

Primary Succession of Surface Active Beetles and Spiders in an Alpine Glacier Foreland, Central South Norway

Authors: Bråten, Anders Thon, Flø, Daniel, Hågvar, Sigmund, Hanssen, Oddvar, Mong, Christian E., et al.

Source: Arctic, Antarctic, and Alpine Research, 44(1) : 2-15

Published By: Institute of Arctic and Alpine Research (INSTAAR), University of Colorado

URL: <https://doi.org/10.1657/1938-4246-44.1.2>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Primary Succession of Surface Active Beetles and Spiders in an Alpine Glacier Foreland, Central South Norway

Anders Thon Bråten*

Daniel Flo†

Sigmund Hågvar‡

Oddvar Hanssen§

Christian E. Mong¶ and

Kjetil Aakra#

*The Norwegian Water Resources and Energy Directorate (NVE), Region South, Anton Jenssens gate 7, Box 2124, 3103 Tønsberg, Norway

†Norwegian Forest and Landscape Institute, Box 115, 1431 Ås, Norway

‡Corresponding author: Department of Ecology and Natural Resource

Management, Norwegian University of Life Sciences, Box 5003, 1432 Ås, Norway

sigmund.hagvar@umb.no

§The Norwegian Institute for Nature Research NINA, Box 5685 Sluppen, 7485 Trondheim, Norway

¶Brattlien 38, 5019 Bergen, Norway

#Midt-Troms Museum, Box 82, 9059 Storsteinnes, Norway

<http://dx.doi.org/10.1657/1938-4246-44.1.2>

Abstract

Spiders and beetles were pitfall-trapped in the foreland of the receding Hardangerjøkulen glacier in central south Norway. At each of six sampling sites, ages 3 to 205 years, twenty traps covered the local variation in moisture and plant communities. Thirty-three spider species and forty beetle species were collected. The species composition was correlated to time since glaciation and vegetation cover. A characteristic pioneer community of spiders and mainly predatory beetles had several open-ground species, and some species or genera were common to forelands in Svalbard or the Alps. While the number of spider species increased relatively constant with age, the number of beetle species seemed to level off after about 80 years. Half of the beetle species were Staphylinidae, and contrary to Carabidae, most of these were rather late colonizers. Most herbivore beetles colonized after more than 40 years, but the moss-eating Byrrhidae species *Simplocaria metallica* and also certain Chironomidae larvae developed in pioneer moss colonies after 4 years. The large Collembola *Bourletiella hortensis*, a potential prey, fed on in-blown moss fragments after 3 years. In the present foreland, chlorophyll-based food chains may start very early. Two pioneer *Amara* species (Carabidae) could probably feed partly on seeds, either in-blown or produced by scattered pioneer grasses.

Introduction

Norwegian glaciers have receded since the end of the “Little Ice Age” around A.D. 1750. In alpine areas of southern Norway, a marked temperature increase has been noted during the last 2–3 decades (Ytrehus et al., 2008), accelerating this process. As summarized by Kaufmann and Raffl (2002), glacier forelands which contain both pristine ground and dated, older sites, allow for interesting studies in primary succession. The sequence of dated study plots, which mirror the succession in a given site over time, is called a chronosequence. The pattern of botanical succession in European glacier forelands has been rather well studied and understood (e.g. Matthews and Whittaker, 1987; Matthews, 1992; Chapin et al., 1994; Vetaas, 1994, 1997; Raffl, 1999; Moreau et al., 2005; Raffl et al., 2006). Less is known about the simultaneous faunistic succession, and the existing information is mainly from Austria, Italy, and Svalbard. In Austria, early faunistic studies in glacier forelands by Janetschek (1949, 1958) and Franz (1969) were followed by Gereben (1994, 1995) on carabid beetles, and Paulus and Paulus (1997) on spiders. Recently, the foreland of the Austrian Rotmoos glacier has been under intense study, including the invertebrate succession (Kaufmann, 2001, 2002; Kaufmann and Raffl, 2002; Kaufmann et al., 2002; König et al., 2011). In Italy, Zingerle (1999) studied spiders and harvestmen in the Dolomites, and Gobbi et al. (2006a, 2006b, 2007, 2010) have described the epigeal arthropod succession in glacier forelands in the Central Italian Alps. The invertebrate

succession in two glacier forelands in Svalbard has been thoroughly described by Hodkinson et al. (2004).

In Norway, Vater (2006) studied the succession of macroinvertebrates in selected glacier forelands in southern Norway. The few other Norwegian faunistic studies in glacier forelands deal with mites (Acari) (Skubala and Gulvik, 2005; Seniczak et al., 2006; Hågvar et al., 2009) and springtails (Collembola) (Hågvar, 2010).

Purposes of the present study are:

- (1) To describe the primary succession of beetles and spiders in the Midtdalsbreen glacier foreland (Norway) where the succession of mites and springtails has already been studied (see Hågvar et al., 2009, Hågvar, 2010). This allows us to compare the colonization rate of four different taxonomic groups. A general increase in species number was expected with site age, as the vegetation cover developed.
- (2) To compare pioneer communities and the general invertebrate succession in Norwegian glacier forelands with those studied on Svalbard and in the Alps.
- (3) To look for common ecological properties among pioneer species, and to shed light on feeding relationships within pioneer communities. While the youngest site in the earlier mite and springtail study was 32 years, we have now included a barren moraine only 3 years old. Based on the literature, we expected a pioneer fauna of spiders and predacious carabid beetles close to the glacier. The paradox of starting a primary succession with predators has been

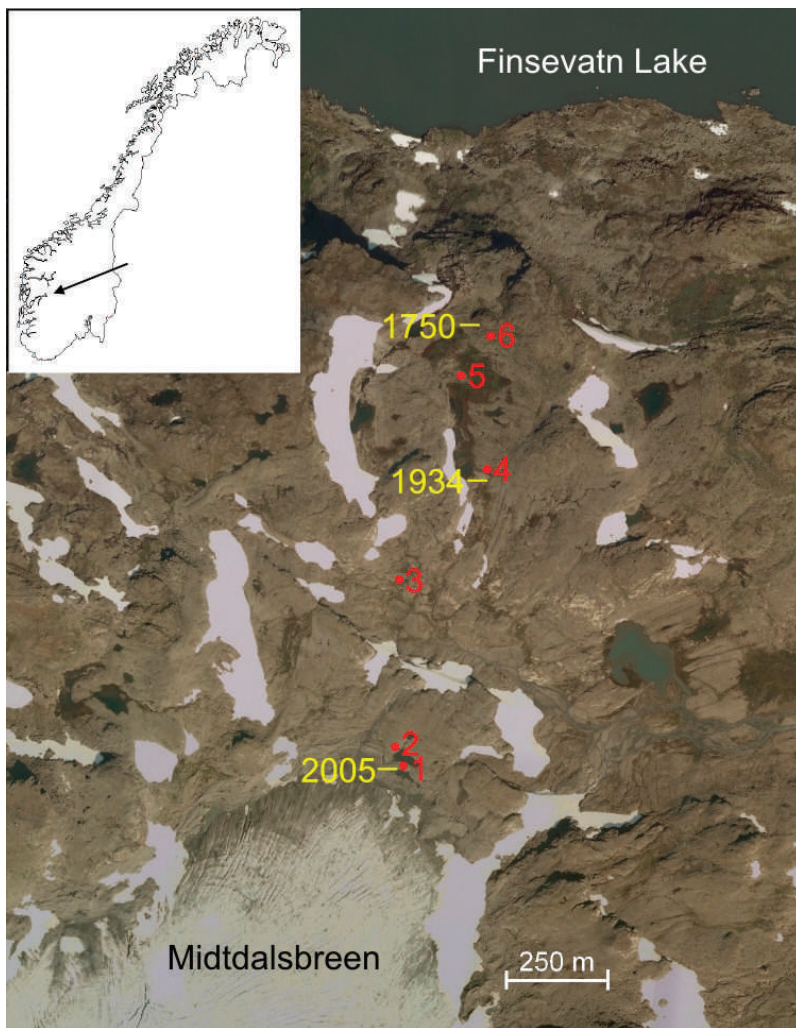


FIGURE 1. Aerial photo showing the position of the six sampling plots close to the receding Midtdalsbreen glacier snout. Moraines from A.D. 1750, 1934, and 2005 are indicated. The location of the study site in south Norway (60°34'N, 7°28'E) is shown on the small map.

discussed by Hodkinson et al. (2002). The food could be wind-blown (or flying) invertebrates or resident decomposers like *Collembola* living on in-blown, dead plant material. Based on the stable isotope ^{15}N in a number of species from early succession in the Austrian Alps, König et al. (2011) suggested that pioneer predators like Carabidae and Araneae were feeding on resident *Collembola*. We also used stable isotopes to sort selected species into trophic levels, and included studies of gut contents in springtails and Carabidae in search of visible proof of food choice. Looking for early chlorophyll-based food chains, the possibility of pioneer mosses as the food source was of special interest.

Methods and Study Area

STUDY AREA AND SAMPLING

The study was performed in front of the receding Midtdalsbreen glacier snout (60°34'30"N, 7°27'40"E), which belongs to the 73 km² large Hardangerjøkulen glacier in central south Norway. Midtdalsbreen has been receding since A.D. 1750, leaving a 1.1-km-long foreland in the treeless low- and mid-alpine zone, between 1300 and 1400 m above sea level (see aerial photo in Fig. 1 with three major moraines from 1750, 1934, and 2005 indicated). Various sites in this chronosequence have been well dated and described, and they have not been subject to reworking

(Sørli, 2001; Hågvar et al., 2009). Figure 1 shows the position of our six sampling sites, where epigeal arthropods were sampled using pitfall traps. The method is efficient in catching surface-active arthropods. However, catches depend both on density and surface activity of the various species, as well as vegetation density and weather (e.g. Spence and Niemelä, 1994), so quantitative data should be treated with care. While site 1 was sampled only in the snow-free period of 2008 (between 14 June and 23 August), the other sites were sampled during two snow-free periods including the winter between 23 June 2007 and 23 August 2008. Twenty traps of 6.5 cm diameter, covered by a plywood roof about 3 cm above the ground, were operated at each site. The traps contained a 50% ethylene glycol solution with a drop of detergent added. During sampling each second week, an inner cup with 0.2 mm mesh size in the bottom was replaced with an empty one, so that the preserving fluid remained. The material was lightly flushed with water and transferred to 70% alcohol. All adult beetles and spiders were identified to species.

According to Ottesen (1996), soil moisture is the most important ecological factor for habitat choice in Norwegian alpine, ground-living beetles. Therefore, in each collection site the 20 traps were placed in a gradient from dry to moist habitats in order to catch as many species as possible. In this way we also covered the main variation of plant communities. The vegetation cover was estimated and dominant plants were noted in 1 m² around each trap. Mean vegetation cover for all 20 traps in a given

site was calculated. The distance between traps was usually 1–1.5 m along a line, or in two or three parallel lines several meters apart, to cover local variation as well as possible. Relative soil moisture was found by collecting soil samples of about 30 cm³ in the upper 3 cm layer, about 20 cm from each trap. Holes were refilled with similar soil to avoid changing the microtopography. After stones larger than 2 mm had been removed by sieving, water percentage of the remaining substrate was calculated on weight basis by drying at 105 °C. The soil samples were taken on the same day after a relatively dry period, since rain would temporarily wet even naturally dry sites.

Information on the depth of the organic soil layer was based on 10–16 soil cores from each site, taken in *Salix herbacea* vegetation in connection with soil animal studies (Hågvar et al., 2009). Since *S. herbacea* belongs to the pioneer species, these measures are probably maximum values at each site.

Site 1: age 3 years. The traps were placed in a long line, covering the topographic variation on a fresh, undulating moraine. The nearest m² around each trap was completely free of vegetation and organic layer, except for one individual of *Poa alpina* and a tiny moss patch of a few cm² near two of the traps, respectively.

Site 2: age 38–39 years. In this nearly flat area, traps were placed in two parallel rows 15 m apart, with 10 traps in each row. Only 2–10% of the ground was covered with vegetation (mean value 6%). Vegetated patches usually consisted of a mixture of mosses, *Deschampsia alpina*, *Salix herbacea*, and *Saxifraga oppositifolia*. A few small specimens of *Salix glauca* and *S. lanata* occurred. There was no organic layer.

Site 3: age 62–63 years. The traps were situated in two parallel rows about 3 m apart, each row with 10 traps covering a gradient from a dry sandy ridge to a moist depression with snow bed vegetation. The ridge had 5–30% open sand and gravel, with a vegetation dominated by *Rhacomitrium* mosses and *Stereocaulon* lichens. The lowest part was a continuous, wet mat of *Anthelia* mosses. Mean vegetation cover in the site was 91%. In the medium part, the field layer covered up to 30–70%, being dominated by *Salix herbacea*, small bushes of *S. glauca* and *S. lanata*, as well as *Empetrum hermaphroditum*, *Carex lachenalii*, *Luzula frigida*, and *Festuca vivipara*. In paths dominated by *S. herbacea*, there was a mean organic layer of about 2 mm.

Site 4: age 78–79 years. The local variation was covered by three trap lines, about 4 m between each. Ten traps were situated in a moist snow bed with continuous vegetation. Various mosses including *Anthelia* sp. covered 60–80% of the ground, the rest being mainly *S. herbacea*, with some graminoids and other herbs. Small bushes of *S. lanata* occurred. The remaining 10 traps were set in two lines on a rather dry slope with 5–92% open sand and gravel around the traps. Here, *Stereocaulon* lichens and *Rhacomitrium* mosses dominated the vegetation, while there were also some *F. vivipara*, *E. hermaphroditum*, *S. herbacea*, and various graminoids. Mean vegetation cover in this site was 80%. In *S. herbacea* vegetation, there was a mean organic layer of 3–4 mm.

Site 5: age 159–160 years. Two rows of traps were situated about 3 m apart on a slope covering a gradient from dry, partly open ground to a continuous vegetation in the lower part. In the upper half of the gradient, 5–60% of the ground was open sand and gravel, with *Cetraria nivalis*, *Stereocaulon*, and *Cladonia* lichens combined with *Empetrum hermaphroditum* as dominant vegetation. In the lowest part, *Salix herbacea*, *Empetrum hermaphroditum*, and *Vaccinium uliginosum* dominated, together with various green mosses. Small *Salix* bushes, mainly *S. glauca*, occurred throughout the gradient, especially in the lower half.

Mean vegetation cover was 80%. In *S. herbacea* vegetation, there was a mean organic layer of 16 mm.

Site 6: age 204–205 years. Also here, two rows of traps, 2–3 m apart, covered a gradient in a slope, with moistest conditions at the bottom. In the uppermost part, a species-rich meadow was dominated by graminoids, various weeds, and *Empetrum hermaphroditum* in the field layer, combined with *Cladonia* and *Stereocaulon* lichens and various mosses. Most of the gradient, however, was dominated by *Salix herbacea* in combination with several weeds, including graminoids. Mean vegetation cover was 96%. In *S. herbacea* vegetation, there was a mean organic layer of 11 mm.

The gradual establishment of moss vegetation on the youngest site was followed from 2005 to 2011 by estimating the moss cover in 20 random plots, each 1 m². To illustrate potential food resources on the barren moraine, we counted all invertebrates, as well as in-blown seeds and moss fragments, in the pitfall traps in 2008, at 3 years of age. Furthermore, the gut content of various Collembola and Carabidae species was microscopied in search of identifiable structures. We also analyzed pioneer moss and 8 species of pioneer macroinvertebrates for stable isotope ratios of ¹⁵N/¹⁴N and ¹³C/¹²C to arrange them into trophic levels. All specimens were taken from the 3-year-old moraine, except for *Byrrhus fasciatus* and *Curimopsis cyclolepidia*, which were taken from 63-year-old soil where they first appeared. In autumn 2010, after a 34-m-long glacial retreat that summer, pioneer springtails were searched for on freshly exposed ground by flotation.

NUMERICAL ANALYSES

We employed multivariate statistics in an exploratory data analysis mainly as a graphical tool. Common methods assume that species have a linear or a unimodal response to underlying gradients. Communities on glacier forelands will often display strong gradients that are correlated and difficult to disentangle (Mong and Vetaas, 2006; Hågvar et al., 2009; cf. Matthews, 1992). Consequently, these methods often suffer from a distortion of the second ordination axis (the arch effect, the horseshoe effect) when applied to such data.

The non-parametric and iterative method Non-metric Multidimensional Scaling (NMDS) was chosen (cf. Borg and Groenen, 1997). Species occurring in less than 5 sampling sets were disregarded, leaving 51 species and 61 sampling sets for analysis. All analyses were performed with R (R Development Core Team, 2008) and the packages *mgcv*, *vegan* (Oksanen et al., 2008), and *MASS* (Venables and Ripley, 2002).

First the data were square root transformed due to high variance in observed abundance of species (highest observed abundance: *Patrobis septentrionis*, 254). Then dissimilarity indices based on the Bray-Curtis distance parameter were identified in order to detect underlying gradients (Faith et al., 1987). Finally, the NMDS was performed with centered data, PC rotation, and half-change scaling. Convergence was found after 5 iterations. The root mean square errors between predictions and observations is 0.000067 and maximum residual is 0.00027. The model has two dimensions and the stress-parameter is 18.098.

The present analysis was based on the total material, where the innermost site differed from the others by having only one sampling season. We also tested separately the 2008 material where the catching effort was equal in all six sites. However, since there was no significant difference in catches between the two seasons in sites 2–6, the overall result became very similar when the total material from both years was used.

TABLE 1

Significant responses to soil moisture among beetles, described by Spearman rank correlation. The three upper species prefer relatively dry ground, while the three lower species prefer relatively moist ground.

Species	β (corrected)	t	2-sided t -value (5%)	P	SE	N
<i>Amara quenseli</i>	-0.72	-3.83	2.16	0.007	38.64	15
<i>Byrrhus fasciatus</i>	-0.76	-5.82	2.06	<0.001	114.72	26
<i>Cymindis vaporariorum</i>	-0.40	-2.19	2.06	0.050	123.64	27
<i>Geodromicus longipes</i>	0.60	2.87	2.14	0.017	43.89	16
<i>Liogluta alpestris</i>	0.31	2.38	2.04	0.019	184.14	33
<i>Patrobis septentrionis</i>	0.73	5.95	2.04	<0.001	173.22	32

Results

BEETLES AND SOIL MOISTURE

Several beetle species showed a significant response to soil moisture (Table 1), confirming the importance of sampling along a moisture gradient within each site. *Amara quenseli*, *Byrrhus fasciatus*, and *Cymindis vaporariorum* showed significantly highest catches on the driest soil, while *Geodromicus longipes*, *Liogluta alpestris*, and *Patrobis septentrionis* were mainly trapped on high moisture soil.

SPECIES NUMBERS ALONG THE CHRONOSEQUENCE

Species lists and total catches of spiders and beetles from all sampling sites are shown in Tables 2–3. While the number of spider species increased rather evenly with age, the number of beetle species increased rapidly up to about 80 years age, but then seemed to drop or level off. Cumulative curves for species numbers of spiders, beetles, springtails, and oribatid mites are combined in Figure 2 for comparison. A common trend is a rapid colonization during the first 60–80 years. Microarthropod data were, however, from soil samples in *Salix herbacea* vegetation and did not cover the local variation in vegetation types, as in the pitfall trapping (Hågvar et al., 2009; Hågvar, 2010).

NUMERICAL ANALYSES

Table 4 shows correlations between environmental variables and the two NMDS axes. Distance, age, and vegetation cover were significantly correlated with the axes, whereas day number (change in the community through the summer) and sampling year (2007/2008) were not.

The best subset of environmental variables with maximum rank correlation with community (Bray-Curtis) dissimilarities was determined. Out of the 5 environmental variables, the best model included 2, age and vegetation cover, with a correlation of 0.8125.

The NMDS plot in Figure 3 shows the position of different species along the two first axes. The first axis is correlated to time since deglaciation and vegetation cover; the NMDS1 scores thus represent a statistical estimation of the sequence of succession. Species with negative scores are pioneers, and species with high scores are late seral. Correlation with the first NMDS axis is given for each species in Tables 2–3. High correlations between the three significant environmental variables age, distance, and vegetation cover (Table 5) makes interpretation of the second axis scores difficult.

FEEDING CATEGORIES

Beetles were sorted into feeding categories according to various sources (e.g. Thayer, 2005; Böcher, 1988; and references in Table 7). The present species within Chrysomelidae, Curculionidae, Byrrhidae, and Hydrophilidae are herbivores. *Hydnobius* and

Atomaria are mycophages, while *Oxytelus* are saprophages. The food of Omalinae within Staphylinidae is not quite clear in literature, and we have put them in the category “predators/saprophages?” (*Acidota*, *Anthophagus*, *Arpedium*, *Boreaphilus*, *Deliphrum*, *Eucnecusum*, *Geodromicus*, *Omalium*). The other Staphylinidae (Aleocharinae and Tachyporinae) are considered predators. The Carabidae species are predators, except the two *Amara* species which are usually considered omnivores, i.e. both predators and herbivores. Our material shows a surprisingly similar combination of feeding categories throughout the gradient (Fig. 4). True predators always dominated the species number, with some higher numbers of spider species than predatory beetles at all sites. The category “predators/saprophages?” represented by Omalinae made up a minor but relatively constant fraction at all ages. True herbivore species were always relatively few, with highest numbers (seven) at 79 years. Still more rare were omnivores or saprophages/mycophages.

The results from stable isotope analyses are shown in Figure 5. Three trophic levels were identified, with moss at the bottom. All three Byrrhidae species, *Amara alpina*, and one *Amara quenseli* plot were grouped as herbivores, while *Mitopus morio*, *Nebria nivalis*, *Bembidion hastii*, and one *A. quenseli* plot were grouped as predators.

PITFALL CATCHES OF OTHER TAXA ON BARREN GROUND

Pitfall catches of other taxa on the youngest site (Table 6) indicate possible food items for pioneer spiders and beetles, which have to depend either on eolian resources or resident decomposers. As much as 8 Collembola species were trapped. This illustrates the value of applying different sampling methods for Collembola. Large, surface-active species may escape during ordinary soil sampling, which revealed only three species after 32 years (Hågvar, 2010). Filled guts and the presence of different developmental stages indicated a resident Collembola fauna on the youngest site. Certain Collembola species, and also Actinedida mites, showed a considerable surface activity. The large Sminthuridae springtail *Bourletiella hortensis* dominated the catches. Also a number of adult Chironomidae dropped into the traps throughout the season. Furthermore, Table 6 documents that small, living moss fragments were regularly blown into the barren ground. The presence of sand grains in all traps confirmed a continuous wind transport at ground level.

Discussion

THE PIONEER COMMUNITY

Comparison among Svalbard, Norway, and the Alps

Certain species or genera seem to be general pioneers in European glacier forelands. Within southern Norway, Vater

TABLE 2

Total catches of spiders per 20 traps at different distance and age. The youngest site was sampled only in 2008, while numbers from the other sites are the sum from 2007 and 2008. For species occurring in at least five samplings, the correlation with the first NMDS-axis is given.

Family	Species	NMDS1	Distance (m)	15	70	472	807	1012	1100
Age (years)				2008	2007/2008	2007/2008	2007/2008	2007/2008	2007/2008
	<i>Erigone tirolensis</i>	-1.119		3	39-40	62-63	78-79	159-160	204-205
Linyphiidae				7.7	63.5	2.7	2.2	7.2	3.5
Linyphiidae	<i>Collinsia holmgreni</i>	-1.063		3.3	115	1.1	5.3	10.5	4
Lycosidae	<i>Pardosa trailli</i>	-0.775		10.3	48.9	12.2	68.1	3.4	4
Linyphiidae	<i>Erigone arctica</i>	-0.670		7.1	7.7	34.7	47.2	0	2.4
Linyphiidae	<i>Hilaira cf. frigida</i>	-0.831		0	100.3	10.2	26.6	26.5	47.4
Linyphiidae	<i>Bathypantes gracilis</i>	0.333		0	2.5	1.3	1	10.9	5.5
Lycosidae	<i>Alopecosa aculeata</i>			0	1	0	0	1.1	0
Lycosidae	<i>Arctosa alpigena</i>	0.367		0	0	55.4	44.6	42.5	0
Linyphiidae	<i>Pelecopis mengei</i>	0.493		0	0	6.4	0	46	2.2
Linyphiidae	<i>Tiso aestivus</i>	0.666		0	0	71.6	60.2	32.9	156.2
Linyphiidae	<i>Agyneta nigripes</i>	0.690		0	0	2.7	1.1	12.4	1.2
Linyphiidae	<i>Scotinotylus evansi</i>	0.742		0	0	13.5	4.4	97.8	37.7
Linyphiidae	<i>Oreonetides vaginatus</i>	0.577		0	0	0	1.1	14.1	20.6
Linyphiidae	<i>Tenuiphantes tenebricola</i>			0	0	0	1	0	0
Linyphiidae	<i>Mecynargus morulus</i>	0.650		0	0	0	0	1	11.1
Lycosidae	<i>Pardosa septentrionalis</i>	0.685		0	0	0	0	31.3	0
Thomisidae	<i>Ozyptila arctica</i>	0.694		0	0	0	0	29.8	2
Lycosidae	<i>Pardosa paludicola</i>	1.049		0	0	0	0	1	314.2
Linyphiidae	<i>Gonattium rubens</i>	1.287		0	0	0	0	2.1	66.6
Linyphiidae	<i>Tenuiphantes flavipes</i>			0	0	0	0	1.1	0
Linyphiidae	<i>Ceratella brevipes</i>			0	0	0	0	0	3
Linyphiidae	<i>Walckenaeria karpinskii</i>	1.098		0	0	0	0	0	8.4
Gnaphosidae	<i>Gnaphosa leporina</i>	1.145		0	0	0	0	0	28.5
Linyphiidae	<i>Oedothorax retusus</i>	1.304		0	0	0	0	0	80
Linyphiidae	<i>Oedothorax sp.</i>	1.367		0	0	0	0	0	6.7
Linyphiidae	<i>Incestophantes kochiellus</i>			0	0	0	0	0	1
Linyphiidae	<i>Lepthyphantes antroniensis</i>			0	0	0	0	0	1
Linyphiidae	<i>Mecynargus paetulus</i>			0	0	0	0	0	1
Gnaphosidae	<i>Micaria alpina</i>			0	0	0	0	0	2
Lycosidae	<i>Pardosa hyperborea</i>			0	0	0	0	0	2
Linyphiidae	<i>Poecilometes variegata</i>			0	0	0	0	0	1
Linyphiidae	<i>Improphantes complicatus</i>			0	0	0	0	0	1.2
Linyphiidae	<i>Lepthyphantes sp.</i>			0	0	0	0	0	1.2
	Number of species			4	7	11	12	18	28
	Cumulative number of species			4	7	12	14	20	33

TABLE 3

Total catches of beetles per 20 traps at different distance and age. The youngest site was sampled only in 2008, while numbers from the other sites are the sum from 2007 and 2008. For species occurring in at least five samplings, the correlation with the first NMDS-axis is given.

Family	Species	NMDS1	Distance (m)	15	70	472	807	1012	1100
Age (years)				2008	2007/2008	2007/2008	2007/2008	2007/2008	204-205
Sampling year				171.1	69.1	0	0	0	0
Carabidae	<i>Bembidion hastii</i>	-1.441		3	39-40	62-63	78-79	159-160	207-208
Byrrhidae	<i>Simpliocaria metallica</i>	-1.226		171.1	28.5	0	2	0	0
Carabidae	<i>Nebria nivalis</i>	-0.925		2.1	31.1	11	35.9	1.1	3
Carabidae	<i>Anara alpina</i>	-0.354		7.7	74.1	54.6	70.7	22.7	168.5
Staphylinidae	<i>Geodromicus longipes</i>	-0.096		3.5	32.8	76.8	86.1	9.2	27.6
Carabidae	<i>Anara quenseli</i>	0.188		5	0	390.7	413.9	2.1	22.3
Staphylinidae	<i>Arpedium quadrum</i>	0.326		1.1	0	0	5.8	0	6
Hydrophilidae	<i>Helophorus glacialis</i>	-0.417		0	1.4	0	2.2	1.1	1
Carabidae	<i>Nebria rufescens</i>	0.058		0	4.4	19.2	175.8	1	7.1
Carabidae	<i>Patrobus septentrionis</i>	0.146		0	71.9	377.3	633.9	320.8	228.6
Staphylinidae	<i>Boreaphilus hemingianus</i>	0.270		0	3	6.7	16.5	3.2	24.3
Curculionidae	<i>Otiorynchus nodosus</i>	0.358		0	1	10.8	24.9	2.4	19
Staphylinidae	<i>Oxypoda amularis</i>			0	1.1	0	0	0	0
Carabidae	<i>Nothophilus aquaticus</i>	0.239		0	0	34.5	26	5.9	16.1
Byrrhidae	<i>Curimopsis cyclolepidia</i>	0.256		0	0	121.8	61.9	0	0
Staphylinidae	<i>Cephalococcyx nivalis</i>	0.395		0	0	6	21.7	7.1	10.1
Byrrhidae	<i>Byrrhus fasciatus</i>	0.425		0	0	10.4	51.5	26.8	26
Carabidae	<i>Cynmidis vaporariorum</i>	0.447		0	0	57.9	28	77.4	19.1
Staphylinidae	<i>Atheta hyporum</i>	0.559		0	0	17.3	10	6.6	24.3
Staphylinidae	<i>Liogluta alpestris</i>	0.667		0	0	87.2	217.9	33.6	608.2
Staphylinidae	<i>Acidota crenata</i>	0.780		0	0	4.8	0	5.2	3.5
Staphylinidae	<i>Deliphrum tectum</i>			0	0	1.1	0	0	0
Staphylinidae	<i>Oxytelus laqueatus</i>			0	0	1.1	0	0	0
Staphylinidae	<i>Gnypeta caerulea</i>	0.144		0	0	0	7.9	0	0
Carabidae	<i>Pelophila borealis</i>	0.446		0	0	0	35.1	5.4	4.1
Staphylinidae	<i>Eucnecosum brachypterum</i>	0.768		0	0	0	13.8	0	13.1
Chrysomelidae	<i>Chrysomela collaris</i>	0.836		0	0	0	2.2	10.1	145
Staphylinidae	<i>Bryoporus rugipennis</i>	0.841		0	0	0	1	0	7
Staphylinidae	<i>Anthophagus alpinus</i>	0.883		0	0	0	18.1	33.8	238.8
Staphylinidae	<i>Omalium caesum</i>	1.068		0	0	0	2.4	17.8	85.5
Curculionidae	<i>Apion cruentatum</i>			0	0	0	2.2	0	0
Cryptophagidae	<i>Atomaria sp.</i>			0	0	0	1	0	0
Staphylinidae	<i>Atheta laevicauda</i>			0	0	0	0	1.4	2
Staphylinidae	<i>Mycetoporus inaris</i>			0	0	0	0	1.1	0
Staphylinidae	<i>Tachinus elongatus</i>	1.192		0	0	0	0	0	24.1
Staphylinidae	<i>Mycetoporus nigrans</i>	1.197		0	0	0	0	0	6
Staphylinidae	<i>Mycetoporus erichsonianus</i>	1.367		0	0	0	0	0	31.5
Staphylinidae	<i>Mycetoporus niger</i>			0	0	0	0	0	2
Chrysomelidae	<i>Gonioctena arctica</i>			0	0	0	0	0	4
Letiidae	<i>Hydrobius spinipes</i>			0	0	0	0	0	1
	Number of species			7	11	19	27	22	30
	Cumulative number of species			7	13	23	32	34	40

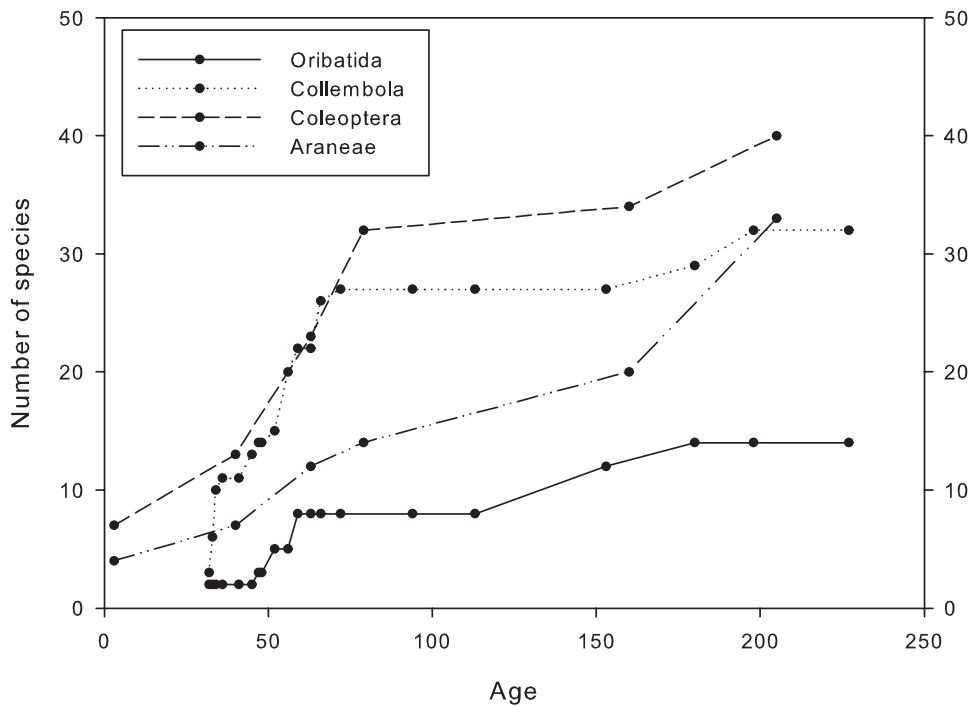


FIGURE 2. Cumulative species numbers of Oribatida, Collembola, Coleoptera, and Araneae in the Middalsbreen glacier foreland. Data for the first two groups are from *Salix herbacea* vegetation, which is found throughout the foreland.

(2006) studied eight forelands in two other glacial areas, Jostedalbreen and Jotunheimen. In several sites younger than 20 years, she found pioneer species or genera common to the present study: *Pardosa trailli* among spiders; and *Amara alpina*, *A. quenseli*, *Nebria* sp. (in one case confirmed as *N. nivalis*), and *Bembidion* sp. among beetles. In the Rootmostal foreland in the Austrian Alps, Kaufmann (2001) recorded *Amara quenseli*, four *Nebria* species, a *Bembidion* species and a *Simplocaria* species, as well as the spiders *Erigone tirolensis* and two *Pardosa* species in sites younger than 20 years. In the Forni glacier foreland in the Italian Alps, Gobbi et al. (2006a) found *Pardosa saturator* and *Oreonebria castanea* active on supraglacial detritus, and *Amara quenseli* present after 24 years. It is also a common feature between forelands in Norway and the Alps that two other carabid beetles arrive somewhat later: *Notiophilus aquaticus* and *Cymindis vaporariorum* (Kaufmann, 2001; Gobbi et al., 2006a, 2010). The two Svalbard forelands studied by Hodkinson et al. (2004) had no beetles, but contained *Erigone arctica* after 16 years, a spider common to the present 3-year-young moraine. *Mitopus morio* (Opiliones) was trapped in large numbers throughout our chronosequence, including on the 3-year-old moraine. This is a large and very active generalist predator, eating both living and dead invertebrates (Phillipson, 1960a, 1960b). Also Vater (2006) found it to be an early colonizer in southern Norwegian forelands. In the Alps, the species was one of the pioneers together with *M. glacialis* (Kaufmann, 2001). Even among springtails and mites, certain taxa are typical pioneers both on Svalbard, in Norway, and in the Alps (Hågvar et al., 2009; Hågvar, 2010).

TABLE 4

Correlations between environmental variables and the two first NMDS-axes. Significant correlations are bold-faced.

Axis	Distance	Age	Vegetation cover	Day number	Year
NMDS 1	0.96	0.83	0.97	0.29	-0.61
NMDS 2	0.29	0.56	-0.24	-0.96	0.79

Open-Ground Species

A common factor for most beetles and spiders present on the 3-year-old moraine is their preference, or tolerance, for living on open ground with stones and gravel (Table 7). The most specialized species in this respect is the carabid *Bembidion hastii*, with high catches both at 3 and 40 year age, but which disappeared as vegetation developed. However, Alfredsen (2010) found it on a local, bare patch which was 75 years old. More tolerant for vegetation are the two *Amara* species, which had high catches on older plots. In contrast to *B. hastii*, they are xerophilic, and newly exposed ground may be rather moist. The fourth pioneer carabid, *Nebria nivalis*, is a cold-tolerant, hygrophilous species which is a classic inhabitant close to glaciers and snow fields. It was rare in the two oldest sites. While three pioneer carabids are typically alpine species, *B. hastii* may also occur in lowland sites, where its demand for open, gravelly ground is seen on river banks, shores of lakes, and even on seashores in northernmost Fennoscandia. Among pioneer spiders, *Pardosa trailli* and the two pioneer *Erigone* species are characterized in literature as typical alpine, open-ground spiders.

Dispersal Ability

Pioneers both must be good dispersers and tolerate tough environmental conditions, and some of the species in Table 7 do even occur on Svalbard. The beetles from the 3-year-old moraine had functional wings. We assume that *M. morio* is able to colonize pristine ground by walking. On Svalbard, Coulson et al. (2003) showed that certain spiders easily dispersed by ballooning. Using water traps in various Svalbard habitats, Magnussen (2010) showed that both mites and springtails could be transported by air. We think that surface living springtails may be able to follow the retreating glacier edge by their own movements, and *B. hortensis* was seen to jump about 10 cm in the field. During 2010, Middalsbreen receded 34 m (Atle Nesje, personal communication), and *A. bidenticulata* was collected by flotation on newly exposed ground at the end of August, some specimens only 4 m from the ice edge. They had filled guts and jumped actively close

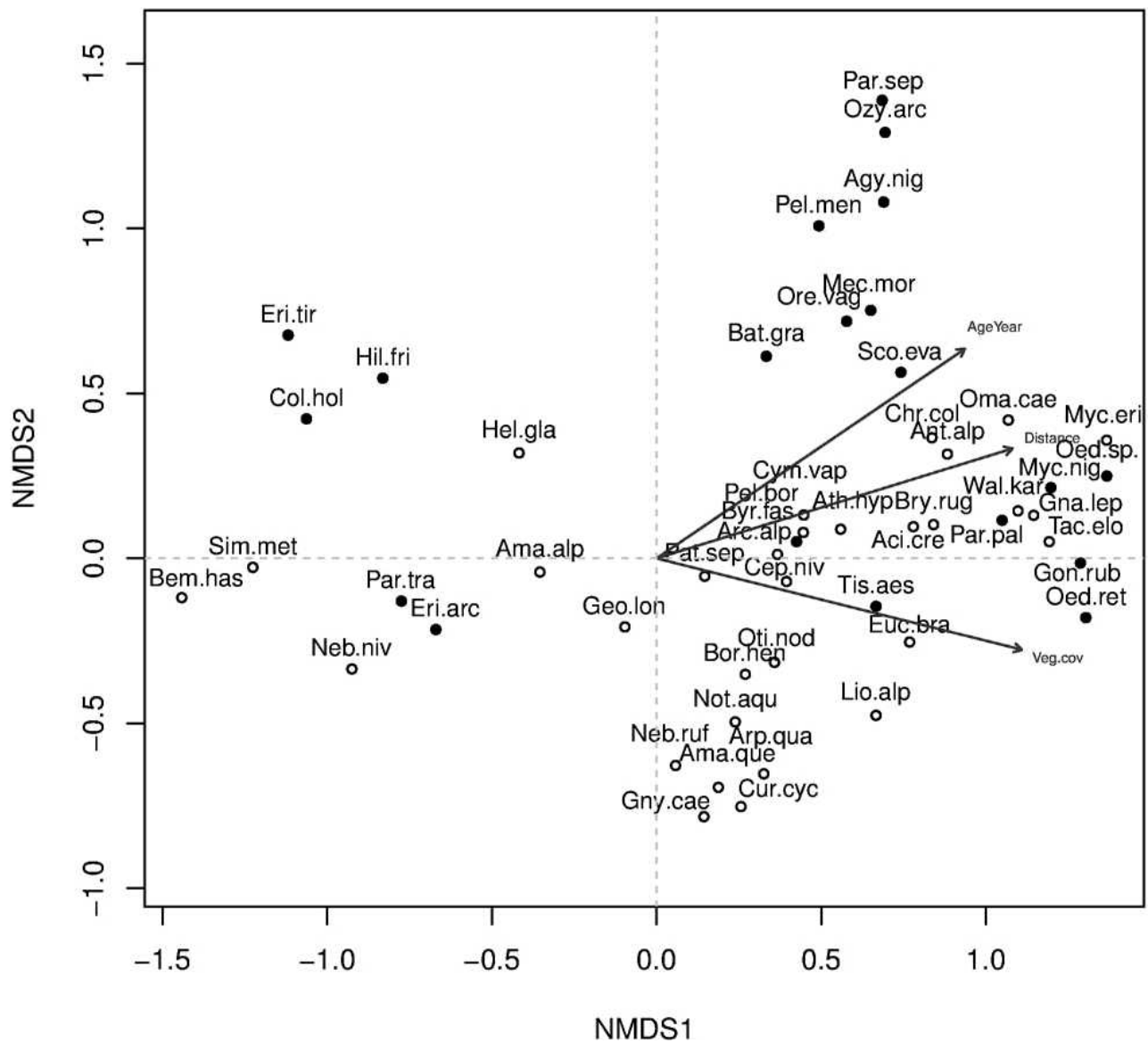


FIGURE 3. NMDS-plot showing the position of spiders (filled circles) and beetles (open circles) along the first two axes. Pioneer species are situated at the negative part of the first axis. Full species names are given in Tables 2–3. Environmental vectors are age, distance, and vegetation cover.

to the melt water. Maybe this species is a super-pioneer in this rapidly expanding foreland, even before predators are established.

Pioneer Communities: a Predictable Mix of Ecologically Different Species?

Pioneer communities consist of an interesting mix of specialists and generalists, parthenogenetic and bisexual species, and species with either a short or a long life cycle. Specialists may

TABLE 5

Correlations between environmental variables. Correlations larger or smaller than $|0.325|$ are significant and bold-faced (Zar, 1999).

	Distance	Age	Vegetation cover	Day number	Year
Distance	1.00				
Age	0.90	1.00			
Vegetation cover	0.85	0.69	1.00		
Day number	0.07	0.09	0.04	1.00	
Year	-0.15	-0.16	-0.15	-0.36	1.00

be open-ground species such as the springtail *Bourletiella hortensis* and various species in Table 7, or “cold-loving” species such as the carabid *Nebria nivalis* and the springtail *Agrenia bidenticulata*. Examples of ecological generalists are the harvestman *Mitopus morio*, the carabid *Amara quenseli*, the springtail *Isotoma viridis*, and the oribatid mite *Tectocepheus velatus*. Among pioneer microarthropods, there are both parthenogenetic and bisexual species, and species with both short and long life cycles (Hågvar et al., 2009; Hågvar, 2010). It remains to be understood fully how pioneer invertebrate communities can be so predictable when they contain species with such different ecology in several respects. Maybe good dispersal ability is a major common feature, combined with a tolerance for a lack of vegetation and soil.

Pioneer Ground: a Relatively Good Habitat?

Barren ground near a glacier may not be as hostile for invertebrates as it appears. A microclimatic aspect is that the surface temperature of stones, gravel, and sand may become very high in sunny weather. The heat is slowly released at night to

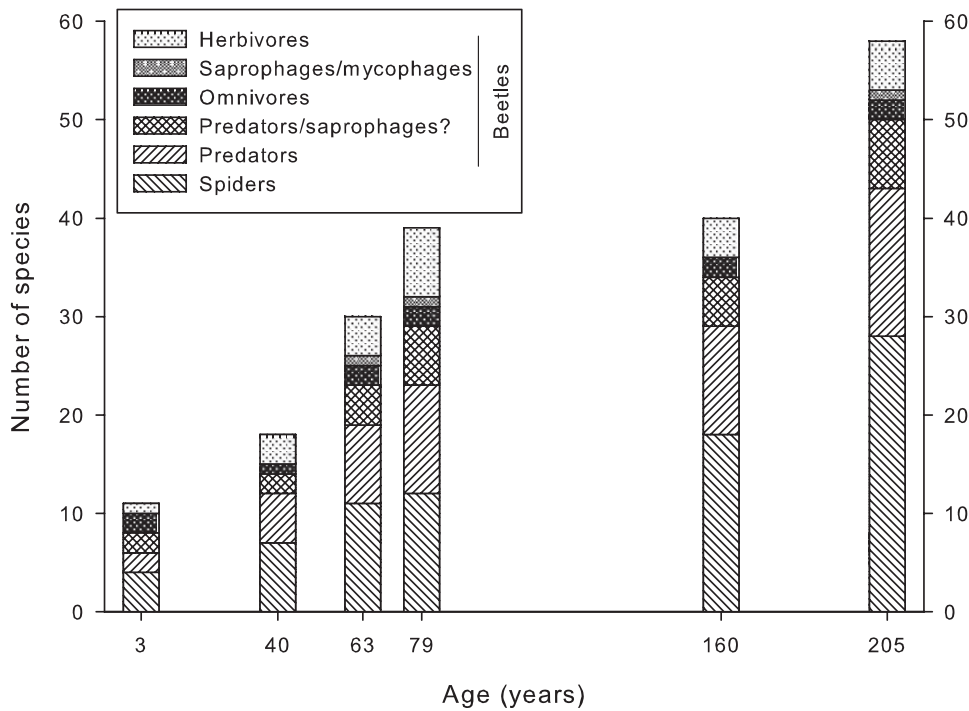


FIGURE 4. Distribution of feeding categories among spiders and beetles which were pitfall-trapped at different ages in the Middalsbreen foreland. Because spiders are predators, this feeding category dominated throughout the gradient.

microhabitats under and between stones. Periodically, ground-living invertebrates may probably experience higher temperatures on barren ground than in vegetated sites. Also, the varied microtopography between stones and gravel of different size creates shelters from wind, as well as hiding places during inactive periods. Due to a limited number of species, interspecific competition may be low. Given a sufficient food supply, pristine ground may in fact be a good habitat for certain invertebrates.

The Key Question: What Do the Pioneers Eat?

Pioneer communities of macroinvertebrates in glacier forelands are typically predator-dominated, and Hodkinson et al. (2002) pointed to the ecological paradox that heterotrophic organisms establish before autotrophic. They assumed that the

predators were fed by an allochthonous input of invertebrates. Aerial transport of invertebrates into pioneer ground was demonstrated in Svalbard by Hodkinson et al. (2001) and Coulson et al. (2003). However, König et al. (2011), studying pioneer invertebrates in an Austrian foreland, suggested that resident Collembola, which decompose allochthonous humus, could be the main food of pioneer predators. Their suggestion was based on stable isotope ratios of $^{15}\text{N}/^{14}\text{N}$ and $^{13}\text{C}/^{12}\text{C}$. Their data also indicated that with time, predators switched their diet to include other predators. Our data based on corresponding isotopes (Fig. 5) indicated two trophic levels among animals in pioneer communities: herbivores and predators. Moss-eating Byrrhidae species are early herbivores. Furthermore, Figure 5 indicates herbivory in *A. alpina* and both herbivory and predation in *A. quenseli*. This means that both herbivores and omnivores occur

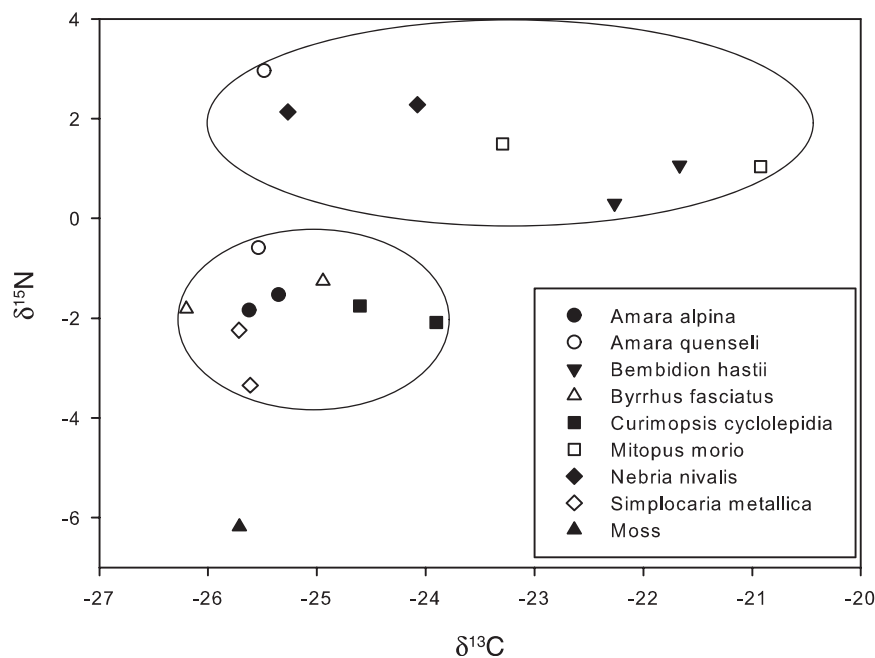


FIGURE 5. $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of various pioneer organisms. Except for the moss sample, there were two replicates of each species. The lower circle indicates herbivores, and the upper one predators.

TABLE 6

Pitfall catches of potential food items for beetles and spiders on a barren, three-year-old moraine. Total numbers in 20 traps are given for 4 two-week periods in 2008.

Collecting date	12 July	26 July	9 August	23 August
COLLEMBOLA				
<i>Bourletiella hortensis</i>	685	300	116	24
<i>Agrenia bidenticulata</i>	196	74	123	30
<i>Isotoma viridis</i>	11	25	26	30
<i>Desoria olivacea</i>	29	36	49	34
<i>Desoria infusata</i>		3	9	16
<i>Desoria tolya</i>			1	1
<i>Lepidocyrtus lignorum</i>	1			6
<i>Ceratophysella scotica</i>			1	
ACARI				
Actinedida	276	83	46	44
OTHER INVERTEBRATES				
Hemiptera: Aphididae	6		3	1
Thysanoptera	1		1	
Diptera: Chironomidae	93	36	23	36
Diptera: Tipulidae	3	1		
Diptera: Brachycera		1	3	4
Hymenoptera parasitica	4	3	1	3
PLANT MATERIAL				
Moss fragments	13	44	14	31
Seeds		1		

very early in the present foreland. Our data on stable isotopes did not include springtails.

The ultimate answer on food selection lies in the gut content. DNA analyses would probably be the best method, but visual inspection of gut content may also tell a lot. Preliminary gut analyses of *N. nivalis* and *B. hastii* from 3-year-old ground showed only animal remains, while the two *Amara* species contained both invertebrate and plant food. Brink and Wingstrand (1949) observed that *A. alpina* could feed even on dead insects on snowfields, and Chernov (1988) found that on the tundra, it climbed up on different plants during night and fed on seeds, for instance of *Poa arctica*. On the present 3-year-old moraine, there were a few *Poa alpina* plants, and in-blown seeds may also have been eaten.

We also studied microscopically the squeezed gut content of Collembola species which were pitfall-trapped on the 3-year-old moraine, and found that the gut of the large and numerous *B. hortensis* often contained fragmented moss leaves. This species is probably able to find and feed on small, living moss fragments which are blown into the moraine (Table 6). Tiny moss colonies were observed within seventeen of twenty m² plots studied the following autumn when the moraine was 4 years old, with highest cover on the moraine slope away from the glacier. Two years later (2011), mosses were visible on all of twenty m² plots studied and covered about 0.4% of the ground on the slope towards the ice, and 6% on the other slope. Scattered higher plants were also present. If predators can eat moss-eating Collembola, moss could be an important element in evolution of the invertebrate community. A resident, moss-eating springtail fauna could represent a significant and stable food source for pioneer predators, while transport of eolian food might be more unpredictable and periodic. Also the moss-eating beetle *Simplocaria metallica* was found to develop in a pioneer moss patch after 4 years, and even some terrestrial Chironomidae larvae were living there. Moreover, aphids were present early, being extracted from the first, scattered,

individual grasses: from *Trisetum spicatum* after 4 years, and from *Festuca vivipara* and *Deschampsia alpina* after 5 years. Chlorophyll-based food chains may start very early in this foreland.

SPIDER SUCCESSION

The cumulative number of spider species increased nearly linearly with age, and most species stayed after colonization. Two other patterns were found in the Alps: Kaufmann (2001) found that most spiders colonized within 40 years, and Gobbi et al. (2006b) observed a threshold effect with a sudden increase in spider diversity after 100–150 years. On Svalbard, spiders colonized newly exposed ground immediately, with 4 of 5 species present after 16 years, probably feeding on airborne Chironomidae (Hodkinson et al., 2001; Coulson et al., 2003; Hodkinson et al., 2004). However, if spiders continuously colonize by ballooning, it is difficult to decide whether the species are thriving and reproducing there, or if the pioneer ground may be a sink for certain species.

BEEBLE SUCCESSION

Contrary to spiders, relatively few new beetle species were added after about 80 years. Most carabids were early colonizers, as also shown by Alfredsen (2010) in the same gradient. A drop in beetle species after 160 years remains unexplained. In the Rotmoostal foreland in Austria, Kaufmann (2001) and Kaufmann and Raffl (2002) concluded that most beetles were present already after 40 years, which is much earlier than in the present study. The difference may be partly due to the lack of species identification of Staphylinidae by Kaufmann (2001), and in Kaufmann and Raffl (2002) only some low species numbers of Staphylinidae were given, without species names. The present study may be the first to identify the majority of beetle species in a glacier foreland. Staphylinidae made up 21 of the 40 beetle species, and the succession pattern was strongly influenced by this family. Half of our Staphylinidae species were found only in sites older than 63 years. Many species live typically among decomposing plant debris, and this group may be favored by the development of an organic soil layer. One species, *Anthrophagus alpinus*, is a climber of small bushes (Palm, 1948). Still, we agree with the general conclusions by Kaufmann and Raffl (2002) that certain carnivorous Carabidae are among the first colonizers, that Staphylinidae are generally later colonizers, and that herbivorous families like Chrysomelidae and Curculionidae are not typical until some vegetation is present. Although slow-moving herbivore beetles may be underrepresented in pitfall material, the low number of herbivore beetles in Figure 4 may be relatively correct since some herbivores were indeed trapped in high numbers, and there are relatively few additional herbivore beetle candidates known from the Finse area (Østbye and Hågvar, 1972). *Chrysomela collaris* is a specialist on *Salix herbacea* (Hågvar, 1975), but was not sampled until about 80 years although its food plant is one of the pioneer species. It may be a slow disperser, and is typically present in snow beds with a well-developed carpet of the food plant (Hågvar, 1975). Kaufmann (2001) recorded it after about 30 years. An interesting family is the moss-eating family Byrrhidae, where the genus *Simplocaria* represented the earliest herbivore beetles during the very first years both in the present study and in the Alps (Kaufmann, 2001). There are several other herbivore candidates in the present foreland, for instance within Lepidoptera, Homoptera, and Symphyta among Hymenoptera, but these groups demand other sampling methods.

TABLE 7
Ecological characteristics of pioneer beetles and spiders living on a barren, three-year-old moraine. Compiled from Andersen (1969), Andersen and Hanssen (1993), Böcher (1988), Brundin (1934), Fjellberg (1972), Kronstedt (2004), Lindroth (1945, 1961, 1985, 1986), Munster (1927–1928), Palm (1948), Palmgren (1976), and Aakra (unpublished).

Species	Habitat: Degree of openness	Hygrophil/Xerophil	Altitude: Alpine/lowland	Arctic Species?	Cold tolerant?	Food
<i>Simpliocaria metallica</i> (Byrrhidae)	Open areas, as river banks, heaths, and herb vegetation	Mainly hygrophil	Mainly alpine (boreal to low Arctic)	On Svalbard and Greenland		Mosses
<i>Anura alpina</i> (Carabidae)	Both on open ground and in dry heaths	Xerophil	Alpine			Omnivorous
<i>Anura quenseli</i> (Carabidae)	Both on open ground and in sparse vegetation	Xerophil	Alpine and on dry, sand/gravel areas in lowland	On Svalbard		Omnivorous
<i>Bembidion hastii</i> (Carabidae)	Open gravelly or stony sites, including river banks and lake shores	Hygrophil	Mainly alpine, may occur in lowland			Predator
<i>Nebria nivalis</i> (Carabidae)	Often on open ground. Mainly along glaciers, snow fields, cold rivers	Hygrophil	Alpine, mainly upper zone	Arctic/alpine distribution on mainland	Cold tolerant	Predator
<i>Geodromicus longipes</i> (Staphylinidae)	Mainly on open ground, often along river banks and shores of lakes	Hygrophil	Mainly alpine			Probably predator
<i>Arpedium quadrum</i> (Staphylinidae)	Moist slopes with vegetation	Hygrophil	Low alpine zone and in forest			Probably saprophagous
<i>Collinsia holmgreni</i> (Linyphiidae)	Not a typical open ground species, often in alpine heaths		Alpine		Early spring active when still snow	Predator
<i>Erigone arctica</i> (Linyphiidae)	Typically on nearly vegetation-free ground, including river banks and sea shores		Alpine and lowland	On Svalbard		Predator
<i>Erigone itroloensis</i> (Linyphiidae)	As above		Mainly alpine	On Svalbard		Predator
<i>Pardosa trailli</i> (Lycosidae)	Open habitats with stones and gravel		Alpine in south Norway			Predator

GENERAL TRENDS IN SUCCESSION

There is, as in common on forelands, three strong overriding factors structuring the community. These factors are a composite of time since deglaciation, distance to the glacier, and vegetation cover. That these three environmental variables are connected is common sense, supported by strong correlations (R-squared) and by other work on glacier foreland (cf. Matthews, 1992). Variations in catches between seasons and years were not structuring factors in this foreland.

Hodkinson et al. (2004), Vater (2006), and Gobbi et al. (2007) all pointed to age as a main factor explaining invertebrate succession in glacier forelands. As vegetation develops with age, vegetation cover turned out to be a main explanatory factor together with soil formation in the study by Kaufmann (2001). Gobbi et al. (2010) showed that an abrupt increase in vegetation cover and plant species richness between 40 and 150 years was correlated with a shift to larger, more diverse, less mobile carabid species with longer larval development. The present study highlights how a rather rich invertebrate community can be established even before any visible vegetation. Therefore, when explaining invertebrate succession, the absence of vegetation is as important as the gradual development of vegetation.

Figure 2 illustrates the simultaneous rapid colonization of Collembola, Oribatida, and Coleoptera during the first 60–80 years, with slower addition of new species later. Spiders colonized more gradually in our foreland. A faster colonization by beetles and spiders in the Rotmoostal glacier may be due to a milder climate, since certain taxa absent in the present site occur there, e.g. Lumbricidae, Formicidae, and Diplopoda (Kaufmann, 2001). In southern Norway, Vater (2006) illustrated how altitude and local climate influence the rate of invertebrate succession in different glacier forelands, even within a small geographical area. While the colonization rate of macroarthropods was rapid in glacier forelands situated in the forested subalpine zone, the succession was very slow in a high alpine foreland. She proposed a “geoecological model” to explain three distinctive pathways of succession, representing the subalpine, the low/mid-alpine, and the high alpine zones, respectively. Certain characteristic species could, however, be pioneers at very different altitudes.

Vater (2006) concluded that in southern Norwegian forelands, few invertebrate taxa were “dropping out” of the chronosequence after their initial establishment. This conclusion was based on a limited taxonomical resolution. While our spider data support this principle, the gap between present and cumulative beetle species at our two oldest sites illustrates a turnover of species. Also, in the Alps several pioneer species of spiders and beetles are absent in later successional stages (Kaufmann, 2001; Gobbi et al., 2006b, 2007).

CONCLUSION ABOUT EARLY SUCCESSION

Summing up for the actual foreland, the cold-loving springtail *A. bidenticulata* is a super-pioneer, following the ice edge closely. Several predators among spiders, harvestmen, and carabid beetles follow rapidly, with options to feed on decomposers, eolian invertebrates, or each other. However, already after a few years, various plant food is available and may be important in structuring the invertebrate community. In-blown moss fragments are fed upon by the springtail *B. hortensis* after 3 years, and the moss-eating beetle *S. metallica* and certain Chironomidae develop in pioneer moss patches after 4 years. The scattered grass plants after 4–5 years contain aphids. Seeds, either in-blown, or from pioneer grasses may be fed upon by the two omnivorous *Amara*

species. The present case study indicates that a pioneer community may be more complicated structured, and also change more rapidly, than signaled by the “predator first”-term.

FUTURE ASPECTS

More case studies from different geographical areas are needed to understand better how invertebrate communities establish and develop in glacier forelands. Which processes can be generalized, and how are local successional pathways explained? To what degree is dispersal a limiting factor? A key question is to find out what pioneer species are eating. To what degree are pioneer predators fed by resident decomposers, and to what degree by eolian prey? How fast do chlorophyll-based food chains establish, and can pioneer mosses be a driver in the young community? Furthermore, studies should have a good taxonomic resolution and preferably combine different sampling methods.

Increased global warming may increase the rate of colonization in the whole foreland, making it difficult to treat it as a chronosequence. Also, the surrounding source communities can be influenced. Long-term monitoring of specific sites in the foreland gradient would be valuable.

Specialized pioneer species may become locally extinct if permanent glaciers or snow patches melt away. Examples from the present study are two cold-adapted species, *Agrenia bidenticulata* (Collembola) and *Nebria nivalis* (Carabidae), but also certain pioneers preferring open, barren ground.

Acknowledgments

Torstein Solhøy is thanked for good advice, and Preben Ottesen kindly loaned us especially designed pitfall traps. Kristine Maraldo helped to get stable isotopes analyzed, and Atle Nesje gave information on the rate of glacier retreat. Thanks to Finse research station for hospitality.

References Cited

- Alfredsen, A. N., 2010: Primary succession, habitat preferences and species assemblages of carabid beetles in front of the retreating glacier Midtdalsbreen, Finse, southern Norway. Master thesis. University of Bergen, Bergen, Norway, 83 pp.
- Andersen, J., 1969: Habitat choice and life history of *Bembidiini* (Col., Carabidae) on river banks in central and northern Norway. *Norsk entomologisk Tidsskrift*, 17: 17–65.
- Andersen, J., and Hanssen, O., 1993: Geographical distribution of the riparian species of the tribe *Bembidiini* (Col., Carabidae) in south and central Norway. *Fauna norvegica Series B*, 40(2): 59–69.
- Böcher, J., 1988: The Coleoptera on Greenland. Copenhagen: *Meddelelser om Grønland, Bioscience*, 26, 100 pp.
- Borg, I., and Groenen, P., 1997: *Modern Multidimensional Scaling. Theory and Applications*. New York: Springer, 614 pp.
- Brink, P., and Wingstrand, K. G., 1949: The mountain fauna of the Virihaure area in Swedish Lapland. *Lunds Universitets Årsskrift*, 45: 1–70.
- Brundin, L., 1934: *Die Coleopteren des Torneträskgebietes. Ein Beitrag Zur Ökologie und Geschichte der Käferwelt in Schwedisch-Lappland*. Dissertation, Lund University, Lund, Sweden, 436 pp.
- Chapin, F. S., Walker, L. R., Fastie, C. L., and Sharman, L. C., 1994: Mechanisms of primary succession following deglaciation at Glacier Bay, Alaska. *Ecological Monographs*, 64: 149–175.
- Chernov, Y. I., 1988: *The Living Tundra*. Cambridge: Cambridge University Press, 228 pp. (English translation).

- Coulson, S. J., Hodkinson, I. D., and Webb, N. R., 2003: Aerial dispersal of invertebrates over a high-arctic glacier foreland: Midtre Lovénbreen, Svalbard. *Polar Biology*, 26: 530–537.
- Faith, D. P., Minchin, P. R., and Belbin, L., 1987: Compositional dissimilarity as a robust measure of ecological distance. *Vegetatio*, 69: 57–68.
- Fjellberg, A., 1972: Coleoptera from Hardangervidda. Oslo: Universitetsforlaget. *Fauna of the Hardangervidda*, 1: 1–74.
- Franz, H., 1969: Besiedlung der jüngst vom Eise freigegebenen Gletschervorfelder und ihrer Böden durch wirbellose Tiere. Neue Forschungen im Umkreis der Glocknergruppe. *Wissenschaftliche Alpenvereinshefte*, 21: 291–298.
- Gereben, B. A., 1994: Habitat-binding and coexistence of carabid beetles in a glacier retreat zone in the Zillertal Alps. In Desender, K., Dufrene, M., Loreau, M., Luff, M. L., and Maelfait, J.-P. (eds.), *Carabid Beetles: Ecology and Evolution*. Dordrecht: Kluwer, 139–144.
- Gereben, B. A., 1995: Co-occurrence and microhabitat distribution of six *Nebria* species (Coleoptera: Carabidae) in an alpine glacier retreat zone in the Alps, Austria. *Arctic and Alpine Research*, 27: 371–379.
- Gobbi, M., De Bernardi, F., Pelfini, M., Rossaro, B., and Brandmayr, P., 2006a: Epigeal arthropod succession along a 154-year glacier foreland chronosequence in the Forni Valley (Central Italian Alps). *Arctic, Antarctic, and Alpine Research*, 38: 357–362.
- Gobbi, M., Fontaneto, D., and De Bernardi, F., 2006b: Influence of climate changes on animal communities in space and time: the case of spider assemblages along an alpine glacier foreland. *Global Change Biology*, 12: 1985–1992.
- Gobbi, M., Rossaro, B., Vater, A., De Bernardi, F., Pelfini, M., and Brandmayr, P., 2007: Environmental features influencing carabid beetle (Coleoptera) assemblages along a recently deglaciated area in the Alpine region. *Ecological Entomology*, 32: 682–689.
- Gobbi, M., Caccianiga, M., Cerabolini, B., Luzzaro, A., De Bernardi, F., and Pierce, S., 2010: Plant adaptive responses during primary succession are associated with functional adaptations in ground beetles on deglaciated terrain. *Community Ecology*, 11(2): 223–231.
- Hågvar, S., 1975: Studies on the ecology of *Melasoma collaris* L. (Col., Chrysomelidae) in alpine habitats at Finse, south Norway. *Norwegian Journal of Entomology*, 22: 31–47.
- Hågvar, S., 2010: Primary succession of springtails (Collembola) in a Norwegian glacier foreland. *Arctic, Antarctic, and Alpine Research*, 42: 422–429.
- Hågvar, S., Solhøy, T., and Mong, C., 2009: Primary succession of soil mites (Acari) in a Norwegian glacier foreland, with emphasis on oribatid species. *Arctic, Antarctic, and Alpine Research*, 41: 219–227.
- Hodkinson, I. D., Coulson, S. J., Harrison, J., and Webb, N. R., 2001: What a wonderful web they weave: spiders, nutrient capture and early ecosystem development in the high Arctic—Some counter-intuitive ideas on community assembly. *Oikos*, 95: 349–352.
- Hodkinson, I. D., Webb, N. R., and Coulson, S. J., 2002: Primary community assembly on land—The missing stages: why are the heterotrophic organisms always there first? *Journal of Ecology*, 90: 569–577.
- Hodkinson, I. D., Coulson, S. J., and Webb, N. R., 2004: Invertebrate community assembly along proglacial chronosequences in the High Arctic. *Journal of Animal Ecology*, 73: 556–568.
- Janetschek, H., 1949: Tierische Successionen auf hochalpinem Neuland. *Berichte des naturwissenschaftlich-medizinischen Vereins Innsbruck*, 48/49: 1–215.
- Janetschek, H., 1958: Über die tierische Wiederbesiedlung im Hornkees-Vorfeld (Zillertaler Alpen). *Schlern-Schriften*, 188: 209–246.
- Kaufmann, R., 2001: Invertebrate succession on an Alpine glacier foreland. *Ecology*, 82: 2261–2278.
- Kaufmann, R., 2002: Glacier foreland colonisation: Distinguishing between short-term and long-term effects of climate change. *Oecologia*, 130: 470–475.
- Kaufmann, R., and Raffl, C., 2002: Diversity in primary succession: The chronosequence of a glacier foreland. In Körner, C., and Spehn, E. (eds.), *Global Mountain Biodiversity: a Global Assessment*. London: Parthenon, 177–190.
- Kaufmann, R., Fuchs, M., and Gosterxer, N., 2002: The soil fauna of an alpine glacier foreland: colonization and succession. *Arctic, Antarctic, and Alpine Research*, 34: 242–250.
- König, T., Kaufmann, R., and Scheu, S., 2011: The formation of terrestrial food webs in glacier foreland: evidence for the pivotal role of decomposer prey and intraguild predation. *Pedobiologia*, 54: 147–152.
- Kronstedt, T., 2004: Studies on species of Holarctic *Pardosa* groups (Araneae, Lycosidae). VI. On the identity of *Pardosa luciae* Tongiorgi with notes on *P. trailli* (O.P.-Cambridge) and some other species in the *P. nigra*-group. In Thaler, K. (ed.), *Diversität und Biologie von Webspinnen, Skorpionen und anderen Spinnentieren*. *Denisia*, 12: 281–290.
- Lindroth, C. H., 1945: *Die Fennoskandischen Carabidae. I. Spezieller Teil*. Göteborgs Kungliga Vetenskaps- och Vitterhets-Samhälles Handlingar, Sjätte Följden. Serie B, Band 4, No. 1: 1–709.
- Lindroth, C. H., 1961: Fam. Carabidae. *Svensk insektfauna*, 9 (Rekv. nr. 35): 1–209.
- Lindroth, C. H., 1985: The Carabidae (Coleoptera) of Fennoscandia and Denmark. Part 1. *Fauna Entomologica Scandinavica*, 15(1): 1–226.
- Lindroth, C. H., 1986: The Carabidae (Coleoptera) of Fennoscandia and Denmark. Part 2. *Fauna Entomologica Scandinavica*, 15(2): 227–498.
- Magnussen, T., 2010: Aerial dispersal of invertebrates on Svalbard and the influence of weather. Master thesis. University of Oslo, Oslo, Norway, 40 pp.
- Matthews, J. A., 1992: *The Ecology of Recently-Deglaciated Terrain: a Geoecological Approach to Glacier Forelands and Primary Succession*. Cambridge: Cambridge University Press, 386 pp.
- Matthews, J. A., and Whittaker, R. J., 1987: Vegetation succession on the Storbreen glacier foreland, Jotunheimen, Norway: a review. *Arctic and Alpine Research*, 19: 385–395.
- Mong, C. E., and Vetaas, O. R., 2006: Establishment of *Pinus wallichiana* on a Himalayan glacier foreland: stochastic distribution or safe sites? *Arctic, Antarctic, and Alpine Research*, 38: 584–592.
- Moreau, M., Laffly, D., Joly, D., and Brossard, T., 2005: Analysis of plant colonization on an arctic moraine since the end of the Little Ice Age using remotely sensed data and a Bayesian approach. *Remote Sensing of Environment*, 99: 244–253.
- Munster, T., 1927–1928: Tillæg og bemerkninger til Norges koleopterfauna. *Norsk Entomologisk Tidsskrift*, 2(3–4): 158–200, 262–298.
- Oksanen, J., Kindt, R., Legendre, P., O'Hara, B., Simpson, G. L., Solymos, P., Henry, M., Stevens, H., and Wagner, H., 2008: *Vegan: Community Ecology Package*. R package version 1.15-0 (<http://cran.r-project.org/>, <http://vegan.r-forge.r-project.org/>).
- Østbye, E., and Hågvar, S., 1972: List of terrestrial invertebrates of the Finse area, Hardangervidda, south Norway. Preliminary list. *Reports from The High Mountain Ecology Research Station, Finse, Norway*, 1972(2), 21 pp.
- Ottesen, P. S., 1996: Niche segregation of terrestrial alpine beetles (Coleoptera) in relation to environmental gradients and phenology. *Journal of Biogeography*, 23: 353–369.
- Palm, T., 1948: Kortvingar: Fam. Staphylinidae. Underfam. Micropeplinae, Phloeocharinae, Olisthaerinae, Proteininae, Omaliinae. *Svensk insektfauna*, 9 (Rekv. nr. 38): 1–133.

- Palmgren, P., 1976: Die Spinnenfauna Finnlands und Ostfennoskandiens. VII. Linyphiidae 2. *Fauna Fennica*, 29: 1–126.
- Paulus, U., and Paulus, H. F., 1997: Die Zönologie von Spinnen auf dem Gletschervorfeld des Hornkees in den Zillertaler Alpen in Tirol (Österreich) (Arachnida, Araneae). *Berichte des naturwissenschaftlich-medizinischen Vereins Innsbruck*, 80: 227–267.
- Phillipson, J., 1960a: A contribution to the feeding biology of *Mitopus morio* (F) (Phalangida). *The Journal of Animal Ecology*, 29: 35–43.
- Phillipson, J., 1960b: The food consumption of different instars of *Mitopus morio* (F) (Phalangida) under natural conditions. *The Journal of Animal Ecology*, 29: 299–307.
- R Development Core Team, 2008: R: a language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing, ISBN 3-900051-07-0 (<http://www.R-project.org>).
- Raffl, C., 1999: *Vegetationsgradienten und Sukzessionsmuster in einem Gletschervorfeld in den Zentralalpen (Öztaler Alpen, Tirol)*. Diploma thesis. University of Innsbruck, Innsbruck, Austria, 102 pp.
- Raffl, C., Mallaun, M., Mayer, R., and Erschbamer, B., 2006: Vegetation succession pattern and diversity changes in a glacier valley, central Alps, Austria. *Arctic, Antarctic, and Alpine Research*, 38: 421–428.
- Seniczak, A., Solhøy, T., and Seniczak, S., 2006: Oribatid mites (Acari: Oribatida) in the glacier foreland at Hardangerjøkulen (Norway). *Biological Letters*, 43: 231–235.
- Skubala, P., and Gulvik, M., 2005: Pioneer oribatid mite communities (Acari, Oribatida) in newly exposed natural (glacier foreland) and anthropogenic (post-industrial dump) habitats. *Polish Journal of Ecology*, 53: 395–407.
- Sørli, R., 2001: Ectomycorrhiza on *Salix herbacea* L. in the glacier foreland of Midtdalsbreen, Finse, Norway. Cand. Scient. thesis. University of Oslo, Department of Biology, Oslo, Norway, 75 pp. and 6 appendices.
- Spence, J. R., and Niemelä, J. K., 1994: Sampling carabid assemblages with pitfall traps: the madness and the method. *The Canadian Entomologist*, 126: 881–894.
- Thayer, M. K., 2005: Staphylinidae Latreille, 1802. In Kristensen, N. P., and Beutel, R. G. (eds.), *Handbook of Zoology IV Arthropoda: Insecta*, Part 38: 296–344.
- Vater, A. E., 2006: Invertebrate and arachnid succession on selected glacier forelands in southern Norway. PhD thesis. University of Wales Swansea, U.K., 372 pp.
- Venables, W. N., and Ripley, B. D., 2002: *Modern Applied Statistics with S*. Fourth edition. New York: Springer, 495 pp.
- Vetaas, O. R., 1994: Primary succession of plant assemblages on a glacier foreland—Bødalsbreen, southern Norway. *Journal of Biogeography*, 21: 297–308.
- Vetaas, O. R., 1997: Relationships between floristic gradients in a primary succession. *Journal of Vegetation Science*, 8: 665–676.
- Ytrehus, B., Bretten, T., Bergsjø, B., and Isaksen, K., 2008: Fatal Pneumonia Epizootic in Musk ox (*Ovibos moschatus*) in a period of extraordinary weather conditions. *EcoHealth*, 5: 213–223.
- Zar, J. H., 1999: *Biostatistical Analysis*. Fourth edition. Upper Saddle River. New Jersey, U.S.A.: Prentice Hall, 660 pp.
- Zingerle, V., 1999: Spider and harvestman communities along a glaciation transect in the Italian Dolomites. *Journal of Arachnology*, 27: 222–228.

MS accepted November 2011