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# Primary Succession of Springtails (Collembola) in a Norwegian Glacier Foreland

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## Abstract

The Collembola succession was studied in the Hardangerjøkulen glacier foreland in south-central Norway. Twenty sampling plots 30 to 230 years of age were distributed along a chronosequence where a glacier snout had been receding since 1750. Also, five plots 10,000 years of age were sampled. All soil samples were taken in *Salix herbacea* vegetation, in order to standardize the microhabitat. The youngest zone (30–50 years) contained 14 springtail species, mainly large, surface active generalists. Additional pitfall catches here revealed considerable surface activity of several species, also on vegetation-free areas. Even a three-year-young moraine contained at least three springtail species. Most pioneers also occurred in older soils. The cumulative number of species increased rapidly up to about 70 years, at which age 72% of all species had been recorded. Only five species in low numbers were confined to 10,000-year-old soil. A high density of *Folsomia quadrioculata* and *F. brevicauda* was noted at 50–70 years of age, and of *Tetracanthella brachyura* at about 100 years. Compared to oribatid mites, a higher number of springtail species colonized pristine ground. While the two pioneer oribatids were parthenogenetic, the dominant springtail pioneers were bisexual. Springtails are among the earliest colonizers along receding glaciers.

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## Introduction

As in several other countries, most glaciers in Norway are receding due to climate change (Norwegian Water Resources and Energy Directorate, 2009). Large areas of barren ground are made available for colonization of organisms, and a gradual development of organic soil. Such chronosequences represent unique possibilities for studying primary succession. Soil formation and plant succession in glacier forelands is rather well described and understood (e.g. Matthews, 1992; Raffl et al., 2006, and references therein). Succession of invertebrates is less well described, but has achieved increased focus during the last decade (e.g. Kaufmann, 2001, 2002; Kaufmann and Raffl, 2002; Kaufmann et al., 2002; Hodkinson et al., 2004; Gobbi et al., 2006; Hågvar et al., 2009). Still, the endogenous soil fauna has been little studied (Kaufmann et al., 2002; Hodkinson et al., 2004; Skubala and Gulvik, 2005; Seniczak et al., 2006; Hågvar et al., 2009). There seems to be only two such studies which have included Collembola at species level: Kaufmann et al. (2002) in the foreland of the Rotmoos glacier in Austria, and Hodkinson et al. (2004) in two forelands at Svalbard. These glaciers are among the southernmost and northernmost in Europe. A large part of the European glaciers are, however, situated in Norway, and the present study allows for comparisons about springtail succession in quite different parts of Europe.

The present work is part of an invertebrate study in a glacier foreland in Norway. The primary succession of mites in the foreland, with emphasis on oribatid species, was published by Hågvar et al. (2009). Based on the two earlier studies, Collembola were assumed to be early colonizers, and with increasing species diversity with time. Pioneer species were expected to be surface active generalists, while species demanding an organic layer were assumed to colonize gradually as the soil profile developed. A comparison with the mite succession would reveal which microarthropod group was the most efficient colonizer of pristine ground.

## Methods and Study Area

### *STUDY AREA*

Hardangerjøkulen glacier covers 73 km$^2$ and is situated in central south Norway, between 1050 and 1850 m above sea level (a.s.l.). In front of a northern glacier snout named Midtdalsbreen (60°34′30″N, 7°27′40″E), there is an 1100-m-long foreland gradient where the glacier has receded since A.D. 1750 (see map in Hågvar et al., 2009). Twenty sampling plots, each 10 × 10 m, were distributed along this gradient, in sites with rather well known age. The sampling sites have not been subject to reworking. Since patches of more or less pure *Salix herbacea* L. vegetation occurred in the whole chronosequence, it was decided to standardize the sampling to such vegetation. *S. herbacea* is one of the general pioneer species, but when the vegetation becomes closed, its optimal habitat is in snowbeds. Five additional sampling plots were situated in 10,000-year-old soil, in *S. herbacea* snowbeds outside the 1750 moraine. The gradient studied lies in the treeless low- and mid-alpine zone, between 1200 and 1400 m a.s.l. Detailed information on age, distance, and soil characteristics in each of the 25 samplings plots was given by Hågvar et al. (2009).

### *SAMPLING*

In every plot, 10–16 soil cores were taken, each 10 cm$^2$ in surface area and 3 cm deep. Half of the cores in each plot were sampled on 25 August 2001, and the rest two weeks later. No significant phenological changes were expected during two weeks,




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and the samples were pooled. A total of 320 soil cores were distributed so that 80 cores were from each of four main zones in the chronosequence (Sørlie, 2001; Hågvar et al., 2009). Plots within each zone were fairly homogeneous in respect to vegetation cover and geomorphological features. Zone A had scattered patches of pioneer vegetation and covered plots 1–8, with ages about 30–50 years. In zone B, the vegetation cover was still sparse, but *S. herbacea* tended to develop more continuous carpets and distinct patches. This zone covered plots 9–13, with ages about 50–70 years. Zone C contained a closed vegetation with some *Salix* shrubs and covered plots 14–20, with ages about 70–230 years. Zone D was the 10,000-year-old soil, with plots 21–25. Microarthropods were extracted with a modified high-gradient apparatus (Macfadyen, 1961).

To achieve a more complete picture of the pioneer springtail community, pitfall traps were operated for 15 days during a warm period, from 24 August 2003 in plots 1–7. In each plot, six traps of 4 cm diameter were operated, two in vegetation-free ground, two in *S. herbacea* patches, and two adjacent to pioneer tussocks of *Deschampsia alpina* (L.) and *Festuca* sp. For comparison, eight pitfall traps were operated simultaneously in the old soil of plot 23. More details about sampling were given by Hågvar et al. (2009).

The nomenclature of Collembola follows Fjellberg (1998, 2007).

### *NUMERICAL ANALYSES*

Multivariate statistics was employed as an exploratory data analysis. Common methods assume that species have a linear or a unimodal response to underlying gradients. Communities on glacier forelands will often display very strong gradients that are correlated and difficult to disentangle (Mong and Vetaas, 2006; Hågvar et al., 2009; cf. Matthews, 1992). Common methods often suffer from a distortion of the second ordination axis (the arch effect, the horseshoe effect) when applied to such data. Therefore, a non-parametric, iterative method, Non-metric Multidimensional Scaling (NMDS), was chosen (cf. Borg and Groenen, 1997). Species occurring in less than five sites were disregarded. All analyses were performed with R (R Development Core Team, 2008) and the packets *mgcv*, *vegan* (Oksanen et al., 2008), and *MASS* (Venables and Ripley, 2002).

First the dissimilarity indices based on the Bray-Curtis distance parameter were identified in order to detect underlying gradients (Faith et al., 1987). Then the NMDS was performed, and convergence was found after nine iterations. The root mean square errors between predictions and observations is 0.003 and maximum residual is 0.0083. The model has two dimensions and the stress-parameter is 13.015, compared to the initial value of the null-model, which is 18.495.

## Results

### *SOIL SAMPLES*

The mean number per soil core of each species in the four main zones is shown in Table 1. As many as 14 species were found in the youngest zone A, with *Desoria olivacea* as the dominant pioneer species. Other species with a density higher than an average of 1 specimen per soil core were *Tetracanthella wahlgreni*, *Desoria infuscata*, *Ceratophysella scotica*, and *Isotoma viridis*. Total springtail density in this zone was about 16 per soil core. In zone B, the species number increased markedly to 23, with 12 new species. Among these, *Folsomia brevicauda* and *Folsomia quadrioculata* dominated with mean densities of 12–14 specimens per soil core. *Desoria olivacea* had a similar density, and the mean total springtail density in zone B was 57 per soil core. Five new species were added in zone C, of which four were rare. However, *Tetracanthella brachyura* was very numerous with a mean value of 39 specimens per soil core, which corresponded to its density in the old soil in zone D. Because some rare species found in younger soil were not seen in zone C, the total species number in zone C was 24. Zone D had a springtail fauna very similar to zone C, both in species number and in density of the various species. The five new species in zone D were all in low numbers, and species number and density increased only a little from zone C to D. For most species, Table 1 shows whether they are parthenogenetic or bisexual (Fjellberg, 1974, 1998, 2007, and personal communication). It is also indicated whether each species is epedaphic (surface-living), hemiedaphic (mainly litter dwelling), or euedaphic (deeper living) (Fjellberg, personal communication; Hågvar, 1983).

Figure 1 illustrates how fast the cumulative number of species increased in young soils. After 70 years, 72% of the species in the gradient had colonized. The innermost plot contained only three species: *Desoria olivacea*, *D. infuscata*, *and Agrenia bidenticulata*. However, the other plots in zone A contained 5–11 species each. Figure 1 also shows that the plots in zone C had species numbers almost comparable to zone D.

The dominance structure of the springtail community changed greatly during succession (Fig. 2). The dominance value of the most abundant pioneer species, *Desoria olivacea*, was strongly reduced with time. The two oldest zones had a remarkable similar community structure, although soil age was very different.

Density data for the most abundant species (with maximum mean density above 3 specimens per soil core), as well as for total Collembola, are visualized in Figure 3 for all 25 plots. All these species were recorded in the 10,000-year-old soil, and only *Tetracanthella brachyra* and *Isotomiella minor* were lacking in soil younger than 70 years. Four species were found throughout zones A and B: *Desoria olivacea*, *Desoria infuscata*, *Isotoma viridis*, and *Ceratophysella scotica*. Their density in older soils varied. Four species lacking in zone A were more or less stable throughout zones B–D: *Folsomia quadrioculata*, *F. brevicauda*, *Friesea truncata*, and *Mesaphorura tenuisensillata*. *Mesaphorura macrochaeta* was mainly present in soils between 50 and 100 years of age. *Tetracanthella brachyura* had not colonized soils younger than 70 years, but was very abundant in most older plots. *Isotomiella minor* was mainly bound to the 10,000-year-old soil, but was also found in some of the oldest plots in zone C. One rare species not shown in Figure 3, *Agrenia bidenticulata*, was found only in the two innermost plots, close to the glacier. Total Collembola numbers were rather low in all plots within zone A, but increased within zone B, and were then rather stable through zone C (lower part of Fig. 3). A high variation in springtail numbers were seen in the five plots of age 10,000 years.

Table 2 shows mean Collembola numbers per soil core and standard error within each sampling plot. Collembola were found in all soil cores along the gradient, except for two of the ten cores in plot 1, and one of the ten cores in plot 4. With increasing age and distance, there was a gradual increase in loss on ignition and the depth of the organic layer, while soil pH decreased due to loss of cations and stabilized after about 150 years. Specific data on these environmental variables for each sampling plot were given by Hågvar et al. (2009). Distance, time, loss on ignition, depth of organic layer, and pH were all significantly, or near significantly, intercorrelated (Hågvar et al., 2009).

**TABLE 1**

**Mean density (specimens per soil core) of Collembola species in glacier foreland zones of different age. + indicates mean densities <0.1. First column indicates if the species is epedaphic (E), hemiedaphic (H), or euedaphic (EU). Second column shows if the species is parthenogenetic (P) or bisexual (B).**

| E: Ep<br>H: He<br>EU: Eu | P: Parth.<br>B: Bisex. | Species | Zone<br>Age (years) | A<br>32–48 | B<br>52–66 | C<br>72–227 | D<br>10,000 |
|---|---|---|---|---|---|---|---|
| E | B | *Agrenia bidenticulata* | | 0.1 | | | |
| E | B | *Desoria olivacea* | | 8.0 | 13.6 | 7.4 | 5.2 |
| E | B | *Desoria infuscata* | | 1.8 | 3.5 | 0.1 | 0.7 |
| E | B | *Desoria tolya* | | 0.5 | 0.1 | | 0.1 |
| E | B | *Isotoma viridis* | | 1.2 | 0.5 | 0.4 | 0.7 |
| H | | *Tetracanthella wahlgreni* | | 2.1 | 0.2 | 2.9 | 0.4 |
| H | B | *Ceratophysella scotica* | | 1.4 | 2.9 | 0.9 | 0.2 |
| H | B | *Lepidocyrtus lignorum* | | 0.1 | 0.1 | + | 0.1 |
| EU | P | *Oligaphorura schoetti* | | 0.2 | 0.3 | | |
| E | B | *Bourletiella hortensis* | | + | 0.1 | + | 0.2 |
| H/EU | P | *Micranurida pygmaea* | | 0.1 | + | 0.3 | 0.1 |
| H | P | *Parisotoma notabilis* | | 0.1 | 1.8 | 1.0 | 2.0 |
| EU | | *Willemia anophthalma* | | + | | 0.4 | 0.1 |
| H | P | *Arrhopalites principalis* | | + | | | |
| H | B | *Folsomia quadrioculata* | | | 12.2 | 5.2 | 6.8 |
| H | B | *Folsomia brevicauda* | | | 14.3 | 15.1 | 26.3 |
| H | B | *Friesea truncata* | | | 1.1 | 6.3 | 6.9 |
| EU | | *Mesaphorura macrochaeta* | | | 3.7 | 0.8 | + |
| EU | | *Mesaphorura tenuisensillata* | | | 1.9 | 5.1 | 1.0 |
| EU | B | *Protaphorura pseudovanderdrifti* | | | 0.2 | 0.2 | 1.1 |
| EU | | *Willemia denisi* | | | 0.2 | 0.1 | 0.1 |
| H | P | *Pseudanurophorus binoculatus* | | | + | | + |
| H/EU | B | *Desoria* cf. *fennica* | | | + | | |
| H | P (?) | *Parisotoma ekmani* | | | 0.1 | 0.1 | + |
| E | B | *Sminthurides malmgreni* | | | + | | |
| H | | *Neanura muscorum* | | | + | + | |
| H | B | *Tetracanthella brachyura* | | | | 39.0 | 39.8 |
| EU | P | *Isotomiella minor* | | | | 1.1 | 7.2 |
| H | | *Folsomia palaearctica* | | | | + | |
| H | B | *Friesea mirabilis* | | | | + | + |
| H/EU | P | *Pseudanurophorus alticola* | | | | 0.1 | |
| H/EU | | *Micranurida forsslundi* | | | | | 0.3 |
| H | | *Megalothorax minimus* | | | | | + |
| E/H | B | *Desoria hiemalis* | | | | | + |
| H | P | *Folsomia bisetosa* | | | | | 0.1 |
| H | B | *Sminthurides* cf. *schoetti* | | | | | + |
| | | Total abundance | | 15.6 | 56.9 | 86.5 | 99.4 |
| | | Number of species | | 14 | 23 | 24 | 28 |

### *NUMERICAL ANALYSES*

Table 3 shows correlations between environmental variables and the two first NMDS-axes. All the environmental variables were significantly correlated to both axes, except pH, which was only significantly correlated to the first axis. The best subset of environmental variables with maximum rank correlation with community (Bray-Curtis) dissimilarities was determined. Out of the five environmental variables, the best model included only one, Distance, which correlates 0.69 to the first axis. At each species name in Figure 3, the score to the first NMDS-axis has been given. Since the first axis is correlated to distance (and age), the scores thus represent a statistical estimation of the sequence of succession. Species with negative correlations were among the pioneers in zone A. The two species with the highest values, *Tetracanthella brachyura* and *Isotomiella minor*, were found only in zones C and D. Figure 4 illustrates the position of each species graphically with the 25 sampling plots and environmental vectors. All plots within zone A (1–8) had negative first axis values, together with plots 9 and 12 from zone B. The other sites in zone B (10, 11, and 13) had values not very far from zero. The mixing of the remaining site numbers 14–25 illustrates the similarity in the springtail fauna between zones C and D. The pH value is negatively correlated to the other four environmental factors. Distance is strongly intercorrelated with organic layer and loss on ignition, but less with relative age.

### *PITFALL TRAPPING*

The pitfall trapping in plots 1–7 (Table 4) gave most of the species recorded in soil samples within zone A (Table 1). Also species usually regarded as hemiedaphic were surface active here. However, the relative number between species was quite different, since pitfall trapping mirrors surface activity. The catches were dominated by *Lepidocyrtus lignorum*, not only in most of the vegetated patches, but also on completely vegetation-free ground. Another abundant species in traps, *Isotoma viridis*, had highest

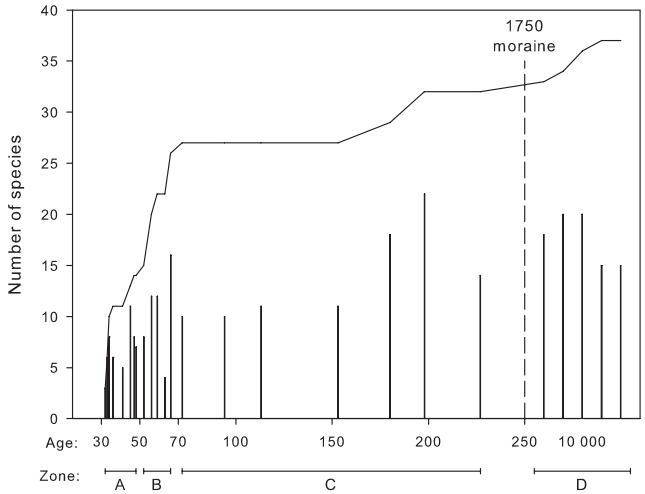


**FIGURE 1. Number of Collembola species in each of the 25 sampling plots (columns) and the cumulative number of species with increasing soil age (continuous curve). The four age zones A–D are indicated.**

catches on vegetation-free ground. The dominant species from soil samples, *Desoria olivacea*, was likewise very active in both vegetated and non-vegetated patches. Four additional species were taken in both vegetated and non-vegetated patches: *Desoria infuscata*, *Desoria tolya*, *Ceratophysella scotica*, and *Bourletiella hortensis*. *Parisotoma notabilis*, *Micranurida pygmea*, and *Tetracanthella wahlgreni* were taken in vegetated patches. Pitfall catches in 10,000-year-old soil gave surprisingly few species, and were strongly dominated by *Lepidocyrtus lignorum*.

Pitfall trapping in August 2008 on a three-year-young, vegetation-free moraine behind plot 1 revealed surface activity of springtails even here. At least three species were present: *Agrenia bidenticulata*, *Desoria olivacea*, and *Bourletiella hortensis*.

## Discussion

### *THE SUCCESSION PATTERN*

All environmental variables were strongly correlated to the first NMDS-axis. This is typical for glacier forelands, including a negative correlation between pH and other variables (e.g. Matthews, 1992; Mong and Vetaas, 2006). The NMDS-analysis confirmed a succession in the Collembola community, especially where the pioneer species of zone A were grouped together. The best model has only one variable because the environmental variables are all correlated—hence, they explain the same variance. Colonization rates of new species were highest before 70 years of age, and very few species were restricted to the oldest soil. A special feature in this foreland was the rather sudden appearance of some very abundant species: two *Folsomia* species in zone B, and *Tetracanthella brachyura* at about 100 years of age in zone C. It is an open question whether their absence in younger soils was due purely to different migration rates, or if each species demands a certain developmental stage of the soil profile.

In the present study, distance explained the springtail fauna better than age. This may be due to local variations along the gradient in factors which were not measured. Also, loss on ignition and the depth of the organic layer showed some unpredictable variations along the gradient (Hågvar et al., 2009). Kaufmann et al. (2002) pointed to local variations in microclimate and soil properties as possible "noise" in their study. Also they found

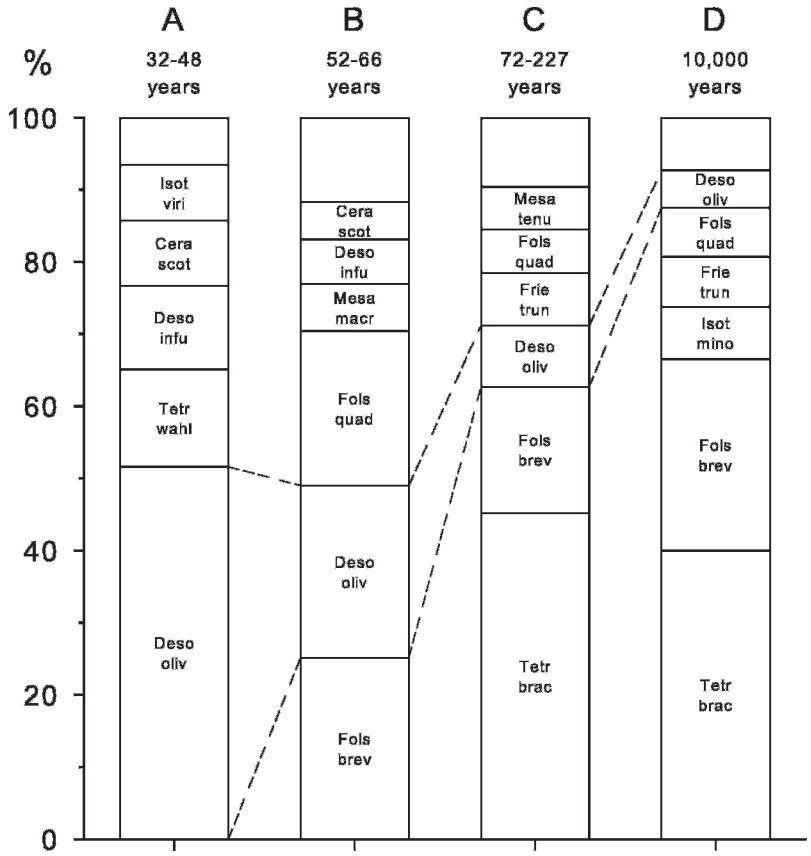


**FIGURE 2. The dominance structure of the Collembola community in the four age zones A–D. Full names are given in Table 1.**

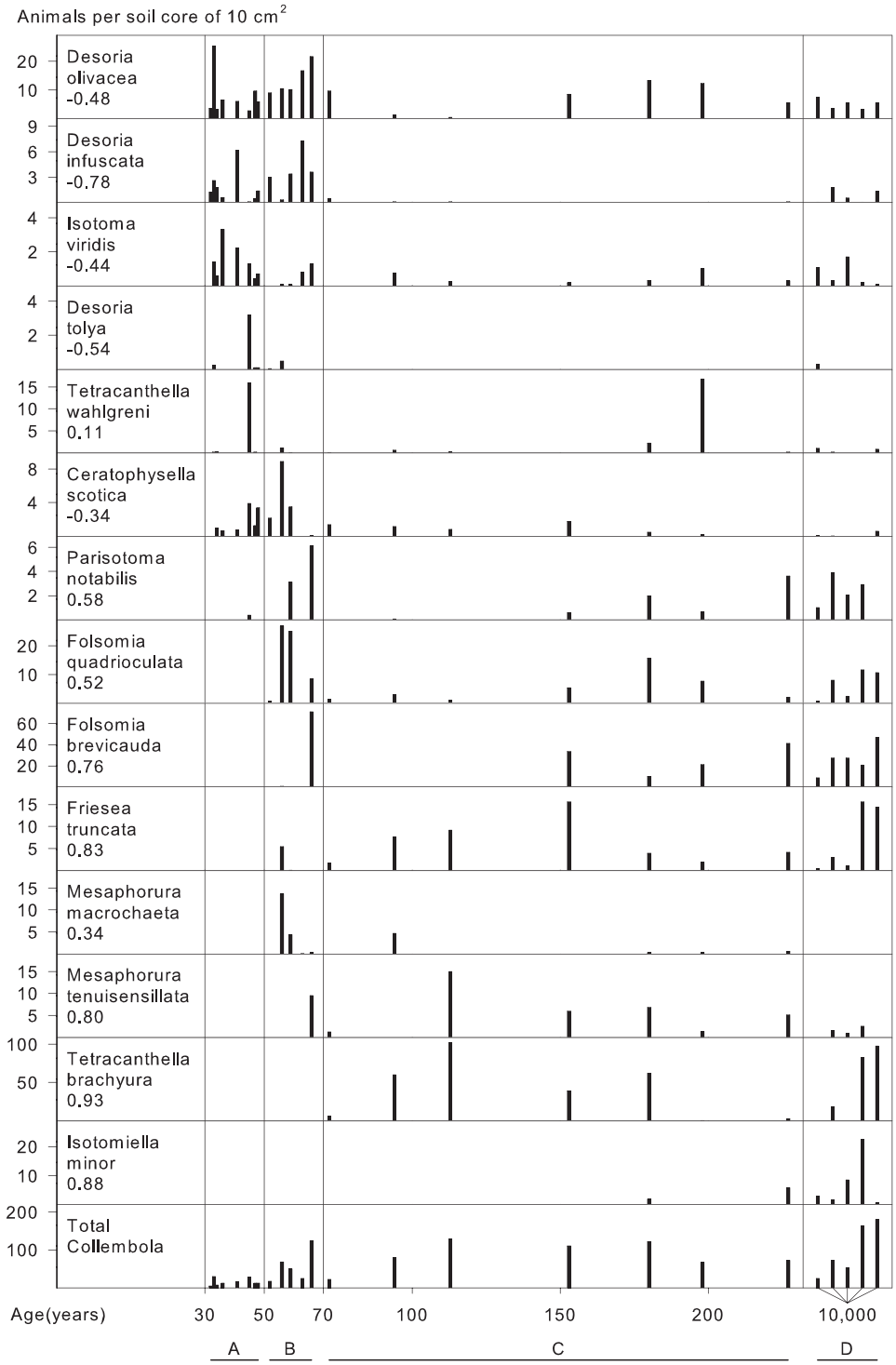


**FIGURE 3. Density of the most abundant Collembola species (above 3 per soil core of 10 cm$^2$) in each of the 25 sampling plots along the age gradient. The score on the first Non-metric Multidimensional Scaling (NMDS)-axis is given for each species. Bottom: total Collembola numbers.**

**TABLE 2**

**Mean number of Collembola per soil core (10 cm$^2$), and standard error, within each of the 25 sampling plots. $n$ = 10–16 cores per plot.**

| Zone | A | | | | | | | | B | | | | | C | | | | | | | D | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Plot | 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 |
| 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 |
| Mean | 5.3 | 29.8 | 7.4 | 12.5 | 15.9 | 28.3 | 12.4 | 12.1 | 17.2 | 69.1 | 50.1 | 24.9 | 124.1 | 22.4 | 79.6 | 129.4 | 111.1 | 122.3 | 66.8 | 72.6 | 25.1 | 72.6 | 54.3 | 164.4 | 179.9 |
| SE | 2.2 | 10.5 | 3.0 | 3.0 | 2.9 | 5.4 | 2.8 | 3.0 | 2.9 | 9.5 | 5.9 | 4.6 | 34.2 | 5.5 | 24.6 | 29.3 | 26.7 | 28.3 | 14.8 | 19.7 | 4.1 | 9.9 | 8.2 | 24.9 | 28.0 |

**TABLE 3**

**Correlations between environmental variables and the two first NMDS-axes. The critical value of a two-sided correlation with a sample size of 25 and α-value 0.05 is |0.396| (Zar, 1999). Significant correlations are bold-faced.**

| Axis | Distance | Relative age LN | Organic layer LN | Loss on ignition LN | pH |
|---|---|---|---|---|---|
| NMDS 1 | **0.84** | **0.68** | **0.80** | **0.79** | **−1.0** |
| NMDS 2 | **−0.55** | **−0.74** | **−0.60** | **−0.61** | −0.02 |

irregular, unpredictable variations in springtail density along the time gradient. It is possible that the springtail succession has a considerable element of randomness. This could be studied by having many replicates of study sites at the same age and distance, both within a given vegetation type, and in different vegetation types. The present study is in that respect limited, since sampling was restricted to one vegetation type along the whole gradient. Furthermore, the material contained low numbers of certain species, so that the absence of a species from a certain plot in Figure 3 may not be correct.

The fact that practically all the sampled pioneer patches of *S. herbacea* in zone A contained Collembola, and that the standard error relative to the mean in most plots within this zone was not very different from later successional stages (Table 2), indicates that establishment of pioneer populations is efficient.

## *COMPARISON WITH THE MITE FAUNA*

The pioneer community of mites in zone A was dominated by two small oribatids, *Tectocepheus velatus* (Michael, 1880), and *Liochthonius* cf. *sellnicki* (Thor, 1930) (Hågvar et al., 2009). As many as 14 Collembola species were present in this zone, mainly large, surface active generalists with pigment, eyes, and furca (Fjellberg, 1998, 2007). *Agrenia bidenticulata*, which was found only in the two youngest plots and on the three-year-young moraine behind, is more specialized and characteristic for cold, moist habitats in arctic and alpine areas (Fjellberg, 2007). Seven different families of Collembola were represented in zone A: Isotomidae, Entomobryidae, Hypogastruridae, Neanuridae, Onychiuridae, Bourletiellidae, and Arrhopalitidae.

While the two pioneer oribatids were parthenogenetic (Hågvar et al., 2009), the dominant pioneer species among Collembola were bisexual (Table 1). This may indicate that dispersal is no problem. Four rare Collembola species in zone A were parthenogenetic, but as in the mites, parthenogenetic Collembola were recorded at all age classes (Table 1). Even if a species may have a good dispersal ability, a short life cycle would increase its possibility to achieve a viable population rapidly in a pioneer site, in competition with other species. According to Fjellberg (1974), the dominant species, *Desoria olivacea*, seems to have a one year life cycle at 1200–1300 m altitude in this alpine area. This is also the case with *Desoria tolya*, *Isotoma viridis*, and *Parisotoma notabilis* from zone A. However, *Tetracanthella wahlgreni*, which probably has a two year life cycle here, also was abundant on one of the plots in zone A (Fig. 3, Table 1). In conclusion, the pioneer microarthropod community is not uniform with respect to parthenogenesis and life cycle length. A combination of good dispersal ability together with a wide habitat tolerance may be the key to the success of each pioneer species.

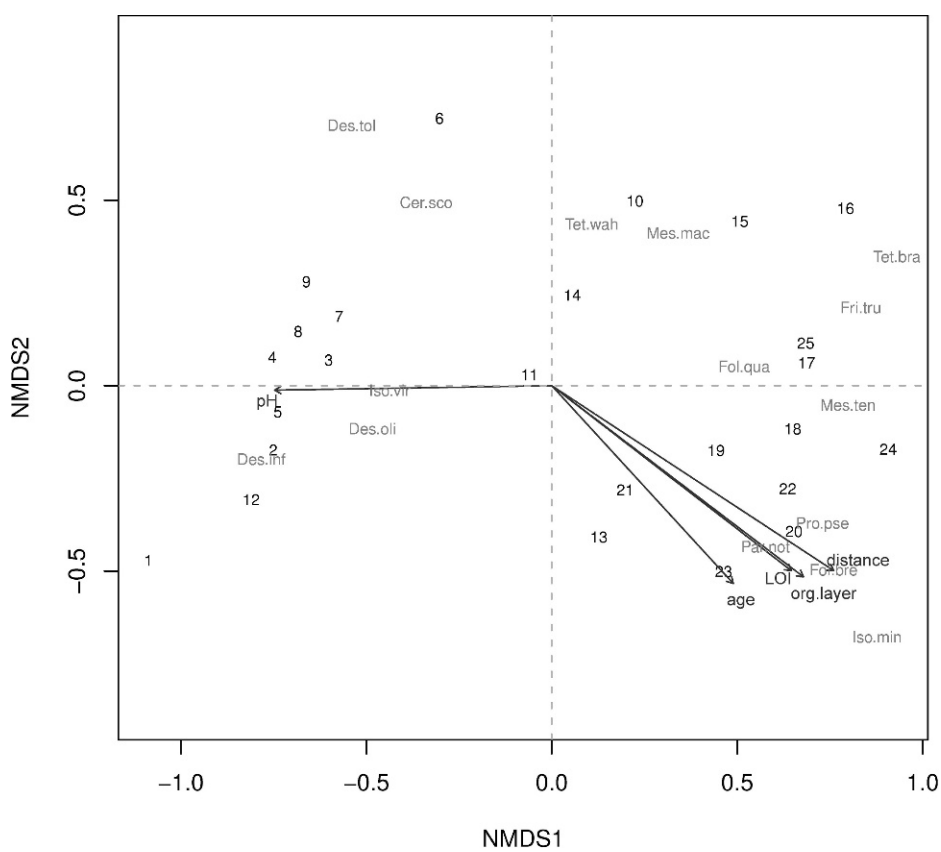


**FIGURE 4. This NMDS-plot of the first two axes illustrates the position of different species and sampling plots, as well as environmental vectors. Full species names are given in Table 1.**

**TABLE 4**

**Pitfall catches of Collembola, 24 August–8 September 2003 (number per 10 traps).**

| Sampling plot no.: | 1–4 | | | 5–7 | | | 23 |
|---|---|---|---|---|---|---|---|
| Age (years): | 34–38 | | | 43–49 | | | 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 |
| *Isotoma viridis* | 32.5 | 15.0 | 25.0 | 23.4 | 20.0 | 18.4 | 16.3 |
| *Desoria olivacea* | 10.0 | 56.3 | 25.0 | 5.0 | 6.7 | 11.7 | |
| *Desoria infuscata* | 7.5 | 12.5 | 10.0 | | | | |
| *Desoria tolya* | 5.0 | | | 3.3 | 3.3 | | |
| *Parisotoma notabilis* | | | | | | 1.7 | 1.3 |
| *Ceratophysella scotica* | 1.3 | 7.5 | 5.0 | 6.7 | 10.0 | 10.0 | |
| *Tetracanthella wahlgreni* | | | 7.5 | | 1.7 | | |
| *Micranurida pygmaea* | | 1.3 | | | | | |
| *Bourletiella hortensis* | 1.3 | | | | 1.7 | | |
| *Lepidocyrtus lignorum* | 57.5 | 21.3 | 110.0 | 71.8 | 116.9 | 223.8 | 191.0 |
| *Neanura muscorum* | | | | | | | 1.3 |
| Total numbers | 115.1 | 113.9 | 182.5 | 110.2 | 160.3 | 265.6 | 209.9 |

Pitfall trapping illustrated a considerable surface activity of both mites and springtails, also on vegetation-free ground. Even species with low density in soil samples could show high surface activity. Among mites, Actinedida dominated the pitfall catches, including the rather large, predatory species *Podothrombium strandi* Berlese, 1910 (Hågvar et al., 2009). The most surface active Collembola species, *Lepidocyrtus lignorum*, was very rare in soil samples. This may partly be due to active escape during sampling, but anyhow illustrates the value of combining soil samples with pitfall trapping in succession studies. Clearly, mites and springtails are not confined to the vegetated patches in the early succession, and many species are actively migrating on vegetation-free ground. While wind dispersal was suggested for small mites by Hågvar et al. (2009), several large springtail species, and also fast-running mites, may have been able to reach the pioneer ground by active migration. In a glacier foreland at Svalbard, Coulson et al. (2003) documented aerial transport of various insects and spiders by using sticky traps, but got no evidence of wind dispersal by springtails or mites.

While only 40% of the oribatid species in the gradient had colonized after 70 years (Hågvar et al., 2009), 72% of the springtail species had. This may be explained by a larger mobility in springtails. Figure 1 illustrates how the cumulative number of springtail species increased abruptly up to about 70 years before it flattened out. A common feature for oribatids and springtails is, however, that colonization rate was highest during zones A and B, and that nearly all species in the 10,000-year-old soil had colonized soils younger than about 200 years.

In zone A, springtail density was half that of mites, similar in zone B, and higher than mites in older soils (Hågvar et al., 2009). The high density of pioneer mites may be due to their smaller size.

## *COMPARISON WITH OTHER GLACIER FORELANDS*

Comparable glacier forelands are geographically far apart, and with a different microarthropod community: the Rotmoos glacier in Austria (Kaufmann et al., 2002), and two glaciers on Svalbard (Hodkinson et al., 2004). However, the springtail succession has several features in common in these three sites: (1) Collembola were among the earliest colonizers, with a documented presence after only 2–4 years. (2) Isotomidae and Hypogastruridae were two characteristic pioneer families, and total abundance reached a rather stable level after 50–70 years. (3) Species numbers tended to flatten out after about 50 years in Austria, after about 70 years in the present study, but on Svalbard species were continuously added during 150 years. The conditions in the High Arctic, with a very slow soil development, may explain this. The generalist *Folsomia quadrioculata* behaved, however, similarly in the present study as on Svalbard, colonizing after about 60 years. The Austrian foreland had three species in common with the present study: *Micranurida pygmaea* and *Isotoma viridis* after about 35 years, and *Parisotoma notabilis* after about 45 years. These ages correlate very closely with the present findings. Surface active Symphypleona may also be early colonizers, present after only two years on Svalbard, after three years in the present study, and after about 90 years in the Austrian site.

Blind, white, euedaphic (deeper-living) species were also present surprisingly early both in the present and the Austrian study. After 30–50 years in the Rotmoos foreland, *Mesaphorura critica* Ellis, 1976 and *Onychiurus* sp. were found. In the present study, *Oligaphorura schoetti* and *Willemia anophthalma* were present after 34 and 45 years, respectively. *Mesaphorura macrochaeta* occurred abundantly in plot 10, which was 56 years old and had an organic layer of only 1.8 mm.

## *HOW PREDICTABLE ARE THE MICROARTHROPOD COMMUNITIES IN GLACIER FORELANDS?*

Microarthropods are clearly pioneer organisms in glacier forelands, and may reach both high species numbers and total abundance during a few decades. In such general terms, both the mite and springtail primary succession close to glaciers may be rather predictable. But how predictable is the species composition at a certain successional stage? Are there many possible pioneer communities? Hodkinson et al. (2004) concluded that the succession of microarthropods in the two high arctic glacier forelands showed great similarity, with similar pioneer communities. This may be explained by the short distance between the sites. Hågvar et al. (2009) concluded that different glacier forelands within South Norway had different pioneer communities of oribatid mites and different succession patterns, depending on local conditions. For instance, different glacier forelands may be situated at quite different altitudes, some surrounded by forest, and others in high-altitude, treeless areas. Both because the microarthropod "source" fauna may have a local character, and

because colonization may be random, further studies will probably reveal alternative patterns of springtail succession in glacier forelands, even within a restricted area. Surface-active generalists of the families Isotomidae, Hypogastruridae, and certain Symphypleona may, however, turn out to be general candidates as pioneers.

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