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Primary Succession of Soil Mites (Acari) in a Norwegian Glacier Foreland, with Emphasis on Oribatid Species

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Abstract

The distribution of soil mites was studied in the foreland of the Hardangerjøkulen glacier in central south Norway, close to a glacier snout, which has been receding since 1750. Twenty sampling plots were distributed along a gradient spanning from 30 to 230 years, and five additional plots were in 10,000-year-old soil nearby. To standardize the microhabitat, all 320 soil cores (each 10 cm^2 and 3 cm deep) were taken in *Salix herbacea* vegetation. The main focus was on oribatids, and most juveniles were identified to species. Two small, parthenogenetic species were pioneers, with high abundance in young soil: *Tectocepheus velatus* and *Liochthonius* cf. *sellnicki*, although their dominance values decreased sharply with time. The youngest soils also contained unidentified Actinedida and Gamasidae, and pitfall traps revealed the rather large, predatory actinedid species *Podothrombium strandi*. The number of oribatid species increased gradually with soil age. The oldest soil contained 19 oribatid species, but only six of them, all in low densities, were unique to this soil. Parthenogenetic species were present in all age classes of soil. Although there exist few earlier studies on mite succession in glacial foreland soil, mites are clearly among the earliest colonizers along receding glaciers.

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Introduction

Alpine glaciers in many countries are receding due to global warming, leaving border areas with barren, pristine ground. Such glacier forelands represent a unique opportunity to study the processes of primary succession. As summarized by Kaufmann and Raffl (2002), chronosequences may be regarded as natural experiments and represent model systems for recovery from severe disturbance.

The botanical succession following glacial recession has been well studied in a number of countries (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). However, the faunal element of primary succession has been much less studied. Some early general faunistic studies in glacier forelands were made by Janetschek (1949, 1958) and Franz (1969), followed by Gereben (1994, 1995) on carabid beetles, Paulus and Paulus (1997) on spiders, and Zingerle (1999) on spiders and harvestmen. More recent and systematic invertebrate studies have been made by Kaufmann (2001, 2002), Kaufmann and Raffl (2002), and Gobbi et al. (2006).

Information about the early faunal succession in glacier forelands has been mainly based on surface-active invertebrates, often collected by pitfall trapping. Very few studies exist on the endogenous soil fauna, as for instance Collembola and Acari. To our knowledge, only four such studies have been published. They indicate that microarthropods are among the earliest colonizers, and species numbers increase with time. Kaufmann et al. (2002) studied the soil mesofauna in the Rotmoos glacier foreland in Austria, and Collembola were identified to species level. Hodkinson et al. (2004) identified species of Collembola, Oribatei, and Rhizopoda in a proglacial chronosequence at Spitsbergen. Skubala and Gulvik (2005) studied soil Oribatei in primary successions in two Norwegian glacier forelands. Seniczak et al. (2006) described mite communities from presumably dry habitats on three moraines of different age in the same study area as ours. Our study, however, covers a much larger number of sampling sites and a different vegetation community than Seniczak et al. (2006).

The present work on mites, with emphasis on Oribatei, is part of a general study of soil microarthropods in a Norwegian glacial foreland. A preliminary report on the Collembola species along the gradient was given by Hågvar (2004). We hypothesized the existence of a pioneer mite community consisting of species with good dispersal abilities, parthenogenesis (thelytoky), and the ability to live in harsh environments with little available organic material. We expected increasing species numbers and more complex communities with increasing substrate age. Comparison with other studies would reveal whether mite successions in glacial forelands have a local character, or whether common patterns or species combinations appear.

Methods and Study Area

STUDY AREA

The Hardangerjøkulen glacier in central south Norway covers 73 km^2 at altitudes between 1050 and 1850 m above sea level (a.s.l.). The study was performed close to a northern glacier snout named Midtdalsbreen (60°34′N, 7°28′E), in a foreland where the glacier has receded about 1100 m since A.D. 1750. The so-called Little Ice Age ended in Norway at that time. Figure 1 illustrates the position of our 25 sampling plots, each 10 × 10 m. We wanted to standardize the vegetation where samples were taken, so all selected plots contained more or less pure *Salix herbacea* L. vegetation. Twenty plots covered the chronosequence of the last

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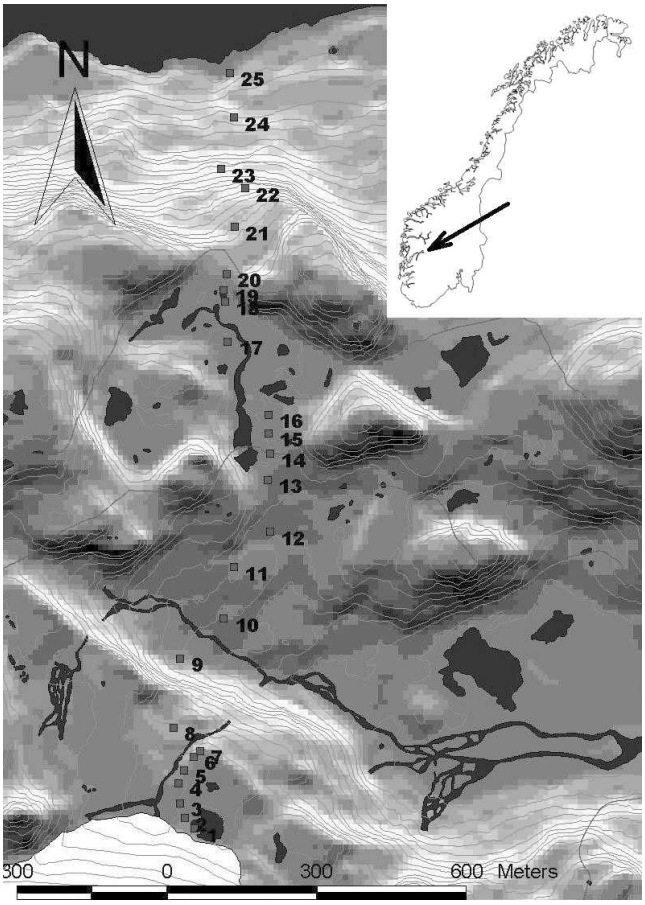


FIGURE 1. Position of the 25 sampling plots, from young soil close to the receding Midtdalsbreen glacier snout, to old soil at lake Finsevatn. The location of the study site in south Norway is indicated on the small map (60°34′N, 7°28′E).

250 years, and five plots represent about 10,000-year-old soil (age estimated by Svein Olaf Dahl, University of Bergen, personal communication) outside the 1750 moraine. Table 1 gives information on age, distance from glacier, and some soil parameters for all 25 sampling plots. Good documentation exists for the ages of plots 1–8, as well as for plot 13 (moraine ridge from 1934) and a 1750 moraine just outside plot 20 (Andersen and Sollid, 1971; Sollid and Bjørkenes, 1978). The ages of plots 9–12 were estimated assuming a constant retreat along a 510-m-long transect, due to the lack of terminal moraine ridges. In the 440-m-long transect between 1750 and 1930, a few small terminal ridges indicate some delays in the retreating process, but the ridges are not well dated. According to Atle Nesje (University of Bergen, personal communication), the retreat has probably been rather constant, although slow in this period. Our sampling sites have not been subject to reworking. The gradient studied lies between 1200 and 1400 m a.s.l., in the treeless low- and mid-alpine zone. More detailed data on vegetation, soil characteristics, etc. in the plots were given by Sørlie (2001).

SAMPLING

Ten to 16 soil cores were taken in each of the 25 plots; cores were 3 cm deep and 10 cm^2 in surface area. Half of the cores in each plot were collected on 25 August 2001, and the rest two weeks later. These were pooled since no significant phenological changes were expected during two weeks. Mites develop slowly in this area, with life cycles up to several years (e.g. Solhøy, 1975). To standardize the microhabitat, all soil cores were made in *Salix herbacea* vegetation. This prostrate shrub is a pioneer plant but occurs throughout the whole gradient. On soil older than about 70 years, it may create continuous carpets mixed with mosses and lichens in places where the snowmelt is late, so-called snow-beds (Moen, 1998). While small vegetation patches from the whole 10 × 10 m area had to be used in plots 1–8, the most homogeneous *Salix herbacea* carpet of 1 m^2 was used in older plots. The 320 soil cores were distributed in such a way that 80 cores were taken in each of four zones in the chronosequence (Sørlie, 2001): zone A (plots 1–8, age about 30–50 years), zone B (plots 9–13, age about 50–70 years), zone C (plots 14–20, age about 70–230 years), and zone D (plots 21–25, age about 10,000 years). Plots within each zone were relatively homogeneous in respect to vegetation cover and geomorphological features. Zone A was an elevated plateau with scattered patches of pioneer vegetation, 1365–1375 m a.s.l. Zones B and C were on a lower plateau, between 1325 and 1335 m a.s.l. The vegetation cover in zone B was still sparse, but *Salix herbacea* tended to develop more continuous carpets and distinct patches. Zone C contained a closed vegetation with some elements of *Salix* shrubs. Samples in zone D were taken in rich and well-established snow-beds on a north-facing slope between 1218 and 1318 m a.s.l.

Microarthropods were extracted with a modified high-gradient apparatus (Macfadyen, 1961). The animals were collected in benzoic acid and further preserved by adding alcohol. After heating to 60 °C, floating animals were submerged with a fine brush. A little glycerol was then added, and the alcohol was evaporated. The animals were stored and counted in a mixture of glycerol and benzoic acid, in the same vials into which they had been extracted. This eliminates the work of transferring animals to new vials, and counting in glycerol is easy because the animals do not float around as they often do in alcohol. Microarthropods were first counted against a black background to spot the smallest, often white animals, and then against a white background for larger animals. Juvenile stages of most oribatids were also identified to species. All the extracted soil cores were analyzed for thickness of the organic layer, organic content (loss on ignition including roots, after drying at 105 °C), and pH. If the organic layer was deeper than our sample, the depth of this layer was taken from Sørlie (2001).

The pioneer fauna close to the glacier was of special interest. Therefore, surface active microarthropods within zone A were sampled with pitfall traps for 15 days from 24 August 2003 in plots 1–7. This period had several warm days with good conditions for arthropod surface activity. Each plot had six traps (diameter 4 cm, with ethylene glycol and a roof to keep precipitation out); two in completely vegetation-free ground with gravel and sand, two in patches of *Salix herbacea*, and two adjacent to small, pioneer tussocks of grasses (*Deschampsia alpina* and *Festuca* sp.). For comparison, eight pitfall traps were operated simultaneously in 10,000-year-old soil, in carpets dominated by *Salix herbacea* in plot 23.

The nomenclature of oribatids follows Weigmann (2006).

NUMERICAL ANALYSES

The data were subject to a detrended correspondence analysis (DCA; Hill and Gauch, 1980) using CANOCO 4.5. This analysis is based on a reciprocal averaging procedure where species and samples are represented in ordination space. Species are assumed to have a unimodal response curve, and the arch effect is removed

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TABLE 1

Age, distance from glacier (m), and some soil parameters for the 25 sampling plots. LOI = loss on ignition in %, including roots. The depth of the organic layer is given in mm. A, B, C, and D indicate four main age groups of the glacial terrain.

Zone	A								B					C							D				
Plot No.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
Distance	4	20	30	48	86	120	145	190	311	416	523	630	704	751	796	843	956	1028	1044	1093	1157	1244	1267	1384	1481
Age	32	33	34	36	41	45	47	48	52	56	59	63	66	72	94	113	153	180	198	227	10,000	10,000	10,000	10,000	10,000
LOI	4.0	5.3	3.3	6.4	7.3	7.8	5.5	11.6	7.6	6.3	5.2	4.6	17.0	16.5	7.8	7.8	43.7	39.3	20.1	23.8	25.2	30.4	39.2	76.3	54.1
pH	5.8	6.3	5.1	5.5	5.9	5.3	5.3	5.3	4.5	4.5	4.9	4.7	4.9	4.6	4.8	4.6	4.3	4.3	4.6	4.3	4.3	4.3	4.7	4.6	4.3
Org. layer	0	0	0	0	1.6	2.6	0.8	1.4	1.3	1.8	1.9	1.0	11.1	3.5	1.8	3.0	16.0	19.2	10.5	12.2	20.0	31.0	51.5	123.0	88.0

by detrending—i.e. dividing the first axis into segments and then centering the second axis on zero (Gauch, 1982).

Species data were log^e-transformed, all other options used the default settings of the program. Environmental variables (Table 1) were included in the analysis, but the axes were not constrained. The DCA was employed to estimate the beta-diversity of the Oribatei community in the foreland, to indicate which environmental factors have the strongest structuring effect on the species composition, and where each taxon has its estimated highest abundance along the time gradient since deglaciation.

Results

SOIL SAMPLES

Table 2 shows the mean densities of different Oribatei species in the four zones of different age. The youngest soils in zone A contained only 3 oribatid species, with *Tectocepheus velatus* as the dominant one (18,900 m^{-2}). The two other pioneer oribatids were *Liochthonius* cf. *sellnicki* (7000 m^{-2}), and a single record of *Oromurcia bicuspidata*. The number of oribatid species increased to 8 in zone B, 13 in zone C, and 19 in zone D. The total density of oribatids was rather high close to the glacier and increased only slowly throughout the age gradient, from about 26,000 in zone A to 41,000 m^{-2} in the oldest soil.

The occurrence of other mite groups is shown in Table 3. In zone A, Actinedida were well represented (6100 m^{-2}), including a few Scutacaridae. Even predatory Gamasidae were recorded close to the glacier (1100 m^{-2}), including both adults and juveniles. The total mite density was rather high here: 33,100 m^{-2}. The densities of Actinedida and Gamasina increased with soil age, although the abundance of Actinedida did not increase from zone C to D. Rather few specimens of Acaridida and Uropodina were recorded.

Figure 2 illustrates the cumulative number of oribatid species in all 25 plots, and also the number of species in each single plot. While there were only two pioneer species in 30- to 40-year-old soil, six new species colonized the 40- to 60-year-old soil. After this phase of rapid colonization, no new species were recorded until about 150-year-old soil, when four new species appeared. Thirty years later, two additional species were found, and no new ones until six additional species appeared in the 10,000-year-old soil.

The dominance structure of the mite community changed markedly during succession (Fig. 3). The pioneer species *Tectocepheus velatus* and *Liochthonius* cf. *sellnicki* became gradually less dominant with time. In contrast, Actinedida increased their dominance value from A to C. The two most similar zones in dominance structure were B and C, indicating that the most dramatic change was early in the succession, from zone A to B. We observed a marked constancy in the dominance of Gamasina in all four zones, in the order of 3–5%.

Density data for all species or groups (except the very rare ones) have been visualized in Figure 4 for all 25 plots. Juveniles often dominated in many species, highlighting the necessity of identifying the juvenile stages. Different abundance scales had to be used for different species, but certain taxa had evident pioneer features, other taxa appeared more gradually, and some arrived late. The figure also illustrates that the occurrence along the gradient could be very irregular for some taxa, indicating local variation along the gradient. We also note that the abundance of a given species could vary considerably between the five plots in 10,000-year-old soil.

The two earliest pioneer species were both rather stable in zones A and B, but displayed different patterns of colonization on older terrain (Fig. 4). *Tectocepheus velatus* occurred at similar densities throughout the gradient, while *Liochthonius* cf. *sellnicki* nearly disappeared after 70 years. Gamasidae were fairly constant but at low abundance throughout the foreland. Actinedida showed generally high abundances in soils older than 150 years. Two species peaked in 50- to 150-year-old soil: *Camisia foveolata* and *Platynothrus punctatus*. Six oribatids (at the bottom of Table 2) were confined to older soils.

All the sampled environmental variables were significantly, or nearly significantly, intercorrelated (Table 4). There was a change in the substrate from the newly deglaciated till which had very little organic material and a relatively high pH, to the oldest soils that were more acidic and with an advanced pedogenesis.

ORDINATION RESULTS

The DCA ordinated the community of Oribatei along a first axis that is 3.1 S.D.-units long. This means that the response of the average taxon had a range of nearly one third of the gradient represented by the first axis and that few taxa occurred at both ends of the axis. This axis had an eigenvalue of 0.63. The subsequent axis values were 0.24, 0.18, and 0.04. An eigenvalue is a measure of how much variation in the data each axis accounts for (Vogt, 1999). The first four axes captured 73.3% of the variability of the taxa, whereas the first axis alone captured 64.1%. The first axis is significantly correlated with all environmental variables, indicating that there is one overriding factor structuring the community of Oribatei throughout the sampled terrain. This factor can be interpreted as a time factor, because the first axis was positively correlated with distance from the glacier ($r = 0.93$), time since deglaciation ($r = 0.89$), loss on ignition ($r = 0.80$), and depth of organic layer ($r = 0.71$), but had a negative correlation with pH ($r = -0.52$). This colinearity of soil variables is a common feature of glacier forelands (Matthews 1992). The critical value of the *r*-coefficient, two-sided and $\alpha = 0.05$, is |0.381| (Zar, 1999). The second DCA-axis was significantly correlated with thickness of organic layer ($r = -0.4$), and loss on ignition was correlated ($r = -0.35$). The other variables fell far short of significance ($r < 0.2$).

A DCA-plot of the first two axes and taxa is shown in Figure 5. *Liochthonius* cf. *sellnicki* was the first species on the first

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TABLE 2

Density (thousands per m^2) of Oribatei species in glacial foreland zones of different age. + indicates densities <0.1. Juveniles were counted in most species. Parthenogenetic species are marked with *.

Taxon	Zone Age (years)	A 32–48	B 52–66	C 72–227	D 10,000
* *Tectocepheus velatus* (Michael, 1880)	adults	3.7	4.2	6.6	3.3
	juveniles	15.2	12.1	11.4	4.2
	sum	18.9	16.3	18.0	7.5
* *Liochthonius* cf. *sellnicki* (Thor, 1930)	adults	—	—	—	—
	juveniles	—	—	—	—
	sum	7.0	9.3	0.9	0.1
Oromurcia bicuspidata Thor, 1930	adults	—	1.1	2.0	2.2
	juveniles	+	1.4	4.0	4.7
	sum	+	2.5	6.0	6.9
* *Camisia foveolata* Hammer, 1955	adults	—	0.4	1.4	0.1
	juveniles	—	2.4	3.8	0.2
	sum	—	2.8	5.2	0.3
* *Platynothrus punctatus* (L. Koch, 1879)	adults	—	0.3	0.5	0.4
	juveniles	—	1.3	2.2	1.6
	sum	—	1.6	2.7	2.0
* *Sellnickochthonius immaculatus* (Forsslund, 1942)	adults	—	—	—	—
	juveniles	—	—	—	—
	sum	—	0.1	—	—
Mycobates sarekensis (Trägårdh, 1910)	adults	—	0.1	1.6	0.9
	juveniles	—	—	—	—
	sum	—	0.1	1.6	0.9
Fuscozetes sp.	adults	—	—	1.0	0.1
	juveniles	—	+	1.2	0.1
	sum	—	+	2.2	0.2
* *Nothrus borussicus* Sellnick, 1928	adults	—	—	—	0.3
	juveniles	—	—	+	2.1
	sum	—	—	+	2.4
* *Suctobelbella acutidens* (Forsslund, 1941)	adults	—	—	0.1	0.3
	juveniles	—	—	—	—
	sum	—	—	0.1	0.3
* *Suctobelbella* cf. *latirostris* (Strenzke, 1950)	adults	—	—	+	0.5
	juveniles	—	—	—	—
	sum	—	—	+	0.5
* *Oppiella neerlandica* (Oudemans, 1900)	adults	—	—	0.8	9.4
	juveniles	—	—	—	—
	sum	—	—	0.8	9.4
Edwardzetes edwardsi Berlese, 1914	adults	—	—	0.4	1.2
	juveniles	—	—	1.2	1.9
	sum	—	—	1.6	3.1
Oribatula tibialis (Nicolet, 1855)	adults	—	—	0.1	3.0
	juveniles	—	—	+	2.2
	sum	—	—	0.1	5.2
* *Brachychthoniidae*, indet.	adults	—	—	—	—
	juveniles	—	—	—	—
	sum	—	—	—	0.1
Eupelops plicatus (C. L. Koch, 1835)	adults	—	—	—	0.7
	juveniles	—	—	—	1.3
	sum	—	—	—	2.0
Melanozetes mollicomus (C. L. Koch, 1839)	adults	—	—	—	0.1
	juveniles	—	—	—	—
	sum	—	—	—	0.1
Chamobates sp.	adults	—	—	—	+
	juveniles	—	—	—	—
	sum	—	—	—	+
Belba verrucosa Bulanova-Zachvatkina, 1962	adults	—	—	—	+
	juveniles	—	—	—	—
	sum	—	—	—	+
* *Oppiella* cf. *nova* (Oudemans, 1902)	adults	—	—	—	+
	juveniles	—	—	—	—
	sum	—	—	—	+
Oribatei, indet.	adults	—	—	—	—
	juveniles	—	—	+	0.2
	sum	—	—	+	0.2

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TABLE 2

Continued.

Taxon	Zone Age (years)	A 32–48	B 52–66	C 72–227	D 10,000
Total abundance of Oribatei		25.9	32.7	39.2	41.2
Number of Oribatei species		3	8	13	19
Number of parthenogenetic species		2	5	8	10

DCA-axis, followed by *Tectocepheus velatus*. These two species thus pioneered the colonization. The next two taxa at the negative end of the first axis were *Fuscozetes* sp. and *Camisia foveolata*. The three species *Mycobates sarekensis*, *Platynothrus punctatus*, and *Oromurcia bicuspidata* had their modes around the middle part of the first axis, whereas the remaining taxa were clustered near the high end of the axis, and these taxa were the latest arrivals in the primary succession.

PITFALL TRAPPING

The pitfall catches are summed up in Table 5. Although mites often move very slowly, and are outnumbered by, for instance, Collembola in pitfall traps, the catches illustrate the following points:

(1) Close to the glacier, various Actinedida and *Tectocepheus velatus* showed activity on the surface, in *Salix herbacea* vegetation, adjacent to grasses, as well as on vegetation-free patches. Actinedida dominated the catches both on 30- to 40-year-old soil and on 40- to 50-year-old soil, and the catches were not very different in the three habitats. Obviously, mites have no problems in passing vegetation-free patches. Among them was the large, fast-running red predatory species *Podothrombium strandi* Berlese, 1910. A few predatory Gamasidae were also trapped on young soils, in vegetation-free patches and adjacent to grasses.

(2) In 30- to 50-year-old soils, the traps contained what we expected among Oribatei, namely *Tectocepheus velatus* and a Brachychthoniidae, probably *Liochthonius* cf. *sellnicki*. However, a juvenile of *Camisia foveolata* on plot 7 (47 years) indicated a slightly earlier colonization than shown in Figure 4.

(3) The catches from plot 23 in old soil illustrate that oribatids do fall into pitfall traps if they are abundant. Among the six species caught, *Oromurcia bicuspidata* dominated, indicating a higher surface activity than the other ones. This species was a rather rapid colonizer, appearing as juvenile already in plot 7, and as adult in plot 13 (Fig. 4).

Discussion

COMPARISON WITH OTHER GLACIER FORELANDS

Our study showed that certain mites colonize virgin soils rapidly, establishing high densities in patches of pioneer vegetation close to the glacier. Half of the oribatid species present in the 250-year-old foreland were established after 60 years. Only six additional species were found in the 10,000-year-old soil.

To our knowledge only three earlier studies exist where oribatid species have been identified from forelands of receding glaciers. One study is from Svalbard in the High Arctic (Hodkinson et al., 2004). The second is from Jostedalsbreen glacier in Norway (Skubala and Gulvik, 2005). Juveniles were not identified in these two, and the latter was without density estimates on species level. The third is by Seniczak et al. (2006), who sampled quantitatively along the same gradient as in the present study. However, they sampled only on three moraine ridges from 1955, 1934, and 1750. The species number increased with age, but their presumably drier habitats may explain some differences in species composition compared with the present samples from moister *Salix herbacea* snow-beds. *Camisia horrida* (Hermann, 1804) and *Liochthonius lapponicus* (Trägårdh, 1910) were common on the 1955 moraine, but were absent in the present study. Instead, *Camisia foveolata*, a more moisture-demanding species (Solhøy,

TABLE 3

Density of Acari (thousands per m^2), except Oribatei, in the glacial foreland zones A, B, C, and D.

Taxon	ZONE Age (years)	A 32–48	B 52–66	C 72–227	D 10,000
ACTINEDIDA					
Scutacaridae		0.1	2.0	1.1	0.1
Other Actinedida		6.0	15.8	26.3	28.6
Sum		6.1	17.8	27.4	28.7
ACARIDIDA					
				1.4	0.1
GAMASINA					
Gamasidae	Adults	0.2	0.4	0.4	0.8
	Juveniles	0.9	1.3	1.0	1.4
	Sum	1.1	1.7	1.4	2.2
Zerconidae			+	0.5	1.6
Gamasina indet.				0.2	
UROPODINA					
Uropodina, indet.			0.1		+
Abundance of Acari except Oribatei		7.2	19.6	30.9	32.6
Total abundance of Acari		33.1	52.3	70.1	73.8

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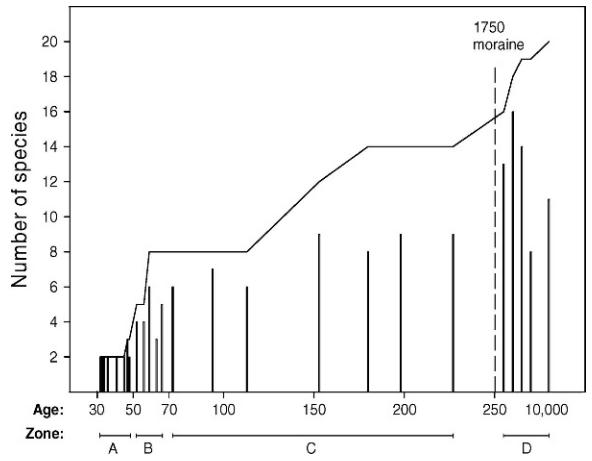


FIGURE 2. Number of oribatid species in each of the 25 sampling plots (columns) and the cumulative number of species with increasing soil age (continuous curve). The four age zones A–D are indicated.

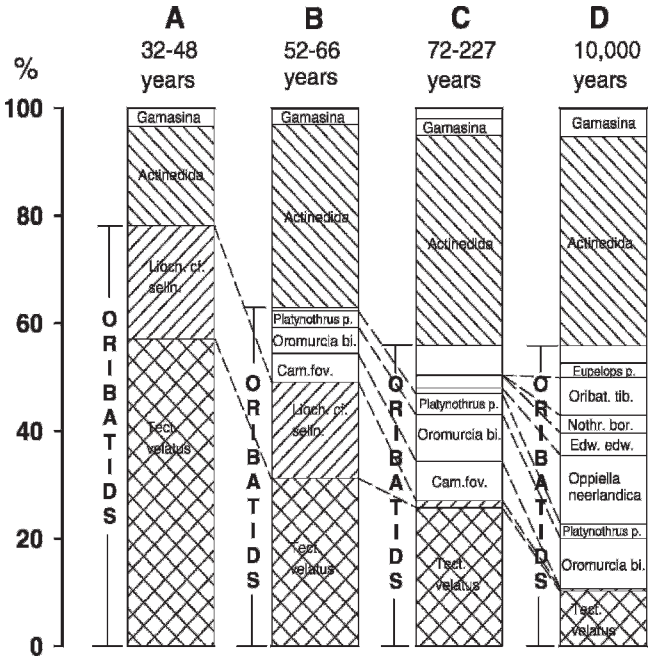


FIGURE 3. The dominance structure of the mite community in the four age zones A–D. Full names are given in Tables 2 and 3.

1976, and unpublished observations from Finse and Svalbard), was present in soils older than 50 years in our plots. Several species were, however, common to these two studies and showed roughly similar succession patterns, e.g., *Edwardzetes edwardsi*, *Fuscozetes* sp., *Platynothrus punctatus*, *Mycobates sarekensis*, *Nothrus borussicus*, *Oromurcia bicuspidata*, and *Tectocepheus velatus*.

The two sampling sites of Skubala and Gulvik (2005) near Jostedalsbreen glacier about 150 km further north, were very different from the harsh, alpine conditions in the present study. Their sites were only 300–375 m a.s.l., there was relatively short dispersal distance from established birch forest, *Salix* and *Betula* bushes were present already after 30 years, and the samples were taken in favorable microsites with accumulated organic matter. Still, the two small pioneer species from the present study, *Tectocepheus velatus* and *Liochthonius sellnicki*, belonged to the pioneers even there. Otherwise, the structure of the pioneer oribatid community differed in their two sites, indicating random colonization. On about 30-year-old ground at the Nigardsbreen snout, typical species were *Oppiella nova* and *Oppiella neerlandica*, while in a young foreland with unknown age at Austerdalbreen snout, *Oromurcia bicuspidata* and *Trichoribates novus* (Sellnick, 1928) were characteristic. About seven of the species near the Nigardsbreen snout can be characterized as typical forest species (Solhøy, unpublished data). Some true arctic/alpine species, common in the present study, were absent in the Jostedalsbreen forelands, e.g. *Camisia foveolata* and *Platynothrus punctatus*.

On Svalbard, Hodkinson et al. (2004) found that the early mite communities were similar in two proglacial chronosequences at Kongsfjord. *Tectocepheus velatus* was a pioneer species in both gradients, present in 16-year-old soil in one site, only surpassed by *Camisia anomia* Colloff, 1993, which was found after only 2 years. These two species were continuously present up to 150 years, and also in old soil of approximately 1900 years. In the better studied gradient, at Midtre Lovénbre glacier, the number of oribatid species increased to four after 37 years, when *Diapterobates notatus* (Thorell, 1871) and *Mycobates sarekensis* came in. The latter was an early colonizer in the present study, turning up after about 60 years.

Clearly, oribatid mites belong to the earliest colonizers of glacier forelands both in Norway and Svalbard, and *Tectocepheus velatus* is a general pioneer species. Also, Gamasina and Actinedida may colonize early. Gamasidae mites feed on a variety of animals, including Collembola (Wallwork, 1970). The lack of Actinedida and Brachychthoniidae in the 150-year-long gradient near Midtre Lovénbre on Svalbard is remarkable.

From Austria, Kaufmann et al. (2002) published the first study of the endogean soil fauna in a glacier foreland. While Collembola were identified to species, mites were only counted collectively. Mites were present after four years and reached a fairly stable density around 50,000 m^{-2} from about 50 years on. Again, mites proved to be among the first colonizers.

COMPARISON WITH PRIMARY SUCCESSION ON POST-INDUSTRIAL DUMPS

The colonization of post-industrial dumps is another case of primary succession. In an extensive work, Skubala (2004) showed that oribatids colonize dumps immediately. Many species might act as pioneers, and there were many possible pioneer communities. Even within the same substrate (e.g. coal mine), different dumps could have different pioneer communities and different succession patterns. Two species, however, were among the pioneers in all studies: *Tectocepheus velatus* and *Oppiella nova*. Also some species of Brachychthoniidae were early colonizers. As in the present study, *Tectocepheus velatus* remained during subsequent succession, but Brachychthoniidae tended to disappear after some time.

CONCLUSIONS

The DCA analysis supported the hypothesis that there is a succession of oribatid species prevailing at different times after deglaciation on the glacial foreland. The first DCA-axis was 3.1 S.D.-units long, which indicates that there is a strong gradient on the terrain. Few, if any, taxa will have a high abundance along all of the gradient, and the environmental variables were all correlated to the first DCA-axis. Terrain age and distance to glacier correlated most strongly to this gradient, but other environmental variables were also correlated and were probably effects of time since deglaciation—high colinearity in environ-

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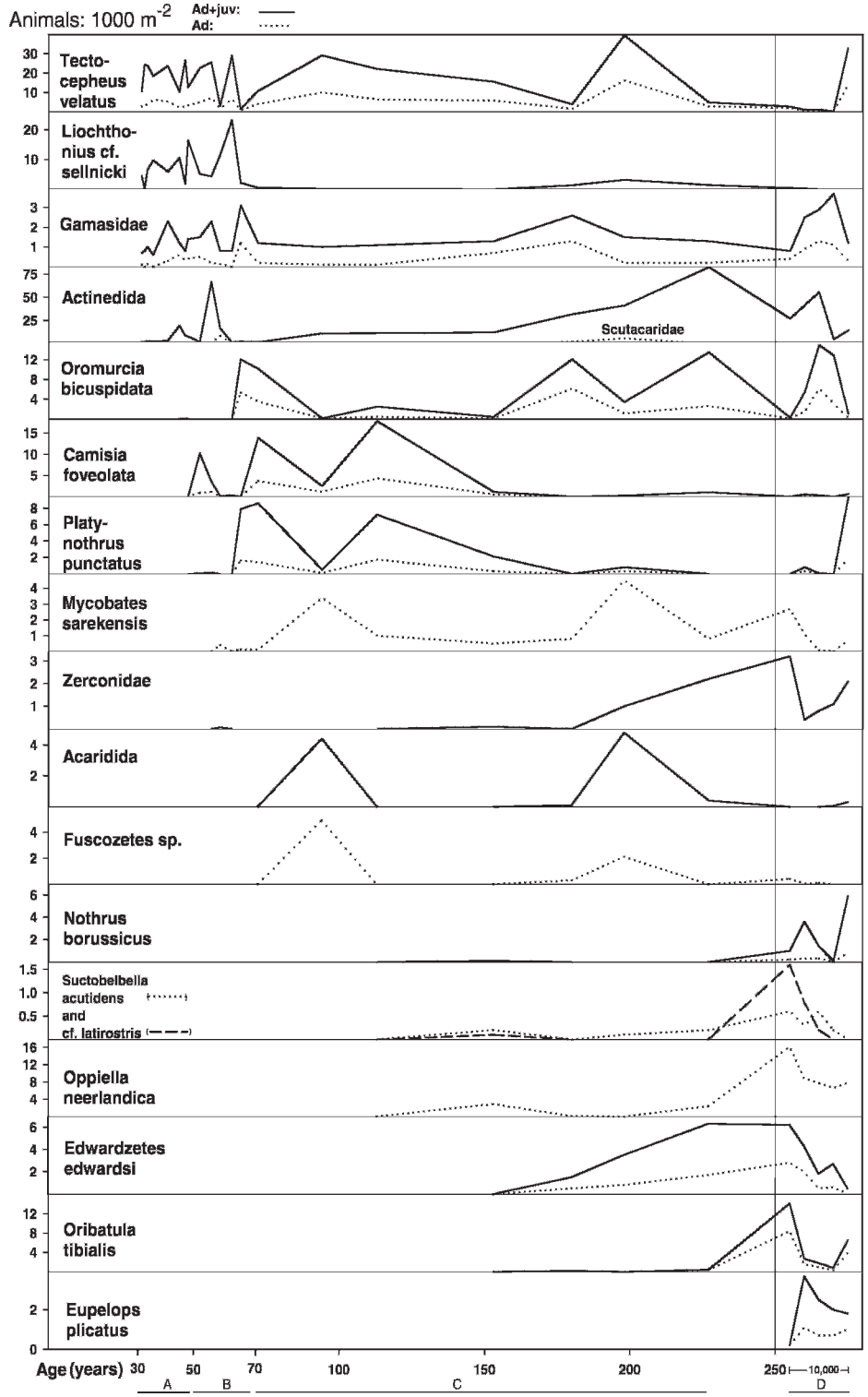


FIGURE 4. Density of the most abundant mites in each of the 25 sampling plots along the age gradient. Ad = adults, juv = juveniles.

TABLE 4

Correlations between sampled environmental variables. LOI = loss on ignition. Significant entries according to critical values of the correlation coefficient *r* (Zar, 1999) are boldfaced. Sample size $n = 25$, critical $|r| = 0.396$ ($\alpha = 0.05$, two-sided).

	Zone	Distance	Time	LOI	pH	Org. layer
Zone	1.00	**0.97**	**0.74**	**0.75**	**−0.80**	**0.66**
Distance	**0.97**	1.00	**0.70**	**0.80**	**−0.81**	**0.69**
Time	**0.74**	**0.70**	1.00	**0.72**	**−0.40**	**0.80**
LOI	**0.75**	**0.80**	**0.72**	1.00	**−0.53**	**0.91**
pH	**−0.80**	**−0.81**	**−0.40**	**−0.53**	1.00	−0.37
Org. layer	**0.66**	**0.69**	**0.80**	**0.91**	−0.37	1.00

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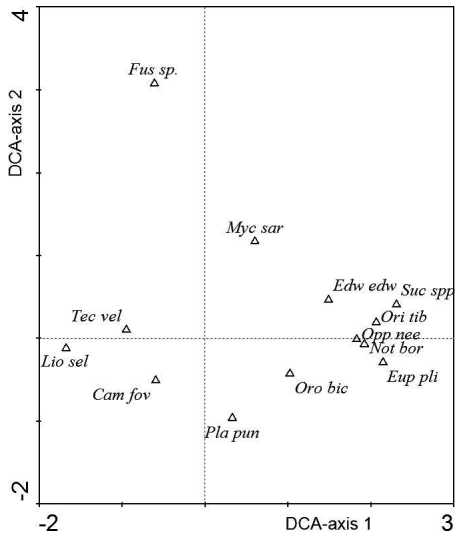


FIGURE 5. A species biplot of a DCA-analysis, where time since deglaciation and all sampled environmental factors strongly correlate to the first axis. Pioneers occur to the left, near the origin, seral species and late seral species are located near the middle and the high end of the axis, respectively. See Table 2 for full names of taxa.

mental variables precludes an analysis of the unique contribution of each factor to the structuring of the faunal community.

Oribatei appeared among the earliest colonizers in primary successions, both close to receding glaciers at different latitudes and altitudes, and on post-industrial dumps. Their great ability to colonize different substrates is due to a combination of easy dispersal, high species diversity including flexible generalists, and parthenogenesis in several species. Since colonization often has a random character, alternative pioneer communities and alternative succession patterns can be observed within the same type of habitat, even within relatively short distances. Skubala (2004) showed that pioneer species on post-industrial dumps were often absent from the neighborhood, and we support his hypothesis that small, pioneer oribatids like *Tectocepheus velatus* and Brachychthoniidae are dispersed by wind. The dispersal distance is relatively short in the present case, as they occur in the surrounding mountain habitats. Because they are also habitat generalists and parthenogenetic, they are successful pioneers. However, parthenogenetic species occurred along the whole gradient, representing more than one half of the species in all four zones (Table 2). While parthenogenesis is obviously an advantage for pioneer species, this way of reproducing is also well represented in more stable environments. Parthenogenesis in oribatids is widespread and occurs for instance in all species of Brachychthoniidae, Tectocephidae, Malaconothridae, Nanhermannidae, and Camisiidae (Norton, 1994). It is questionable whether parthenogenesis has evolved mainly for colonizing purposes.

Mosses were among the pioneer plants, and the cover of mosses varied considerably in soil samples from the inner zone A. However, the abundance of the two pioneer oribatid species or Actinedida was independent of the degree of moss cover. Since the present sampling was performed in one main vegetation type (*Salix herbacea*–dominated, occurring throughout the chronosequence), direct comparison with the botanical succession cannot be made. It is a challenge to describe the microarthropod succession in glacial forelands, with respect to the changes and variation in plant communities along the gradient.

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TABLE 5

Pitfall catches of Acari, 24 August–8 September 2003: Number per 10 traps.

	Sampling plot No.:	1–4			5–7			23
	Age (years):	32–36			41–47			10,000
	No. of traps:	8	8	8	6	6	6	8
	Vegetation:	Absent	*Salix herbacea*	Poaceae	Absent	*Salix herbacea*	Poaceae	*Salix herbacea* snow-bed
ACTINEDIDA								
Podothrombium strandi		10.0	1.3	14.0	7.0	7.0	35.0	
Other indet.		21.0	13.0	19.0	22.0	10.0	22.0	47.0
GAMASINA								
Gamasidae	Adults				1.7		1.7	1.0
	Juveniles	1.3						
	Sum	1.3			1.7		1.7	1.0
ORIBATEI								
Tectocepheus velatus	Adults	1.3						
	Juveniles	1.3	2.5				1.7	
	Sum	2.6	2.5				1.7	
Brachychthoniidae					1.7		1.7	
Camisia foveolata	Juveniles						1.7	
Oromurcia bicuspidata	Adults							71.0
	Juveniles							16.0
	Sum							87.0
Edwardzetes edwardsi	Adults							5.0
Eupelops plicatus	Adults							4.0
Belba sp.	Adults							16.0
Oribatula tibialis	Adults							18.0
Oppiella neerlandica	Adults							1.0
Oribatei indet.	Juveniles	1.3						1.0

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