Williams et al. (2008), *Oreonebria castanea* is an example of one species that may respond to environmental changes through adaptive capacity and therefore via the variation of certain life history traits (e.g., length of larval development) in order to face the different challenges of each successional stage. This strategy of inherent plasticity appears to be infrequent, as few ubiquitous plant or carabid species occur along the entire succession.

This study demonstrates that it is possible to compare plants and animals on the basis of a non-taxonomical, functional approach (i.e., species traits). It also highlights the need for monitoring programmes to investigate a wide spectrum of organisms in order to improve understanding of the interaction between biotic components of the ecosystem and the effects of climate change. Diaz and Cabido (2001) and Kaufmann and Raffl (2002) suggest that analyses at the species, functional group and diversity levels represent a promising field for the understanding of ecosystem functioning. Our study confirms this assumption, and also highlights the life history traits that are predicted to promote community resilience to environmental change triggered by climate warming.

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Appendix. Vascular plant species recorded at each sampling site. The file may be downloaded from the web site of the publisher at www.akademiai.com.