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Initial Colonization of New Terrain in an Alpine Glacier Foreland by Carabid Beetles (Carabidae, Coleoptera)

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Abstract

The melting of glaciers in the European Alps has exposed new terrain in the last decades. Ground beetles (Carabidae, Coleoptera) are among the first colonizers of this new alpine land. Since 1999, we have studied the ground beetle assemblages of the recently deglaciated areas in the Hornkees glacier foreland (Zillertal Alps, Austria). Data were collected in July 1999, 2001, 2007, and 2009. Two species of Carabidae, *Nebria jockischii* and *Nebria germari*, were dominant in the areas immediately below the glacier in all sampling periods. The occurrence of *Nebria jockischii* larvae very close to the edge of the glacier strongly suggests that reproduction occurred in the area which had been ice-free for only one year. Comparison of the carabid beetle assemblages from the recently deglaciated areas with those from neighboring and longer exposed areas indicates that the first colonizers continuously expanded their range following the path of the glacial retreat. We hypothesize that *Nebria jockischii* populated the new alpine terrain by initial migration from the banks of the glacial stream, whereas *Nebria germari* probably colonized the recently deglaciated area by migration from the lateral moraines. These carabid beetles represent the first predatory insects in the initial phase of colonization of the Hornkees foreland.

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Introduction

The formation of alpine landscape is intertwined with the historical events of glaciation. The advance of glaciers in the European Alps in historical times reached a peak at the close of the "Little Ice Age," circa 1850. Since then, glacier retreat has been predominant and interrupted only by short periods of advance. As a result, a considerable amount of land has been exposed. The expanding terrain of the glacial foreland offers an ideal opportunity to investigate the succession of the primary communities of plants and animals in natural terrestrial habitats (Matthews, 1992; Hodkinson et al., 2002; Bardgett et al., 2005). The colonization of the glacier foreland by arthropods has traditionally been described using a chronosequence approach (e. g., Kaufmann, 2001; Hodkinson et al., 2004; Kaufmann et al., 2002; Gobbi et al., 2006, 2007; Johnson and Miyanishi, 2008).

Investigations on the colonization of new land in the Hornkees glacier foreland in the Zillertal Alps began more than 60 years ago (Janetschek, 1958). The last period of advance of the Hornkees glacier ended in 1989 and resulted in the production of a conspicuous terminal moraine. Since then, the Hornkees glacier has steadily melted exposing new terrain (Fig. 1). Studies on the distribution pattern and the microhabitats of carabid beetles were carried out in the 1980s (Gereben, 1994, 1995). They showed that particular ground beetle assemblages occur in different areas of the Hornkees glacier foreland, each characterized by distinct geomorphic and ecological conditions. Syntopic species exhibit similar morphological, behavioral, and physiological characters that are presumed to match the environmental conditions and factors of the habitat and microhabitat, such as vegetation cover, instability, moisture, substrate structure, and stone cover. Previous studies in other alpine forelands (Janetschek, 1949; Kaufmann, 2001; Kaufmann and Juen, 2001; Gobbi et al., 2007) showed also that carabids of the genera *Nebria* and *Oreonebria* were the most abundant predatory insects in such pioneer communities. The present research in the Hornkees glacier foreland utilizes these results as a background to focus on reconstruction of the initial phase of colonization events occurring over the first 20 years following deglaciation by comparing the carabid beetle assemblages in the newly exposed terrain to neighboring areas, which were deglaciated decades ago. Further, the study addresses the capability for colonization of the various carabid beetles to infer the underlying mechanisms of colonization.

Methods and Study Area

The study was carried out in the Hornkees glacier foreland in the Zillertal Alps, Austria. The valley of the glacier foreland extends in a north-south orientation and becomes progressively steeper toward the glacier (Fig. 1). From 1990 to July 2009, the glacier retreated about 430 m, from 2085 m above sea level (a.s.l.) (47°00′54.8″N, 11°49′10.4″E) to 2188 m a.s.l. (47°00′41.8″N, 11°49′15.9″E). The area which has been deglaciated after 1990 is referred to here as "new terrain" (Fig. 1). It is delimited in the north by the conspicuous terminal moraine produced by the last glacier advance in the winter 1989/1990 (Patzelt, 1990) and in the east by a lateral moraine (Fig. 2). The west side is inaccessible due to step rocks and the danger of rock fall.

The new terrain was divided into four areas (sites A–D). In each of the four sampling periods, the newly formed site next to the retreating glacier was assessed (Fig. 2). The glacier retreated about 100 m from 1990 to 1999 and left an exposed area of roughly 0.75 ha according to the annual glacier reports published

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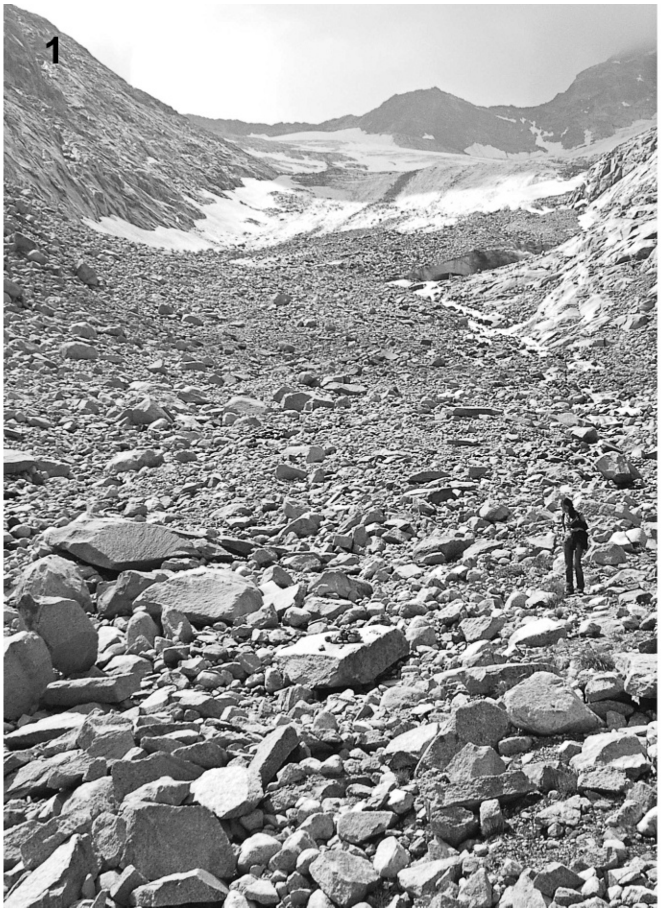

FIGURE 1. Newly exposed terrain of the Hornkees glacier foreland (Zillertal Alps, Austria) (47°00′41.8″N, 11°49′15.9″E) which has been deglaciated since 1990. View from the terminal moraine of the last glacier advance (1989) to the glacier in July 2007.

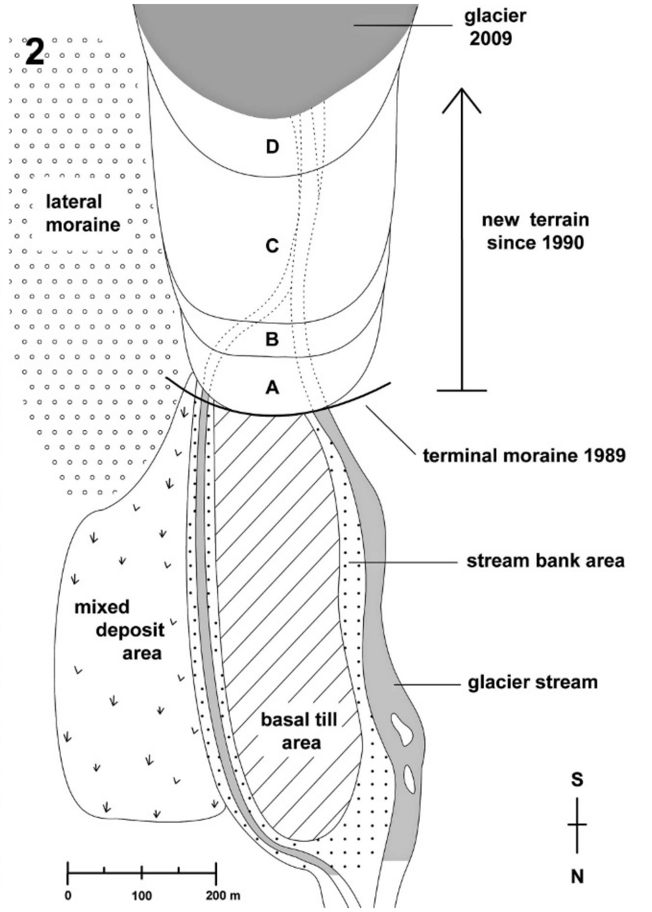

FIGURE 2. Schematic representation of the study area indicates the sampling sites during the 10-year study that followed the retreating glacier. Site (A), exposed since 1990, was sampled in 1999, 2001, 2007, 2009; site (B), exposed since 1999, was sampled in 2001, 2007, 2009; site (C), exposed since 2001, was sampled in 2007, 2009; site (D), exposed since 2007, was sampled in 2009. Stream banks, basal till, and mixed deposit area were sampled in 1999, 2001, 2007, and 2009; lateral moraine was sampled in 1999, 2001, and 2009.

by the Austrian Alpine Club (Patzelt, 1991–2000); this area is our site (A) which was sampled in July 1999, 2001, 2007, and 2009. From 1999 to 2001, the glacier retreated 44 m (Patzelt, 2000–2002); this is our site (B) which was sampled in 2001, 2007, and 2009. From 2001 to 2007 the retreat was roughly 200 m (Patzelt, 2003–2008); this area site (C) was sampled in 2007 and 2009. Between 2007 and 2009, the glacial retreat amounted to 88 m (Patzelt, 2009; Fischer, 2010); this area (site D) was sampled only in July 2009.

The sampling results of the new terrain were compared with those of the older terrain deglaciated before 1989. Four areas of "old terrain" on the glacier foreland are recognized in this paper (Fig. 2): (1) the glacial *stream bank* area, which is stony and nearly vegetation-free; (2) the *basal till* area, which forms a ridge between the anabranches of the glacial stream and has a patchy vegetation; (3) the steep *lateral moraine* of 1850 to the east; and (4) a *mixed deposit* area at the bottom of the valley consisting of basal till and material from the 1850 lateral moraine. The mixed deposit area is mostly covered with alpine vegetation. In this paper, the term lateral moraine refers to the moraine on the eastern side. No data are available for the lateral moraine to the west, due to the high risk of rock fall. In total, 25 chrono-sites were sampled in the new and old terrain over a period of 10 years (Table 1).

Several kinds of glacial deposits are distinguishable in the new area of deglaciated terrain: a flow till which lies immediately in front of the glacier and which varies in size from year to year; a basal till in which the glacial stream flows; and deposits consisting of various material from the basal till and the lateral moraine of 1850.

The presence of Carabidae was assessed by hand collection according to the following scheme. In July of every sampling period (1999, 2001, 2007, 2009), all sites were examined six times for 30 minutes each (thus equivalent to 3 hours) by turning over stones 5–70 cm in size and collecting all adult and larval carabid beetles. The total collecting time over the span of 10 years was 78 hours. Adult specimens were released in their environment shortly after collection and identification. One sampling round was carried out in each site per day. Larvae were stored in 70% ethanol for later determination (Huber, 2004; Strodl et al, 2010). The imagines of *Oreonebria* and *Bembidion* could not be determined at the species level in the field. The species in the respective genera were thus not distinguished from each other in the present study, except for the individuals of *Oreonebria* which were collected in 2009 and stored for later determination.

The vegetation cover was assessed by estimating the ground cover of vascular plants in five randomly chosen plots of 1 m^2 in each study site during 1999 and 2009.

The diversity of beetle assemblages was computed using Shannon-Wiener's index which estimates diversity based on presence and abundance of species (MacArthur, 1965). Statistics

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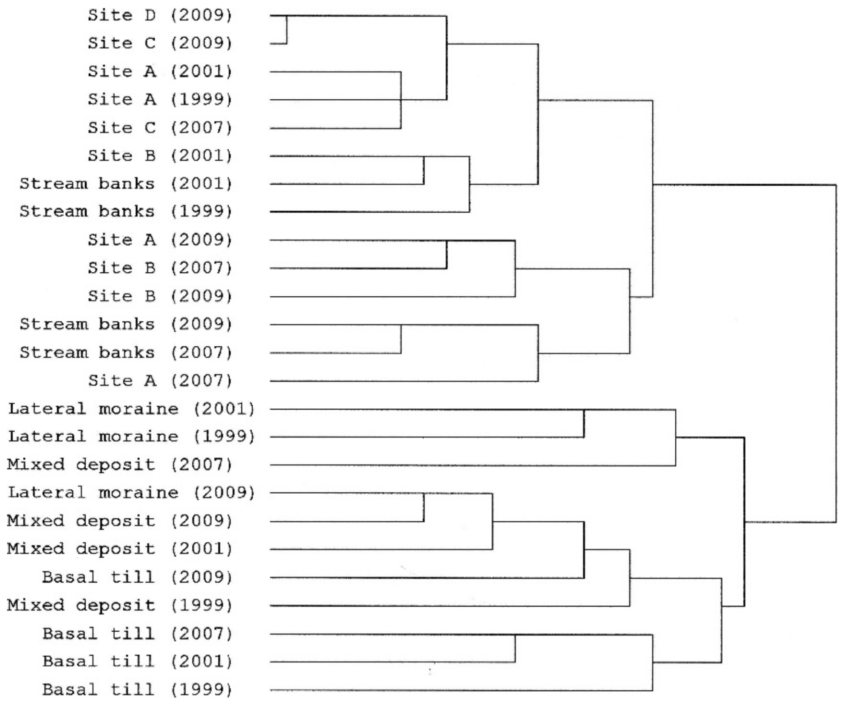

FIGURE 3. Dendrogram calculated by a hierarchical cluster analysis (average linkage between groups) showing the relative similarities of the carabid assemblages from the new terrain (sites A–D) and the old terrain sites (stream bank, lateral moraine, basal till and mixed deposit) of the Hornkees glacier foreland over the complete sampling period (1999, 2001, 2007, and 2009). In total, 25 chrono-sites were investigated; sampling year is given in parentheses. The beetle assemblages of the stream bank sites are intermixed with those of the new terrain (sites A–D) in one clade, while the beetle assemblages of the remaining old terrain sites form a separate clade.

were calculated in SPSS 15. A hierarchical cluster analysis of the in-between distance of Phi-Quadrat-values (Brosius and Brosius, 1996) was performed to show similarity among sites.

Results

In the study areas of the Hornkees glacier foreland, 975 individuals of adult carabid beetles from eight genera were collected (Table 1). The beetles of the closely related genera *Nebria* and *Oreonebria* were dominant in number, totaling 68.9% of all individuals. The number of collected individuals, species richness, and Shannon-Wiener diversity index (Tables 1, 2) were significantly lower in areas of the new terrain compared to the older terrain deglaciated before 1990 (Shannon-Wiener index U-Test, $p = 0.017$, $Z = -2.385$, $N = 25$).

The new terrain (which encompasses all sites exposed since 1990; Fig. 2) was dominated by individuals of *Nebria jockischii* which constituted 54.26% of the total Carabidae (Table 1). In sites adjacent to the glacier (Fig. 2), *Nebria jockischii* amounted to 74.6% of the total number of carabid beetles. The second most frequent species was *Nebria germari* with 19% of the total number of individuals. The greater the distance between sampling sites and the glacier, the more pronounced was the increase in numbers of individuals, species and diversity of the carabid assemblages (Tables 1, 2). In the course of the 10-year study, plant cover in site (A) increased from less than 1% to approximately 20%.

The increase in diversity and abundance of Carabidae in the new terrain was clearly revealed in the 2009 sampling period (Table 1). In the area next to the glacier (site D), only individuals of *Nebria jockischii* and *Nebria germari* were collected. In July 2009, late instars of *Nebria jockischii* were found indicating that reproduction occurred within one year after deglaciation. In site (C), exposed since 2001, *Nebria jockischii, Nebria germari*, and a single individual of *Nebria hellwigii* were found, while in site (B), exposed since 1999, four *Nebria* species and *Oreonebria castanea* were collected in July 2009. Site (A), which was deglaciated between 1990 and 1999, is characterized by a high abundance of *Nebria rufescens* and *Nebria jockischii* as well as *Oreonebria castanea* and *Oreonebria austriaca*. In addition, *Amara erratica, Pterostichus jurinei*, and individuals of *Bembidion* were found in 2009. The highest diversity (Shannon-Wiener Index 1.745) was recorded at site (A) (Table 2).

Succession was most evident in site (A) since it was sampled four times since 1999 (Table 1). This site was about 100 m from the Hornkees glacier in 1999. By 2009, the distance had increased about 430 m (Fig. 2). The comparison of our sampling results revealed an increase in the number of individuals (from 23 specimens in 1999 to 70 in 2009), in species richness (from 3 to 8 species), and Shannon-Wiener diversity index (from 0.56 to 1.745) (Tables 1, 2). The abundance of *Nebria jockischii* decreased from 82.61% in 1999 to 25.71% in 2009. It was remarkable that in 2009, 24.29% of all collected Carabidae belonged to *Nebria rufescens*; whereas only a single individual of this species was found in 2007, and none were found in the previous years in site (A) (Table 1).

The ground beetle assemblages from the new terrain were compared to those of the old terrain (deglaciated before 1989) for each sample period (Table 1). The highest species numbers (up to 10 carabid species per site for a sampling period) and diversity indices up to 1.974 were recorded for the old terrain (Table 2). In the stream bank area, *Nebria jockischii* was the only dominant carabid species, representing 52.17% of all collected Carabidae. The stabilized lateral moraine east of the new terrain (Fig. 2) showed a low number of beetles and diversity (Table 2). The basal till was characterized by a high abundance of individuals of *Oreonebria* (representing 23.57% of the collected Carabidae) and two *Amara* species in all sampling periods. The number of *Nebria rufescens* increased from one in 1999 to 30 individuals in 2009. The mixed deposit area also showed a high number of carabid species, as did the basal till area below the 1989 terminal moraine (Table 1). Likewise, the representatives of the genus *Oreonebria* represented 43.25% of all ground beetles. In the mixed deposit area, *Pterostichus jurinei* was encountered in remarkably high numbers.

A hierarchical cluster analysis showed that for each sampling period the carabid assemblages in the new terrain were most similar to each other and to those from the stream bank. Carabid

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TABLE 1

Species and numbers of specimens of Carabidae collected during the study (1999–2009) in the Hornkees foreland (Zillertal Alps, Austria). Plant cover is indicated in % in the first and last year of the respective site; number of larvae in parenthesis. Shaded blocks of the table represent sites which were covered by the glacier in the respective sampling period.

Study sites	Species	Sampling periods 1999	2001	2007	2009
New terrain					
Site (D), exposed 2007	*Nebria jockischii*	Under glacier	Under glacier	Under glacier	11 (2)
Plant cover: 0%	*N. germari*				7
Site (C), exposed 2001	*Nebria jockischii*			11 (1)	29 (1)
Plant cover: <1%	*N. germari*	Under glacier	Under glacier	1	12
	N. hellwigii				1
	Oreonebria sp.			1	
Site (B), exposed 1999	*Nebria jockischii*		6	6 (1)	13
Plant cover: 0–6%	*N. rufescens*			4	4
	N. germari		1	1	3
	N. hellwigii	Under glacier	1	4 (3)	1
	Oreonebria sp.			1	5
	Bembidion sp.		1	2	
	Amara erratica			1	
Site (A), exposed 1990	*Nebria jockischii*	19 (4)	19 (2)	8 (5)	18 (1)
Plant cover: <1–20%	*N. rufescens*			1	17
	N. germari	3	2		3
	N. hellwigii		1		6
	Oreonebria sp.			2	16
	Notiophilus biguttatus		1	1	
	Bembidion sp.	1		1	1
	Pterostichus jurinei				1
	Amara erratica			2	8
Neighboring areas exposed before 1990					
Stream bank	*Nebria jockischii*	17 (4)	23	3	17 (1)
Plant cover: 0–2%	*N. rufescens*		1		5
	N. germari	2	2		
	N. hellwigii	1	1		1
	Oreonebria sp.	3	3		
	Notiophilus biguttatus		3		1
	Bembidion sp.	3	2		11
	Pterostichus jurinei		1	2	
	Amara quenseli	9	2		
	A. erratica			1	1
Lateral moraine	*Carabus fabricii*	1			
Plant cover: 5–24%	*Nebria jockischii*	1	5 (1)		
	N. germari	4	7		
	N. hellwigii	3	3	No data	1
	Oreonebria sp.	3	4		11
	Notiophilus biguttatus	3			1
	Pterostichus jurinei				2
	Amara erratica		2		2
Basal till	*Carabus fabricii*				2
Plant cover: 24–61%	*C. depressus*				1
	N. jockischii	12	1		1
	N. rufescens	1	6	14	30
	N. germari	1			
	N. hellwigii	4	11	3	6
	Oreonebria sp.	24	10	5	31
	Notiophilus biguttatus	1	3	15	2
	Bembidion sp.	1	3	4	
	Pterostichus jurinei		3	4	7
	Amara erratica	5	10	12	5
	A. quenseli	24	17	10	8

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TABLE 1

Continued.

Study sites	Species	Sampling periods			
		1999	2001	2007	2009
Mixed deposits	*Carabus fabricii*		3	1	
Plant cover: 26–58%	*C. depressus*		1	1	
	N. jockischii	6			
	N. rufescens	3	1		
	N. germari	3		7 (1)	
	N. hellwigii	17 (2)	2	2 (2)	3
	Oreonebria sp.	48	35	6	20
	Notiophilus biguttatus			2	3
	Bembidion sp.		2	2	
	Pterostichus jurinei	4	17	10	21
	P. subsinuatus				5
	Amara erratica		2	9	9
	A. quenseli	1	1		
	Calathus melanocephalus		1	1	3

assemblages from the basal till area, the stabilized lateral moraine area, and the mixed deposit area were similar to each other and distinct from the new terrain and the stream bank area (Fig. 3).

Discussion

This 10-year study demonstrated that the newly exposed terrain of the Hornkees glacier foreland (Zillertal, Tyrol, Austria) was immediately colonized by two species of Carabidae, *Nebria jockischii* and *Nebria germari*. Adults and, especially remarkable, larvae were collected within 10 m of the glacier. These carabid species were likewise documented to be members of the pioneer community of terrestrial arthropods in the Rotmoos foreland (Ötztal, Tyrol) (Kaufmann, 2001).

Nebria jockischii was the dominant species in the youngest vegetation-free areas which are marked by water from melting snow and ice, flow tills, deposits of blocks, and small gravel forming a heterogeneous and instable habitat. The species was also frequent in the glacial stream bank area below the 1989 terminal moraine. We conclude that *Nebria jockischii* initially colonized the newly deglaciated terrain by migrating from the stream bank area and that it expanded its range by following the retreating glacier. The preferred habitat of this ripicolous ground beetle is free of vegetation, unstable, and consists of coarse-grained sediments (Kaufmann and Juen, 2001; Gobbi et al., 2007). *Nebria jockischii* is diurnal and capable of flight (Gereben, 1995). It has the best swimming performance of the investigated species of *Nebria* (unpublished data; Schößwender et al., 2010), which demonstrates a strong link to ripicolous habitats.

In contrast, *Nebria germari* is nocturnal and unable to fly, yet it was also regularly encountered in the most recently deglaciated areas. Since this carabid beetle occurred in considerable numbers in the unstable and barren lateral moraine but in low numbers in other neighboring areas, it probably migrated into the newly exposed terrain initially from the lateral moraine. In general, this species is found on the upper alpine zone, on barren debris-covered slopes with patchy vegetation (Lang, 1975; Christandl-Peskoller and Janetschek, 1976; De Zordo, 1979). In the first 10 years of colonization, the pioneer carabid assemblage of *Nebria jockischii* and *Nebria germari* was characterized by a low diversity, in contrast to the relatively high diversity of carabid assemblages in neighboring, longer exposed terrain. The species diversity and individual numbers of carabids increases in areas which have been exposed over 10 years. This is exemplified by a steady increase in the numbers of individuals of *Oreonebria* in the new terrain throughout the colonization process. We found members of this genus in the older areas of the new terrain in the last two sampling periods only. In contrast to our results, the brachypterous species, *Oreonebria castanea*, was recorded at sites immediately in front of the glacier in the Forni valley (Italy) and even on deposits on that glacier (Gobbi et al., 2007).

Based on the distribution and abundance pattern of the stenotopic carabid beetles in the upper section of the Hornkees glacier foreland, we conclude that the expansion of their range into

TABLE 2

Diversity of carabid beetles in the sampling sites over time. Shannon-Wiener index is followed by the number of species [in brackets]. Values for the Shannon-Wiener index and the number of species increase the longer the area has been exposed to potential colonization.

Study sites	Sampling periods			
	1999	2001	2007	2009
New terrain				
Site (D), since 2007	Under glacier	Under glacier	Under glacier	0.668 [2]
Site (C), since 2001	Under glacier	Under glacier	0.536 [3]	0.702 [3]
Site (B), since 1999	Under glacier	1.003 [4]	1.722 [7]	1.326 [5]
Site (A), since 1990	0.56 [3]	0.643 [4]	1.414 [6]	1.745 [8]
Neighboring areas, exposed before 1990				
Stream bank	1.386 [6]	1.457 [9]	1.011 [3]	1.289 [6]
Lateral moraine	1.679 [6]	1.526 [5]	No data	1.119 [5]
Basal till	1.606 [9]	1.952 [9]	1.923 [8]	1.733 [10]
Mixed deposits	1.274 [7]	1.404 [10]	1.974 [10]	1.634 [7]

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newly exposed terrain is guided by habitat preference and the ability to select appropriate microhabitats.

Previous studies on ground beetle colonization in alpine glacier forelands also showed that areas deglaciated over 30 years ago were more or less equally dominated by several species of *Nebria* and *Oreonebria* (Kaufmann, 2001; Gobbi et al., 2006, 2007). The studies by Gobbi et al. (2006) and Kaufmann (2001) investigated long-term succession (over 150 years), while we focused on the initial phases of colonization. Based on our repeated sampling of the same sites in all study periods between 1999 and 2009, we were able to calculate a fine temporal and spatial scale of species overturn for periods of one to 20 years after deglaciation. Most importantly our results reveal a rapid and initial colonization by few carabid species for the first few years followed by a slow increase in species number and diversity. Thereafter, the formation of a species-rich assemblage of carabid beetles coincided with the development of patches of vegetation, as observed in the oldest areas of the new terrain in 2009. Other studies, as well, noted that the highest increase in diversity on alpine glacier forelands occurred in areas colonized over 20 years ago (Gobbi et al., 2006). The pattern of distinct microspatial distribution with high levels of abundance of the ground beetles in the Hornkees glacier foreland is produced by an interplay of various factors and processes that change over time, such as geomorphic genesis, lateral variation in slope and topography, soil processes, recent encroachments, and vegetation cover. To describe the finely tuned colonization process of the Hornkees glacier foreland using the chronosequence approach alone would be insufficient. Variation, for example, occurs among the carabid beetle assemblages even in areas which were more or less concurrently deglaciated, such as the area immediately below the 1989 terminal moraine.

The method of hand collection and field determination of terrestrial insects without killing them has several advantages over the commonly used pit-fall traps, since it focuses on target species and is not dependent on the activity of insects. Furthermore, the methods used should not significantly impact the faunistic environment. We are convinced that systematically turning over stones and collecting all individuals of carabid beetles is a practical method to answer questions about the micro-distribution of carabids (Spence, 1979; Davies, 1987; Manderbach and Plachter, 1997; Paill, 2005). Particularly at the beginning of the study in 1999, hand collection in combination with field determination and subsequent release of beetles was the most appropriate method, since the newly deglaciated area was considerably small. At that time, setting pitfall-traps could have had a major impact on the initial colonization of carabid beetles that probably would have impaired the results for several years. Hand collection provides valuable information on the distribution patterns of carabid beetles on a small scale and is recommended for vulnerable areas.

One disadvantage to field determination of live specimens in the present study was that we were unable to distinguish the species of the genera *Bembidion* and *Oreonebria*. Since the ecological differentiation of these species has yet to be studied, exact identification would not help to further resolve the colonization pattern.

Examination of the colonization pattern of the newly exposed alpine terrain at a fine spatial and temporal level indicates that certain carabid species rapidly expanded their range by migration from neighboring source habitats. Habitat preference seems to be the main mechanism for the colonization by stenotopic carabid beetles, while the ability of dispersal, the abundance of species in the source habitat, and stochastic events play minor roles.

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