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Animal Successional Pathways for about 200 Years Near a Melting Glacier: A Norwegian Case Study

Sigmund Hågvar, Mikael Ohlson and Daniel Flø

Additional information is available at the end of the chapter

Abstract

Here, we explore 200 years of arthropod succession by using dated moraines in a Norwegian glacier foreland. Surface active beetles (Coleoptera) and spiders (Aranea) were sampled by pitfall trapping, and springtails (Collembola) and mites (Acari) were extracted from soil samples. Newly deglaciated ground was rapidly colonised by a mixture of generalists and specialists, with various life strategies. Interestingly, the pioneer community was fed by three 'invisible' food sources: biofilm with terrestrial diatom algae, tiny pioneer mosses and chironomid midges whose larvae were pond-living and used ancient carbon that was released by the melting glacier as an energy source. The true 'super-pioneers' were biofilm-eating springtails, which tracked the melting ice edge closely. Most species of beetles and springtails colonised within 80 years, while spiders and oribatid mites needed a longer time span to colonise. Topography influenced the succession pattern. Among both surface-living macroarthropods and soil-living micro-arthropods, we distinguished between a 'dry' and a 'wet' successional pathway with different community structure. Most arthropod species persisted after colonisation, but certain species preferring open space or low temperature were gradually excluded. Comparisons are made with botanical succession. Sampling methods, material size, and taxonomic resolution were considered critical factors when studying arthropod succession.

Keywords: succession, beetles, spiders, springtails, mites, glacier foreland, moisture, alternative successional pathways, geo-ecology

1. Introduction

Due to climate change, glaciers are shrinking worldwide [1–3]. Simultaneously, 'waves' of different organisms try to colonise the newly exposed land. Glacier forelands give unique

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possibilities for studying primary succession. Instead of monitoring changes within a fixed plot over time, which indeed would be a very time-demanding approach, successions can be described by studying sites with known ages. Such a gradient in the terrain, where space is used as a substitute for time, is called a chronosequence [4, 5].

Most studies in glacier forelands have dealt with plant succession, and a thorough and long-lasting one has been performed near the glacier Storbreen in Norway [4]. A main conclusion is that age alone cannot predict the plant community. Local variations in microtopography, moisture, nutrients, substrate and exposure contribute in shaping the species composition. Instead of ending up with a 'monoclimax', the succession produces a 'polyclimax' with a mosaic of plant communities. A 'bulk' succession related only to the age of the ground contains 'noise' from a mixture of successional pathways. It has been argued for a 'geo-ecological' view on primary succession, where both biotic and abiotic factors were taken into considerations [4]. A recent study from Nigardsbreen foreland in Norway confirmed the modifying effect of microtopography on the floral succession [6].

Studies on animal succession near receding glaciers are fewer, and are mainly focusing on arthropods. In addition to the present case study, there are studies on arthropod succession in glacier forelands from the Alps [5, 7–11], from Svalbard [12–15], from Iceland [16] and from Norway [17–23].

In the following presentation, we have adopted the geo-ecological perspective. In other recent studies of invertebrate successions in Norwegian glacier forelands, a geo-ecological perspective has been successfully applied, when comparing succession patterns at different altitudes and climatic conditions [19, 20, 22, 23].

Hardangerjøkulen glacier in Southern Norway has been receding since the end of 'the little ice age' for about 250 years ago. The melting rate has been especially high during the last two decades, with about 20-m retreat yearly at one glacier snout near Finse (Midtdalsbreen). We have good data on earlier positions of the ice edge in this glacier foreland due to dated moraines. Since 2001, extensive zoological studies have been performed here to describe and understand arthropod succession patterns (**Figure 1**). These studies include soil-living micro-arthropods [24, 25], surface active beetles, spiders and harvestmen [26, 27], aerial transport of arthropods [28], studies on ancient carbon released by the glacier [29, 30], food choice of pioneers [31], as well as a special focus on early succession [32].

Time has come to combine these fragments into a holistic story about animal succession near a melting glacier. In addition to summing up the main results from these nine papers, the present syntheses will discuss some general aspects of succession:

a. *Comparison between botanical and zoological succession*

- Are there alternative succession patterns for arthropods, in the same way as there are alternative succession patterns for vegetation [4–6, 33]?

- Is there a strong progressive succession of arthropods on terrain ages of 20–50 years, as in plants [33]?

- Does animal and botanical successions differ in their early phases?

Figure 1. Sampling of soil for the extraction of microarthropods (springtails and mites). This snow bed habitat was 180 years old and situated 1 km from the glacier (plot no. 18). It had a well-developed *Salix herbacea* vegetation and a 2-cm thick organic soil layer. Microtopography in the surroundings created gradients from dry ridges to moist depressions.

b. *Questions about zoological succession*

- Do most arthropod species tend to persist after colonising [19, 20, 22, 23]?

- Is a geo-ecological perspective fruitful and relevant when considering mechanisms of facilitation and inhibition in zoological successions?

- Does arthropod succession pattern differ between surface-active macroarthropods and soil-living microarthropods?

- Is soil fauna succession in *Salix herbacea* snow bed vegetation related to the gradual development of an organic layer?

c. *Question about methods*

- Are sampling methods, material size and taxonomic resolution critical factors when studying arthropod succession?

2. Materials and methods

2.1. Study site

The study site was situated close to the 73-km² large Hardangerjøkulen glacier in central Southern Norway, between 1200 and 1400 m a.s.l., in the treeless low- and mid-alpine zone. **Figure 2** shows the foreland of a northern glacier snout named Midtdalsbreen (60°34′N, 7°28′E).
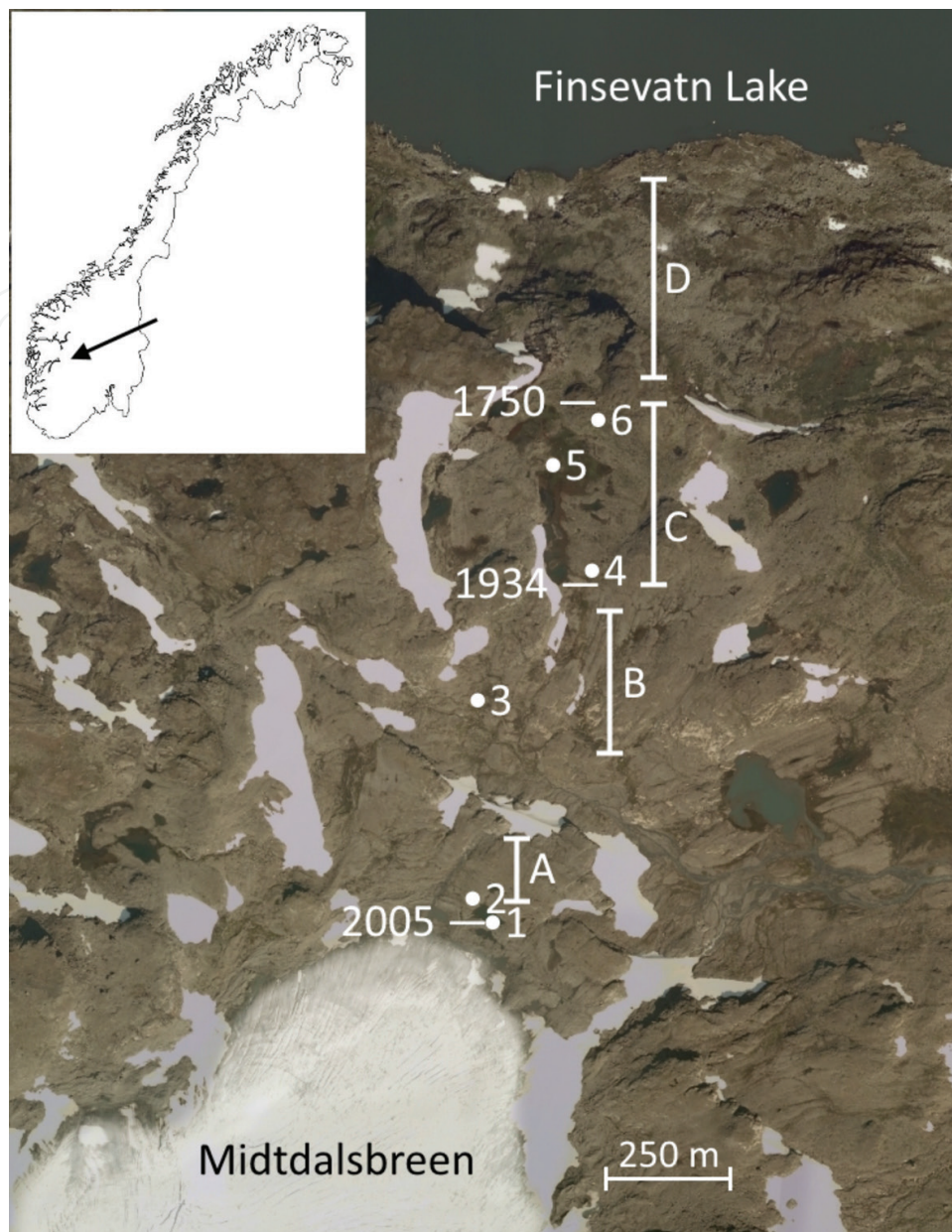
Figure 2. Aerial photograph of the glacier foreland, showing the position of moraines from 1750, 1934 and 2005. Beetles, spiders and harvestmen were sampled on the six numbered plots with the following ages: 3, 40, 63, 79, 170 and 205 years. Springtails and mites were sampled from eight plots in zone A (32–48 years), five plots in zone B (52–66 years), seven plots in zone C (72–227 years) and five plots in zone D (10,000 years). The small map shows the position of the foreland in Southern Norway. Modified from Ref. [26].

2.2. Microarthropod sampling

For the study of soil-living microarthopods, which are springtails (Collembola) and mites (Acari), we chose to keep the vegetation factor as constant as possible. All soil samples were taken in *S. herbacea* vegetation, which was found throughout the gradient. This tiny shrub belongs to the pioneer plants and shows no preference for snow cover on relatively young terrain [34, 35]. However, after about 70 years, it is mainly restricted to patches where snowmelt

is late (the so-called snow beds), where it forms rather continuous carpets. Plots 1–8 (zone A) were 32–48 years old, plots 9–13 (zone B) were 52–66 years old and plots 14–20 (zone C) were 72–227 years old. Plot nos. 21–25 (zone D) were outside the 1750 moraine which mark the end of the 'little ice age' in Norway, so these five plots had an age of about 10,000 years [24]. In each of the 25 study plots, microarthropods were extracted from 10 to 16 soil cores, 3 cm deep and with a surface area of 10 cm^2 [24].

2.3. Macroarthropod sampling

A different sampling strategy was chosen for surface-active macroarthropods, which were beetles (Coleoptera), spiders (Aranea) and harvestmen (Opiliones). Here, we aimed at collecting as many species as possible at each age, by covering a span of vegetation types. Pitfall traps were used at six sites with the following ages: 3, 40, 63, 79, 170 and 205 years. Twenty traps with a diameter of 6.5 cm were operated at each site and emptied every 2 weeks during two snow-free seasons (2007 and 2008) [26]. Traps were usually distributed in a topographic gradient from dry, lichen-dominated vegetation via an *Empetrum hermaphroditum* heath, to moist snow bed. In a nearby foreland of the same glacier (Blåisen glacier snout), these plant communities were characteristic products of succession [35]. Vegetation and the degree of cover were noted around each trap, a number of soil moisture data were taken, and catches from each trap and period were kept separate. Pitfall traps measure surface activity and not density, but they catch a high number of species and may be used in comparison between sites.

Figure 3. A small pond, 8 years old, in which larvae of chironomid midges assimilated ancient carbon from the sediments. From Ref. [30].

Aquatic invertebrates, for instance larvae of Chironomidae midges, were sampled from young ponds using a sieve. **Figure 3** shows a pond on an 8-year-old moraine.

2.4. Sticky traps and fallout traps

We performed extensive sampling of airborne arthropods on 3–6-year-old ground on the 2005 moraine [28]. Two types of traps were used: sticky traps and fallout traps. The sticky traps were placed on poles, up to 1-m height, and turned towards different directions. Fallout traps had their rim 5 or 11 cm above the ground to prevent surface-active arthropods to drop into them (**Figure 4**).

2.5. Gut content analyses

The food choice of different species was studied by analysing their gut contents under the microscope. Crop and gut contents of beetles and harvestmen were dissected out and spread on slides, embedded in glycerol. In most springtails, gut contents could be observed in ordinary slides for species identification. The large, spherical species *Bourletiella hortensis* was squeezed on the slide to spread the gut content.
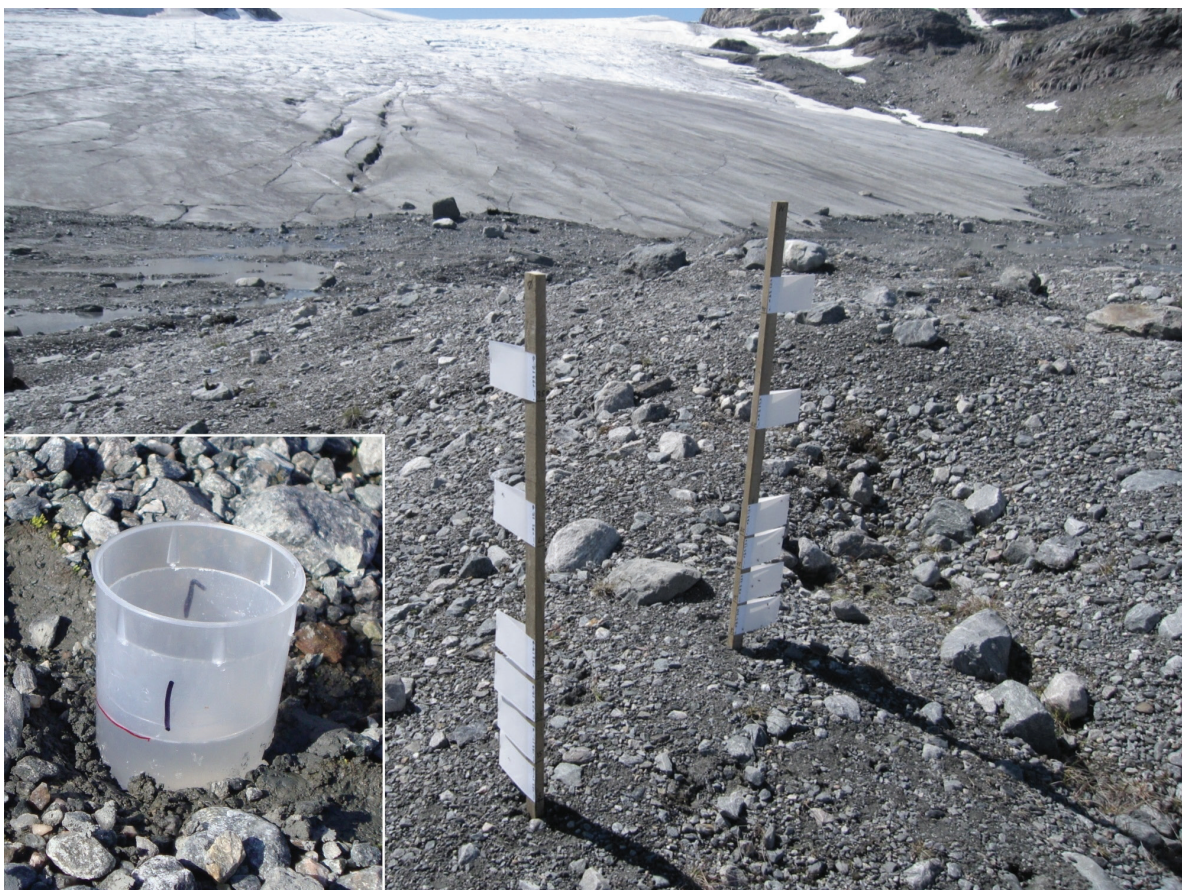

Figure 4. Sticky traps on a 6-year-old moraine, collecting airborne invertebrates from different directions, up to 1-m height. Inserted: open fallout trap with diameter 6.5 cm. From Ref. [28].

3. Succession patterns

3.1. Succession in species numbers

Figure 5 illustrates the cumulative species number for oribatid mites [24], springtails [25], and beetles and spiders [26], with increasing age of the ground. All groups showed a rapid addition of species during the first 80 years. Later, relatively few new species colonised among beetles and springtails. Oribatid mites and spiders, however, increased their cumulative species number considerably during the following 150 years. The five plots in 10,000-year-old soil had about the same number of springtail species as in 200-year-old soil, and with very few new species. Among oribatid mites, six new species were added. Beetles and spiders were not sampled in 10,000-year-old soil.

3.2. Succession in dominance structure

Another way of presenting succession is to examine the relative dominance among species. To illustrate the main changes among mites and springtails, data were lumped into the four mentioned age groups A–D (**Figure 2**), each with a similar number of sampling sites. In zone A (32–48 years), oribatids as a group made up about 80% of all mites, but this value later stabilised around 55%. The mite group Actinedida correspondingly increased their dominance in older soil, while predatory Gamasina mites were rare throughout the age gradient. In 10,000-year-old soil, the pioneer species *Tectocepheus velatus* was still present, but *Oppiella neerlandica* was now the dominant oribatid species [24].
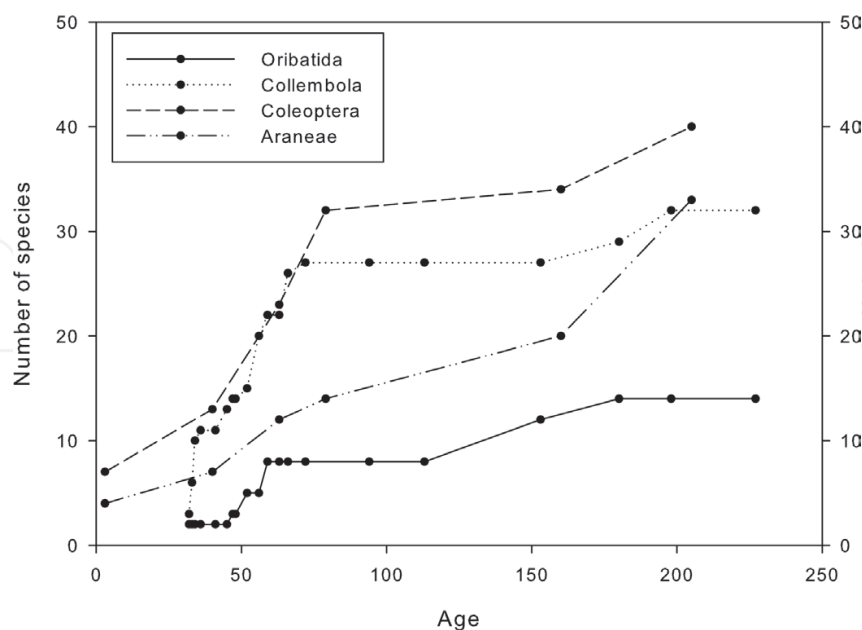

Figure 5. Cumulative species number of different arthropod groups, with increasing age of the ground. Surface active beetles (Coleoptera) and spiders (Araneae) were pitfall-trapped in various vegetation types, while springtails (Collembola) and oribatid mites (Oribatida) were extracted from soil in *Salix herbacea* vegetation. From Ref. [26].

Also, the springtail community showed considerable changes in dominance structure as the soil aged [25]. Two *Folsomia* species took over the dominance in zone B (52–66 years), and later *Tetracanthella brachyura* became the most abundant species. In short, there was a '*Folsomia* front' approaching the pioneer ground, and behind it followed a '*Tetracanthella* front'. The dominance structure of springtails was surprisingly similar in zone C (72–227 years) compared to the very old soil of 10,000 years in zone D [25].

Pitfall catches of beetles and spiders indicated clear changes in community structure during the 200-year study period. This is illustrated for beetles in **Table 1**, which shows the relative catches of the 13 most common species. *Bembidion hastii* dominated the catches strongly on 3-year-old ground but was still well represented on 40-year-old ground, for then to disappear on older ground. On 63- and 79-year-old ground, the community structure was very similar, being dominated by *Amara quenseli* and *Patrobus septentrionis*. While *A. quenseli* became very rare in older sites, *P. septentrionis* increased its dominance further and represented more than half of the catches on 160-year-old ground. However, on 205-year-old ground, *Liogluta alpestris* from the Staphylinidae family took over the dominance.

Table 2 lists the 14 most common spider species in the pitfall material. The catches on newly deglaciated ground was dominated by *Pardosa trailli, Erigone tirolensis* and *E. arctica*, while *Collinsia holmgreni* and *Hilaira* cf. *frigida* took over the dominance after 40 years. As in beetles,

Species	Family	3 yr	40 yr	63 yr	79 yr	160 yr	205 yr
Bembidion hastii	Carabidae	**81**	22	0	0	0	0
Nebria nivalis	Carabidae	**10**	**10**	1	2	<1	<1
Amara alpina	Carabidae	4	**23**	4	4	4	10
Geodromicus longipes	Staphylinidae	2	**10**	6	4	2	2
Simplocaria metallica	Byrrhidae	1	**9**	<1	<1	0	0
Amara quenseli	Carabidae	2	0	**30**	21	<1	1
Curimopsis cyclolepidia	Byrrhidae	0	0	**9**	3	0	0
Nebria rufescens	Carabidae	0	1	2	**9**	<1	<1
Patrobus septentrionis	Carabidae	0	23	29	32	**54**	13
Cymindis vaporariorum	Carabidae	0	0	5	1	**13**	1
Liogluta alpestris	Staphylinidae	0	0	7	11	6	**34**
Anthophagus alpinus	Staphylinidae	0	0	0	1	6	**13**
Chrysomela collaris	Chrysomelidae	0	0	0	<1	2	**8**
Other species		0	2	6	10	10	**16**
Total percentage		100	100	100	100	100	100

Table 1. Dominance structure of the beetle community on the ground of different age, expressed by pitfall catches. For each species, the highest dominance value is shown in bold numbers. Species with dominance values below 5% are collectively listed under 'Other species'.

Species	Family	3 yr	40 yr	63 yr	79 yr	160 yr	205 yr
Pardosa trailli	Lycosidae	**36**	14	6	26	1	1
Erigone tirolensis	Linyphiidae	**27**	19	1	1	2	<1
Erigone arctica	Linyphiidae	**25**	2	16	18	0	<1
Collinsia holmgreni	Linyphiidae	12	**34**	1	2	3	1
Hilaira cf. *frigida*	Linyphiidae	0	**30**	5	10	7	6
Tiso aestivus	Linyphiidae	0	0	**34**	23	9	19
Arctosa alpigena	Lycosidae	0	0	**26**	17	11	0
Scotinotylus evansi	Linyphiidae	0	0	6	2	**26**	5
Pelecopsis mengei	Linyphiidae	0	0	3	0	**12**	<1
Pardosa septentrionalis	Lycosidae	0	0	0	0	**8**	0
Ozyptila arctica	Thomisidae	0	0	0	0	**8**	<1
Pardosa paludicola	Lycosidae	0	0	0	0	<1	**39**
Oedothorax retusus	Linyphiidae	0	0	0	0	0	**10**
Gonatium rubens	Linyphiidae	0	0	0	0	1	**8**
Other species		0	1	2	1	12	11
Total percentage		100	100	100	100	100	100

Table 2. Dominance structure of the spider community on the ground of different age, expressed by pitfall catches. For each species, the highest dominance value is shown in bold numbers. Species with dominance values below 5% are collectively listed under 'Other species'.

spiders showed a similar community structure on 63- and 79-year-old ground, being dominated by *Tiso aestivus*, *Arctosa alpigena* and *E. arctica*. After 160 years, *Scotinotylus evansi* dominated the catches, and *P. paludicola* dominated after 205 years.

3.3. Do species persist after colonisation?

A study of macroarthropod succession in several Norwegian glacier forelands at different altitudes and environmental conditions concluded that most species persisted after colonisation [19, 20, 22, 23]. This was regarded as a fundamental difference as compared to plant succession patterns. However, the taxonomic resolution in these studies was low in certain animal groups. For instance, in the beetle family Staphylinidae, which was represented by a high number of species in our study (21 out of 40 beetles), most species were unidentified in the studies by Vater and Matthews. The number of traps used in their studies was also low in some cases.

The more extensive material from the present case study, where all beetles and spiders were identified to species, confirmed to a large degree the hypothesis of 'adding and persistence' of species [26]. However, there were some exceptions. Among beetles, *B. hastii* disappeared when vegetation became more or less closed after about 60 years. *Simplocaria metallica* became very

rare at the same time, and was not recorded after about 80 years. Likewise, the cold-adapted *Nebria nivalis* nearly disappeared after 80 years. *Curimopsis cyclolepidia* was only recorded in the range of 60–80 years. This range was also the clearly preferred for *A. quenseli*. It is interesting to note that the two last-mentioned species were not found in an extensive pitfall trapping in various neighbouring habitats of 10,000 years of age during 3 years (1969–1971) [36].

Among spiders, *P. trailli* and *E. arctica* nearly disappeared after 80 years. *A. alpigena* was numerous between 60 and 160 years but was absent after about 200 years. At 160 years, two new species appeared as very common: *P. septentrionalis* and *Ozyptila arctica*, but the first one disappeared in 200-year-old soil, and the second one nearly so.

Most soil microarthropods seemed to persist after colonisation. Among oribatid mites, the pioneer species *Liochthonius* cf. *sellnicki* was barely present after about 70 years [24]. Among springtails, the cold-loving pioneer species *Agrenia bidenticulata* gave up after about 50 years. There were several examples of rare species which 'disappeared' in older soils, but the small data do not allow firm conclusions about the presence or absence.

A general persistence of both macro- and microarthropods during succession indicates that these species have a high tolerance for each other and for changes in vegetation. Obviously, the concept of tolerance is as important as facilitation and inhibition when we try to understand succession.

3.4. Relations to environmental parameters

3.4.1. Parameters related to age

A detrended correspondence analysis (DCA) showed that terrain age was strongly correlated to the distance to the glacier, increased organic content in soil and falling pH values [24]. A species biplot of a DCA for mites sorted pioneer species, seral species and late seral species rather well into groups, confirming a successional process [24]. Correspondingly, a non-metric multidimensional scaling (NMDS) plot for springtails separated well the pioneer species. However, in contrast to the mite succession, which showed considerable difference between 72–227 years and 10,000 years, the NMDS plot for springtail communities confirmed a great similarity in these two age groups [25]. Concerning beetle and spider succession, an NMDS plot showed a clear succession, and the pioneer species were best separated. Also, vegetation cover was correlated with age and distance from the glacier [26].

Figure 6 shows a linear relation between age and thickness of the organic layer ($R = 0.83$, $F = 38.4$, $P < 0.001$). However, the variation was large. In **Figure 7**, species numbers of springtails and oribatid mites were related to the depth of the organic layer, and adapted curves indicated that species numbers tended to flatten out at about 10-mm organic layer. Pioneer microarthropod species have to be independent of an organic layer, and able to live on or close to the surface. Surface-living species are called epedaphic, litter-dwellers hemiedaphic and deeper-living species euedaphic. The two first groups typically contain larger species with eyes and pigmented body, while euedaphic species are often small, white and blind. **Figure 8** shows the number of springtail species from each of these categories (or transition
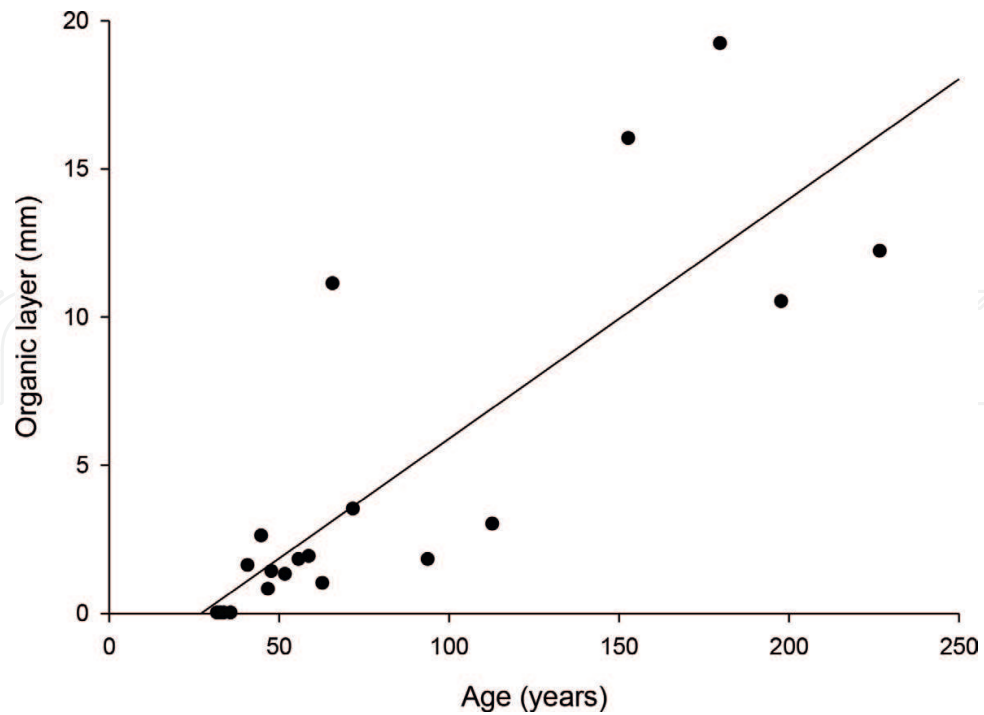
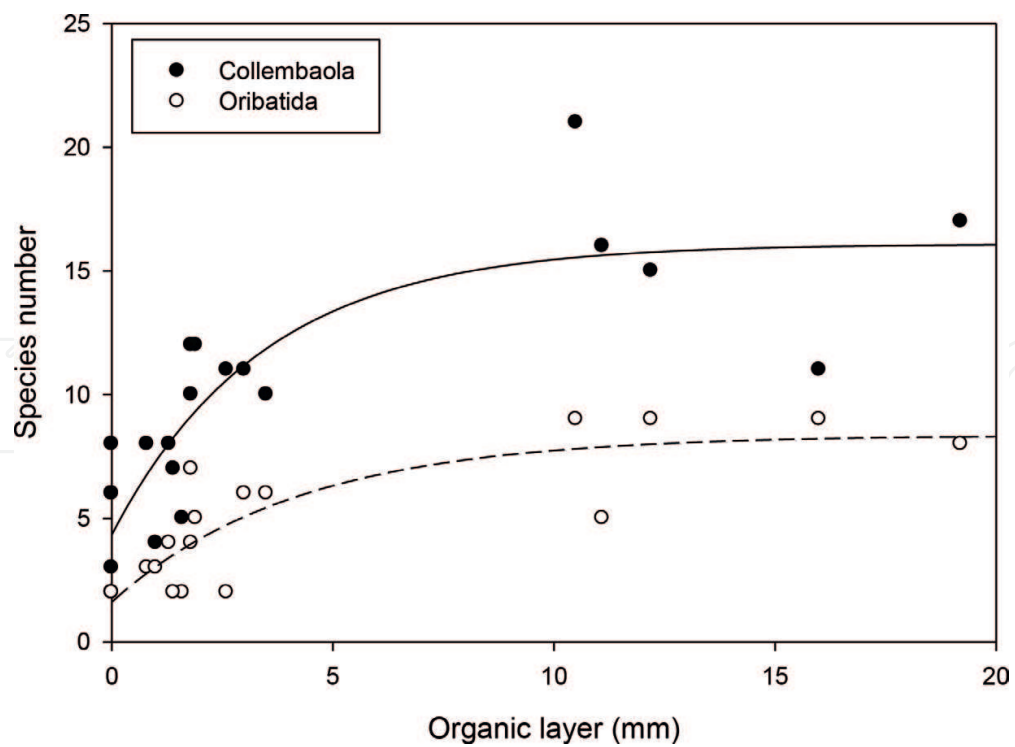**Figure 6.** Relationship between the age of soil and the thickness of the organic layer.

Figure 7. Adapted curves for the relationship between the thickness of the organic layer in soil and species numbers of springtails (Collembola) and oribatid mites (Oribatida).
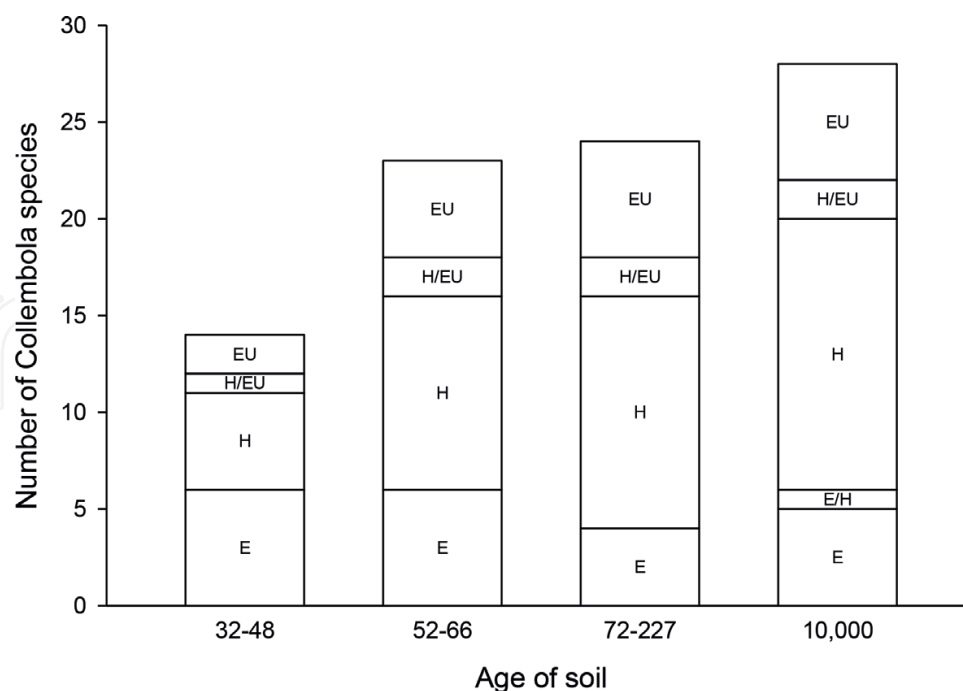
Figure 8. Structure of the springtail (Collembola) community at different age groups of the soil. E = Edaphic species, which are surface-living. H = Hemiedaphic species, which are litter dwellers. EU = Euedaphic species, which are deeper-living soil species.

categories) in soil of different age groups. It is a bit surprising that some hemiedaphic, and even two euedaphic species were recorded already in soil of 32–48 years of age. However, their presence may not be permanent. The organic layer was absent up to 36 years, and 1–3-mm thick in 41–48-year-old plots [24]. Later, the hemiedaphic species gradually became numerous, with 14 species in the very old soil. About five euedaphic species were established already at the age of 52–66 years, and the species number in this category changed little with further age.

3.4.2. A 'wet' and a 'dry' successional pathway

Local variation in soil moisture modified the succession pattern, among both surface-active macroarthropods and soil-living microarthropods. Direct correlation between soil moisture measured close to single traps, and the species collected there showed that the following beetles significantly preferred moist soil: *P. septentrionis, Geodromicus longipes* and *L. alpestris*. Three other species were clearly dry-ground dwellers: *Byrrhus fasciatus, Cymindis vaporariorum* and *A. quenseli* [37]. Among spiders, *T. aestivus* is an example of a dry-ground dweller, as all of 102 specimens were collected on dry ridges with lichen-dominated vegetation.

In **Figure 9**, the 'noise' from varying moisture conditions was identified by separating catches of beetles from typical 'wet' and typical 'dry' traps. We see how *P. septentrionis* dominated strongly in wet sites, while *A. quenseli* dominated the catches in dry sites nearby.

Earlier studies have considered soil moisture to be the most important ecological factor for ground-living beetles in Norwegian alpine areas [38]. This is in accordance with our results. We conclude that surface-active macroarthropods followed two parallel successional trends in the foreland: a dry and a moist pathway.

Also, the succession of soil animals was affected by moisture. In the same glacier foreland, oribatid mites have been studied on dry moraine ridges of known age [18]. This allows for a comparison of the oribatid community in dry soil with neighbouring, moist snow bed soil at two age groups: 45–47 years and 66–72 years. While the generalist *T. velatus* was well represented in both dry and wet habitats, *L. lapponicus* and *Camisia horrida* occurred only on dry ridges, and *L.* cf. *sellnicki* and *C. foveolata* only in the wet snow bed. This illustrates that species within the same genus may have quite different moisture preferences.

Figure 10 illustrates schematically wet and dry succession. Both pathways were reflected in the vegetation mosaic of the foreland. This is in accordance with studies in the Rotmoos foreland in the Austrian Alps, where the effect of local topography and exposure on various invertebrate groups was studied. The moisture regime was an important factor on a local scale, for all site ages [7].
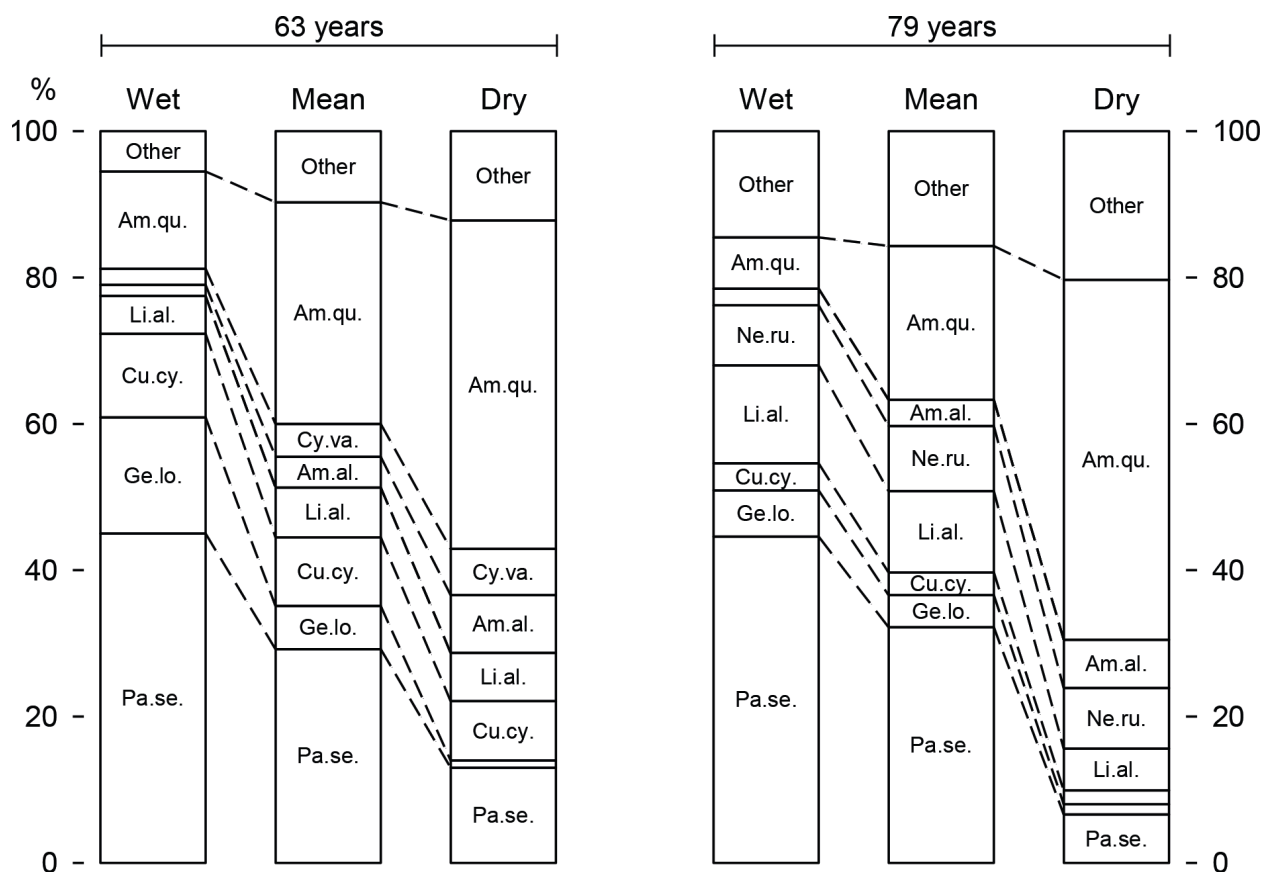

Figure 9. Effect of wet and dry ground on the structure of the beetle community. Both on 63- and 79-year-old plots, *Patrobus septentrionis* (Pa. se.) dominated on wet ground, and *Amara quenseli* (Am. qu.) on dry ground. Full names of the other species are *Amara alpina* (Am. al.), *Curimopsis cyclolepidia* (Cu. cy.), *Cymindis vaporariorum* (Cy. va.), *Geodromicus longipes* (Ge. lo.), *Liogluta alpestris* (Li. al.) and *Nebria rufescens* (Ne. ru.).
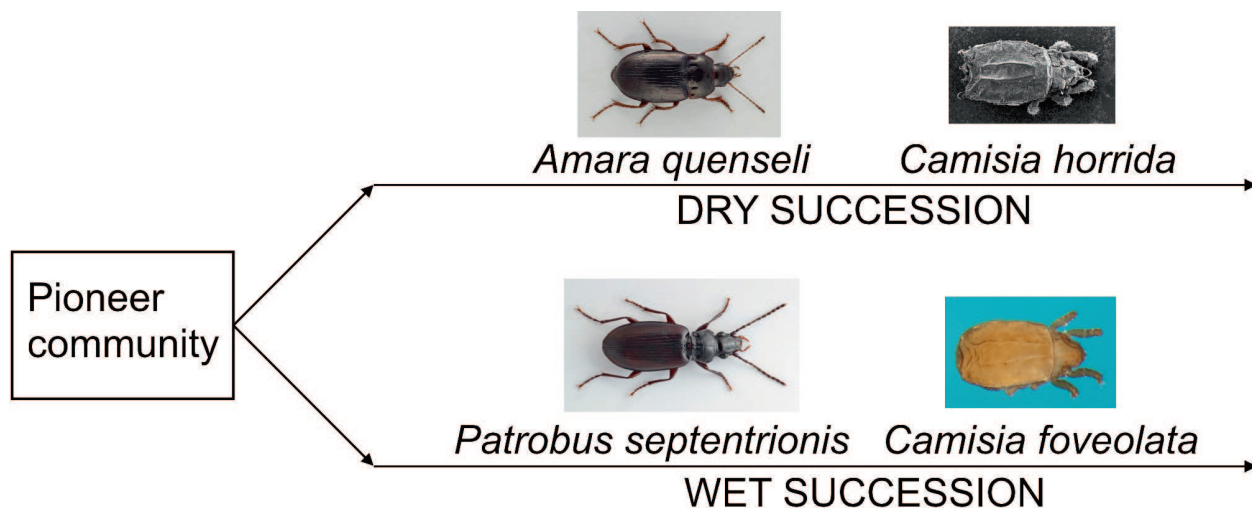
Figure 10. While the pioneer community is rather predictable, the further succession pattern differs in dry and wet patches. The figure shows a characteristic beetle and oribatid mite for a 'dry' and 'wet' succession, respectively.

3.5. Succession of surface animals versus soil animals

Among both surface-active macroarthropods and soil-living microarthropods, species numbers increased markedly during the first 80 years. Both groups had species that were favoured by the glacier retreat, because either they were cold-adapted (the springtail *A. bidenticulata* and the carabid beetle *N. nivalis*) or they preferred open space (the springtail *B. hortensis* and the carabid beetle *B. hastii*). Furthermore, both surface-living and soil-living animals were split into a 'dry' and a 'moist' succession pattern.

The two groups were, however, differently related to the development of vegetation. Soil-living microarthropods were favoured by the gradual development of an organic soil layer. Surface-active macroarthropods were influenced by the gradual closing of vegetation, and for some, to the appearance of food plants. While predators dominated throughout succession among macroarthropods, there were fewer predator species among microarthropods.

3.6. Comparison between plant and animal succession

Several investigators have detected a peak in plant richness early in primary succession, followed by a decline due to increased competition [4]. For instance, in the nearby foreland of Blåisen, there was an early diversity peak in proximal slopes [34]. Most arthropods, however, tend to persist after colonisation (see below), and there is no early peak in species richness.

Plant and animal succession have several features in common. Both plants and animals respond to local soil moisture, resulting in a 'dry' and a 'wet' succession. In the foreland of Blåisen, microtopography and moisture clearly affected plant succession [34].

Another similarity between botanical and zoological succession in the Finse area is that it takes at least 200 years to establish a stable "climax" community. Near Blåisen, only

communities of simple structure, such as snow beds, reached a mature state after 220 years of succession [39].

Furthermore, plants with very narrow niches could attain local optima during early succession on glacier forelands and nunataks [35, 40]. Examples were *Draba cacuminum, Poa herjedalica, P. jemtlandica* and *Sagina intermedia* in the Finse area. Corresponding arthropod examples are two open space-living species: the carabid beetle *B. hastii* and the springtail *B. hortensis*, as well as two cold-loving species: the carabid beetle *N. nivalis* and the springtail *A. bidenticulata*.

A general similarity between plant and animal succession in Norwegian forelands is that the process is markedly affected by altitude and local climate. Glacier forelands in a harsh climate at high altitudes create a slow and species-poor succession, while the succession in both plants and animals is rapid and species-rich in forelands situated below the tree line [4, 19, 20, 22, 23].

3.7. Pioneer arthropods—a heterogenic group

The pioneer community was an interesting mix of generalists and specialists, and of various life strategies [26, 32]. Among early springtails and mites, there were both parthenogenetic and bisexual species, and species with either a short or a long life cycle [24, 25]. Furthermore, there were open-ground species as the springtail *B. hortensis* and the carabid beetle *B. hastii*, and 'cold-loving' species represented by the springtail *A. bidenticulata* and the carabid beetle *N. nivalis*. Several generalists colonised the pioneer ground. The harvestman *Mitopus morio* is a generalist predator, with high catches throughout the whole foreland [27]. Among oribatid mites, *T. velatus* is a well-known generalist, and among springtails we can point at *Desoria olivacea* and *Isotoma viridis*. The carabid *A. alpina* and the staphylinid *G. longipes* are habitat-tolerant beetles, and *E. tirolensis* is a spider example. Despite differences in ecology, pioneer arthropods have certain key abilities in common: they are good dispersers and can live, eat and reproduce on barren or nearly barren ground [32].

4. Dispersal: how to get there?

The rapid colonisation of newly exposed ground indicated that arthropods have a high dispersal ability. On Iceland, springtails and oribatid mites easily colonised recently emerged nunataks, and isolation of a few kilometres did not affect the colonisation [16]. These results strongly indicate aerial dispersal, and our study supports this. Fallout traps and sticky traps collected nine species of springtails and four species of oribatid mites, as well as some Actinedida mites and spiders (**Figure 11**). Among other items were unwinged aphids, some flies, several chironomid midges, a few seeds, and many fragments and diaspores of pioneer mosses [28]. Most aerial transport occurred rather close to the ground, below 0.5-m height. Sand grains in sticky traps up to this level illustrated the mechanical force of wind transport.

Some of the trapped species were assumed not to be able to thrive on pioneer ground, but to depend on a thicker organic layer [28]. In that case, their dispersal ability is high, but the pioneer ground may act as a 'sink' for them, where they will die. A 'real' pioneer species must
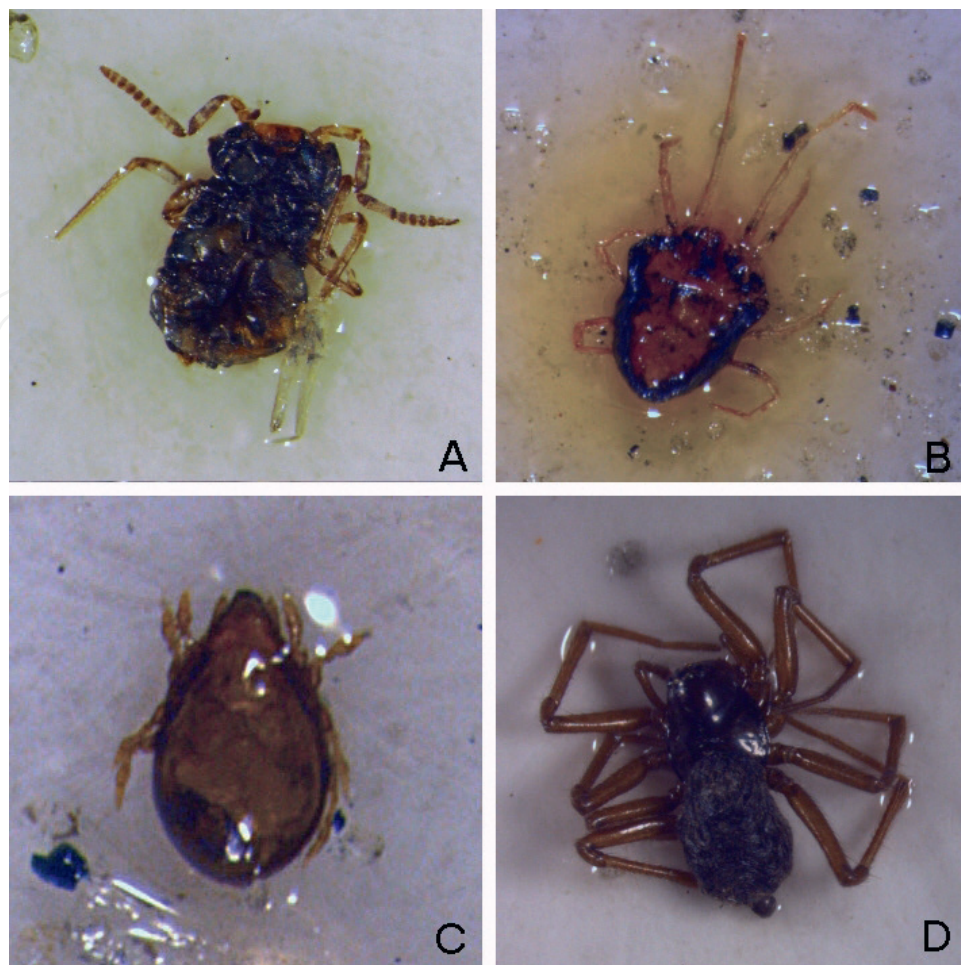
Figure 11. Invertebrates taken in sticky traps, proving airborne transport. A = the springtail *Bourletiella hortensis*. B = the mite *Bryobia* sp. C = the mite *Tectocepheus velatus*. D = the spider *Erigone arctica*. From Ref. [28].

be able both to arrive, to tolerate the harsh environmental conditions, to manage competition, to find food and to reproduce. In other words, pioneers must pass two 'filters': a 'dispersion filter' to arrive and an 'ecological filter' to establish a population.

5. Food sources: how to survive?

How can so many arthropod species—even predators—thrive on bare ground, before higher plants have established, or are very few? Based on analyses of the gut contents in springtails, beetles, harvestmen and chironomid midge larvae, we found that there were three 'invisible' food sources on newly deglaciated ground: biofilm with diatom algae, tiny pioneer mosses and ancient carbon delivered by the glacier.

5.1. Terrestrial biofilm as food

The springtail *A. bidenticulata* (**Figure 12**) was a 'super-pioneer', following the retreating glacier edge closely. Their guts contained a rather compact material dominated by tiny mineral particles, but diatom algae could often be seen [29, 31] (**Figure 13**). We assume that mineral
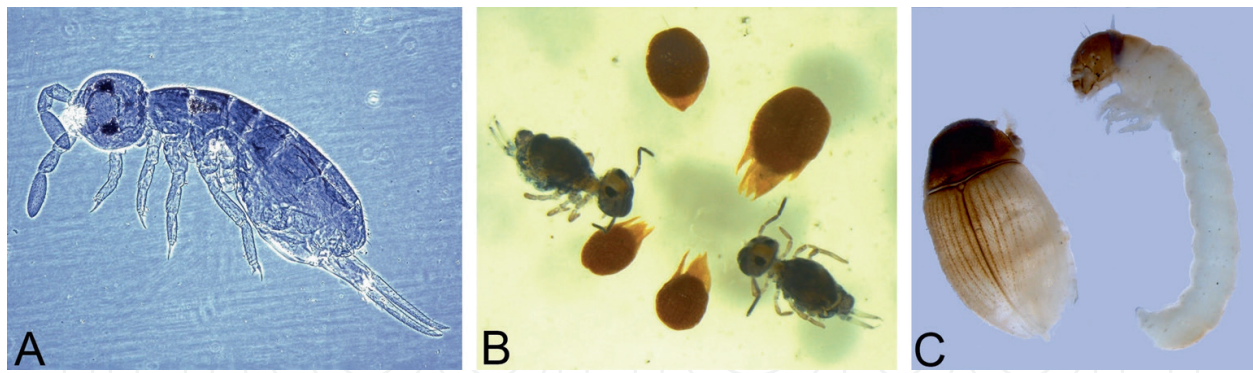
Figure 12. Some pioneer invertebrates. A = the biofilm-eating springtail *Agrenia bidenticulata*. B = the moss-eating springtail *Bourletiella hortensis*, together with four bulbils (dispersal units) of the moss *Pohlia* sp. C = newly hatched adult and a larva of the moss-eating beetle *Simplocaria metallica*. From Ref. [31].

particles were ingested accidentally when 'grazing' on biofilm. Terrestrial diatoms have the ability to establish a slimy, nutrient-rich biofilm on open ground by producing large quantities of extracellular polymeric substances [41, 42]. Diatom algae were also found in some guts of two other pioneer springtails: *D. olivacea* and *I. viridis* [31]. The early presence of terrestrial diatom algae shows that chlorophyll-based food chains start almost immediately after deglaciation.

5.2. Pioneer mosses as food

Already on a four-year-old ground, five mosses were observed: *Ceratodon purpureus, Bryum arcticum, Pohlia filum, Racomitrium canescens* and *Funaria hygrometrica* [31]. On nunataks of
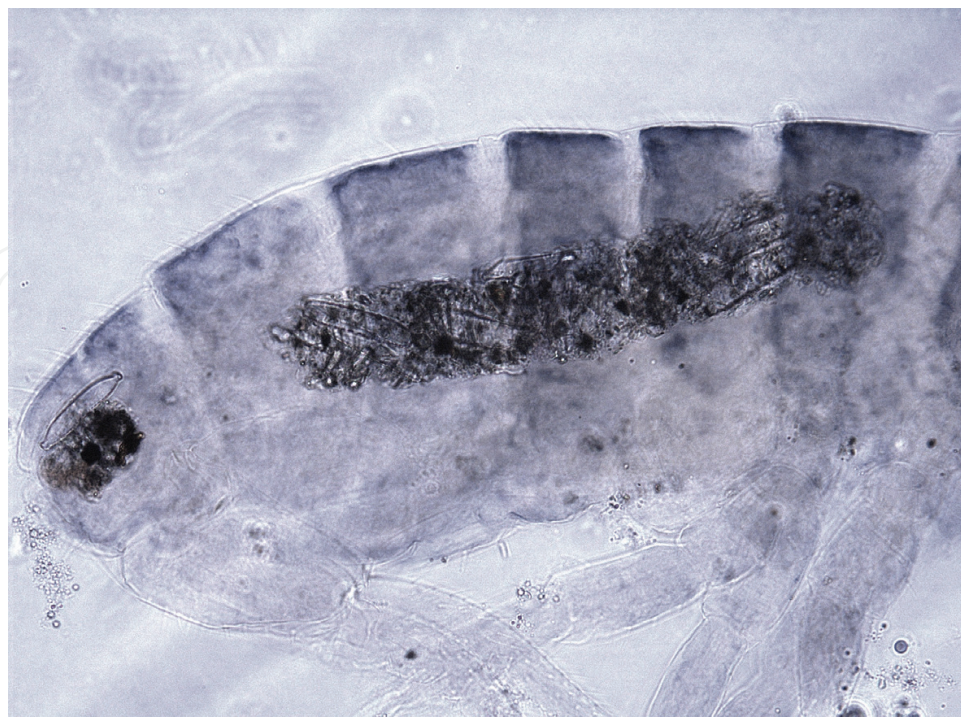

Figure 13. Hind part of the springtail *Agrenia bidenticulata* showing diatom algae in the gut. Most diatoms are densely packed, but a single one is easily seen to the left. From Ref. [31].

Omnsbreen glacier, about 10 km further North, a similar pioneer moss community has been found [40].

Due to characteristic cell structure in each moss species or genus, it was possible to identify small moss fragments in arthropod guts. On a 3-year-old ground, the relatively large and spherical springtail *B. hortensis* (**Figure 12**) had eaten leaves of *C. purpureus*, *Bryum* sp. and *Pohlia* sp., as well as nutrient-rich dispersal units (bulbils) of *P. filum* [31]. Among beetles, the family Byrrhidae is known to have moss-feeders, and on a six-year-old ground, guts of *S. metallica* (**Figure 12**) contained three different mosses (**Figure 14**). Two carabid beetles on three–six-year-old ground were omnivores, as their guts contained both invertebrates and moss fragments: *A. alpina* and *A. quenseli*. Conclusively, as much as four pioneer arthropods grazed on pioneer mosses [31].

5.3. Ancient carbon as food

The identification of this food resource was gradual, and surprising. A publication from a glacier foreland in the Austrian Alps showed that heterotrophic microbial communities used ancient carbon released by the glacier [43]. We wondered whether ancient carbon was released also by our glacier, and if so, whether it could be used as a nutrient source for pioneer arthropods. In September 2010, samples of surface soil (sand and silt) were taken 20 m from the glacier edge. During that summer, the glacier had retreated as much as 34 m. Analyses by Beta Analytic in Florida concluded that the samples contained material which was in average 21,000 years old. Furthermore, radiocarbon dating of chironomid midges and four predators, which were pitfall trapped on a 6–7-year-old ground showed that they all contained ancient carbon. The wolf spider *P. trailli*, had a radiocarbon age of 340 years, the harvestman *M. morio* 570 years, the carabid beetle *N. nivalis* 690 years, the carabid beetle *B. hastii* 1100 years and chironomid midges 1040 years [29]. Even larvae and adults of predatory diving beetles collected in young ponds had a radiocarbon age of 1100–1200 years. Springtails, however, did not contain ancient carbon.

New samples of surface soil taken close to the ice edge 4 years later corrected the age of released organic material to about 5160 years [30]. In the latter analysis, samples were pretreated at a lower temperature so that possible graphite particles from the phyllite-containing bedrock were not combusted and included in the analysis.

We found that chironomid larvae living in the sediment of young ponds assimilated the ancient carbon, and achieved a radiocarbon age up to 3270 years. We assumed that these larvae were eaten by diving beetles (**Figure 15**), and that adult midges ending on the soil
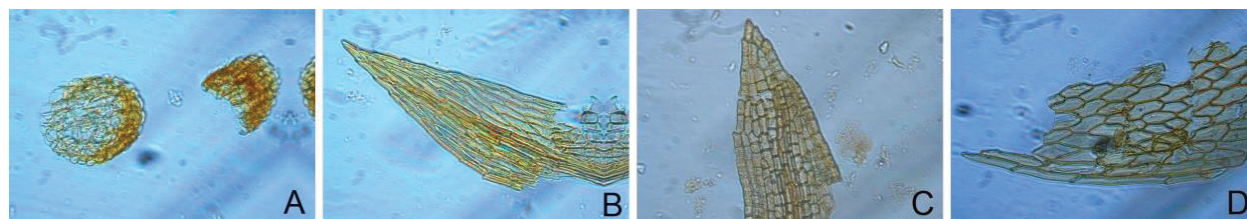

Figure 14. Moss fragments recorded in the gut of the beetle *Simplocaria metallica*. A = cross sections of a moss stem. B = leaf of *Pohlia* sp. C = leaf of *Ceratodon purpureus*. D = typical cell structure of a *Bryum* leaf. From Ref. [31].

surface after swarming fed terrestrial predators. Studies of the gut contents of the carabid beetles *N. nivalis* and *B. hastii*, and the harvestman *M. morio* confirmed that adult chironomid midges were an important part of their diet.

To be sure that ancient carbon was assimilated into the body tissue, measurements were also made on the larvae of Tipulidae (another Diptera group) in the same pond sediment, being careful to remove the gut contents before analysis. The actual body tissue from Tipulidae larvae had a radiocarbon age of 1610 years [30]. Moreover, chironomid larvae collected in the glacier river, and freed from their gut contents, had radiocarbon ages up to 1260 years.

We concluded that ancient organic material released by the glacier was assimilated by chironomid larvae, and transported further to aquatic and terrestrial predators. Chironomid midges thus supported early succession, and bound aquatic and terrestrial food webs together [29, 30].

The remaining question was: What is the source of the ancient carbon that had been stored in the glacier? We gradually abandoned the possibility that it came from old forest, bogs or soils from earlier periods where the glacier had been periodically absent. One reason was that the actual organic particles were probably extremely small. A purely chemical process, where carbon from non-biological bicarbonate served as a CO_2 source for aquatic algae, was also abandoned, since gut contents of chironomid larvae were practically free from algae [30]. Instead, our suspicion was led towards long-transported aerosols, originating from the incomplete combustion of fossil fuels. Such aerosols make up a part of the organic matter that glaciers collect by surface accumulation [30]. These aerosols are C_{14} depleted, and radiocarbon dating will reveal that they are very old [44, 45]. In fact, heavily glaciated watersheds may transport ancient, bioavailable carbon all the way to oceans, where marine microorganisms can assimilate the old carbon [46]. The aerosol hypothesis would fit with all our results [30].

5.4. A pioneer food web

Pioneer ground of 3–7 years of age contained a surprisingly diversity of food sources for pioneer arthropods (**Table 3**). Primary production was represented by invisible biofilm with
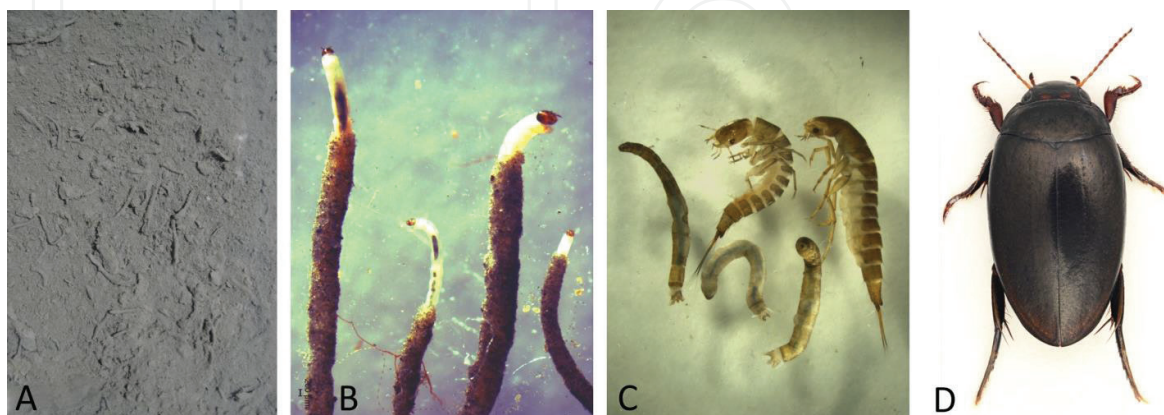

Figure 15. These pond-living invertebrates contained ancient carbon supplied by the melting glacier. A = sediment with chironomid larvae in tubes. B = chironomid larvae which have been partly freed from their tubes. C = two predacious larvae of the diving beetle *Agabus bipustulatus*, and three saprophagous, cylindrical larvae of Tipulidae (crane flies). D = adult predacious diving beetle, *Agabus bipustulatus*. From Ref. [30].

Species	Group	Biofilm	Fungal hyphae	Bryophytes	Vascular plants	Invertebrates	Ancient carbon via Chironomidae
Agrenia bidenticulata	Collembola	x					
Desoria olivacea	Collembola	x					
Isotoma viridis	Collembola	x	x				
Lepidocyrtus lignorum	Collembola		x				
Bourletiella hortensis	Collembola		x	x			
Simplocaria metallica	Coleoptera			x			
Amara alpina	Coleoptera			x	x	x	
Amara quenseli	Coleoptera			x		x	
Nebria nivalis	Coleoptera					x	x
Bembidion hastii	Coleoptera					x	x
Mitopus morio	Opiliones					x	x

Table 3. Food sources of terrestrial invertebrates on 3–6-year-old ground, based on gut content analyses. From Ref. [31].

diatom algae, tiny bryophytes and scattered vascular plants. Fungal hyphae found in some springtail guts were early terrestrial decomposers, and chironomids eaten by several predators were (as larvae) detritus feeders on ancient organic material. In addition, some inblown insects certainly contributed as prey. Two 'super-pioneers' followed the ice edge most closely: the biofilm-feeding springtails *A. bidenticulata* and *D. olivacea*.

To understand the food web on pioneer ground, we must combine aquatic and terrestrial food chains, and distinguish between chlorophyll-produced carbon, inblown carbon and ancient carbon released by the glacier. **Figure 16** summarises these relationships, and distinguishes between autotrophs, herbivores, predators and decomposers.

A pioneer food web can probably be of local character. In the present case, chironomid midges hatching from young ponds fed several terrestrial predators. In the Rotmoos foreland in Austria, however, springtails were found to be the main prey, and intraguild predation was demonstrated [47, 48].

5.5. Feeding categories during succession

Figure 17 shows that throughout the 200-year-old succession, the great majority of trapped macroarthropods were predators. While all spiders are predators, beetles contained a mixture of feeding categories. Pure herbivores were always represented by few species, even in the oldest sites.
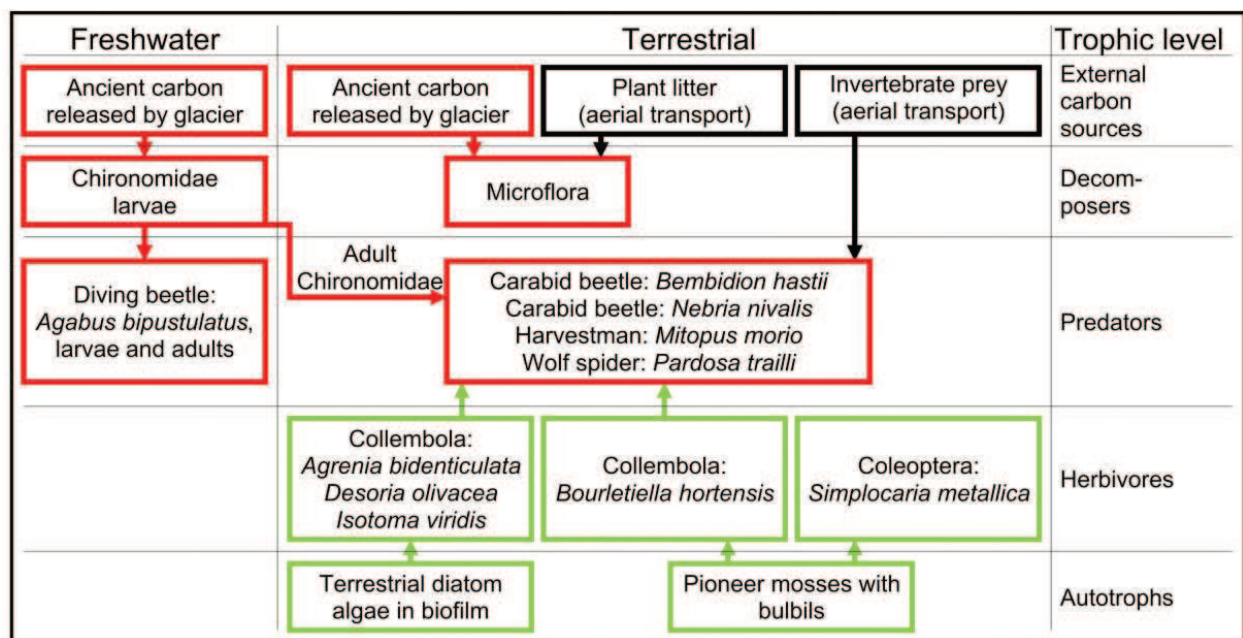
Figure 16. This food web from pioneer ground combines aquatic and terrestrial habitats. Shaded boxes illustrate the flow of ancient carbon, lower boxes with a grey frame show the flow of chlorophyll-produced carbon and the two upper boxes with a black frame show the use of carbon from inblown organic material. It is distinguished between autotrophs, herbivores, predators and decomposers. From Ref. [29].
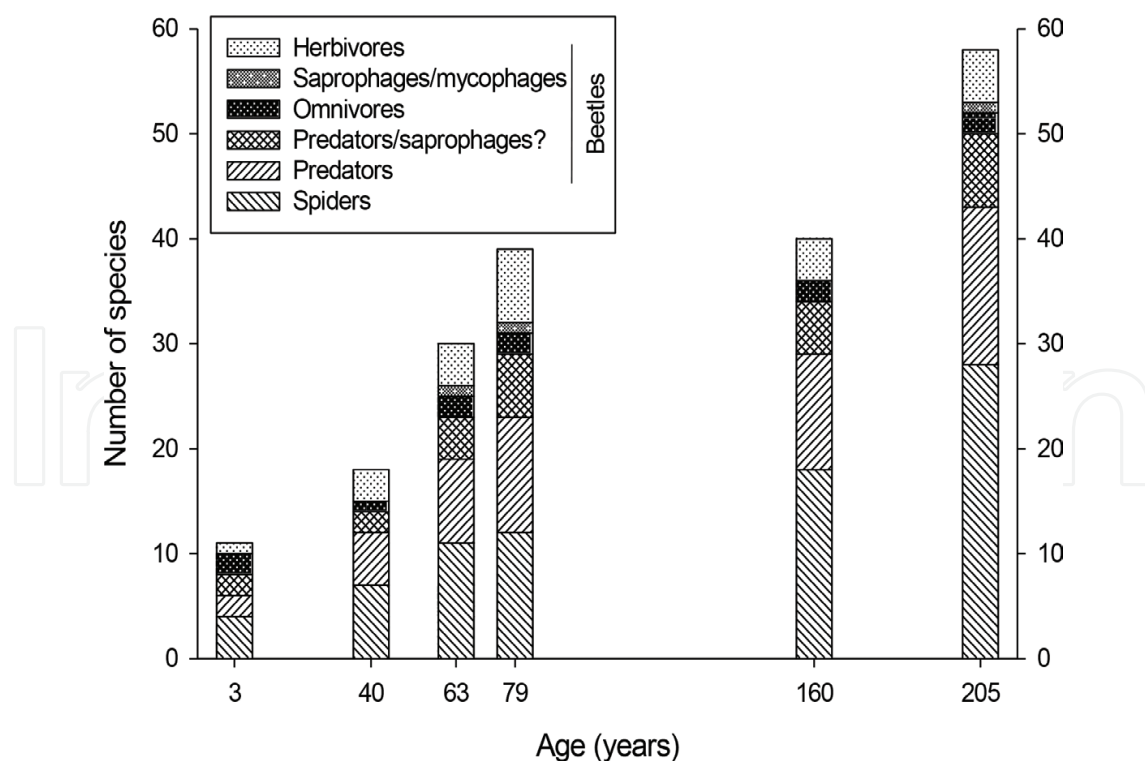

Figure 17. Feeding categories among pitfall-trapped macroarthropods at different ages of the ground. All spiders are predators, while beetles contained various feeding groups. Pure herbivores were rare throughout the gradient. From Ref. [26].

6. Driving forces in various phases of animal succession: facilitating and inhibiting factors

In early succession theory, facilitation, inhibition and tolerance were central concepts [49]. They were all used in a biotic context, and it was assumed that succession was driven by the way species interacted with one other. Early occupants could modify the environment in a way that influenced 'late-successional' species in three possible ways: (a) make the habitat more suitable for other species (facilitation) and (b) less suitable (inhibition), or early occupants had little or no effect on subsequent recruitment of species (tolerance). In the following presentation of four characteristic phases of succession, we use the terms facilitation, inhibition and tolerance in both biotic and abiotic contexts. We want to show that animal succession is only partly driven by the development of vegetation, and that abiotic factors may considerably influence the succession process.

6.1. Age 3–7 years: bare ground or only scattered pioneer vegetation

Wind facilitated transport of invertebrates, prey, algae and mosses into newly exposed ground [28]. In a foreland at Svalbard, aerial dispersal of midges and ballooning spiders was even assumed to add nutrients to virgin soil [12, 14].

The glacier itself facilitated the pioneer community by producing ponds, in which chironomid larvae assimilated ancient carbon. Within ponds, chironomid larvae were eaten by predatory diving beetles. Adult midges transported ancient carbon to terrestrial predators [29, 30]. The presence of predators before visible plants, often referred to as the 'predator first paradox' [13], can to a large degree be explained by local production of chironomid prey from young ponds. Cold-adapted species, like the springtail *A. bidenticulata* and the ground beetle *N. nivalis*, were facilitated by proximity to the glacier. However, a glacier retreat around 20 m per year means that they had to migrate continuously to remain in the cold zone.

6.2. Age about 30–40 years: patchy pioneer vegetation and much open ground

A high soil humidity due to much silt facilitated the colonisation of several plants and animals. Small patches of *S. herbacea* initiated the production of an organic layer. The moist-loving carabid beetle *P. septentrionis* colonised the ground. Pitfall catches documented a high surface activity among larger springtail species, not only within vegetated patches but also on bare ground [32].

6.3. Age about 60–200 years: mainly closed vegetation

A closed vegetation created shelter, reduced wind and maintained humidity. Web-building spiders were favoured by a three-dimensional vegetation. The pioneer ground beetle *B. hastii* disappeared when the vegetation became closed, but a local population survived on a 75-year-old bare patch [21]. The gradually deeper organic soil layer was positive for soil-living springtails and mites (**Figures 6–8**).

For herbivores, the presence of a suitable food plant is crucial. While the moss-eating beetle *S. metallica* was found in the first moss patches on a 3-year-old ground, another moss-eating beetle, *B. fasciatus*, was not trapped until on a 63 years old ground. The beetle *Chrysomela collaris* feeds on *S. herbacea*, which occurs throughout the foreland. However, this beetle colonised late, and was found after 79 years. Clearly, other factors than the presence of the food plant determined the colonisation rate of some herbivorous beetles [26].

Both macro- and microarthropods were split into two main successional pathways: a dry and a wet succession. Due to patchy distribution of dry and moist habitats in the foreland, specialist on dry or moist sites had to overcome dispersal over unfavourable ground. The carabid beetle *C. vaporariorum*, which prefers dry ground, has a disadvantage by its inability to fly, due to rudimentary wings.

6.4. Age about 10,000 years: mature soil

The number of oribatid species increased clearly in this very old soil compared to 200-year-old soil, maybe facilitated by a deep organic layer. However, the increase was small for springtails, which were more efficient in colonising the foreland.

7. Remarks

Glacier forelands offer unique possibilities for the study of succession. We are beginning to understand patterns of arthropod succession by comparing studies from Norway, Svalbard, Iceland and the Alps [26, 32]. Several species or genera among arthropods are common pioneers in Norway and the Alps. However, glacier foreland chronosequences are both variable and complex. More case studies are needed, both to reveal local variations in pioneer communities and succession patterns and to look for general patterns.

Sample size is a critical factor. **Figure 18** shows how 12 soil samples within one plot gradually increased the cumulative number of mite taxa, but none of the samples contained all taxa. Ideally, sample numbers should be so high that the cumulative species number stabilises. If species numbers in different sites shall be compared, corresponding sampling effort should be used in all sites. To cover local variation in species composition, it may be better to take several small samples instead of a few larger covering the same area. During sampling with a soil corer, large, surface active springtails may escape by jumping. Some pitfall traps in addition may give valuable information.

Pitfall traps are much used for beetles and spiders in comparative studies, but the number of traps is often low. Even in the present study, with 20 traps operating during 2 years at each site, several species were taken in very few specimens [26]. Traps should be operated throughout the snow-free season, since certain species may have restricted seasonal activity.

The term 'primary succession' is questionable when both aquatic and terrestrial pioneer communities use ancient carbon released by the glacier. Young ponds acted as 'biological oases'
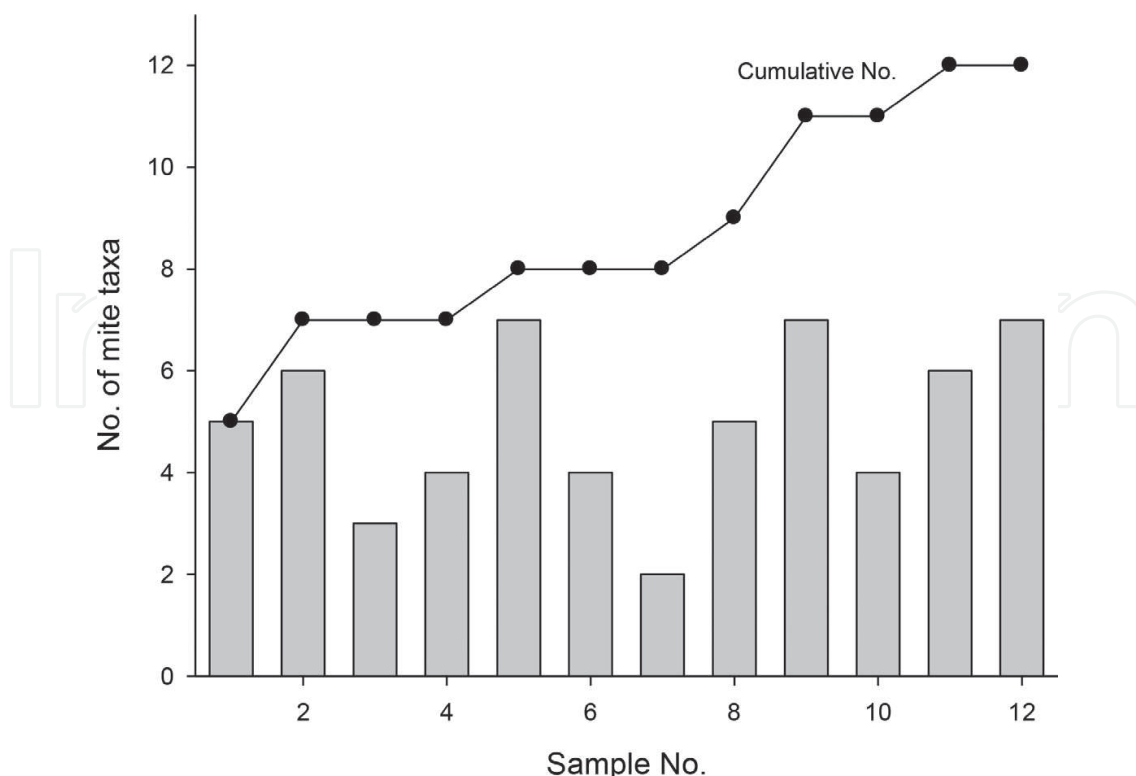
Figure 18. In plot no. 18 (age 180 years, see Figure 1), 12 soil cores were taken. This example shows how the cumulative number of mite taxa increased with increasing number of cores. However, none of the single cores contained all taxa (columns).

where ancient carbon was assimilated by Diptera larvae, mainly Chironomidae. In a foreland without ponds, a possible release of ancient carbon can be checked by radiocarbon dating chironomid larvae from the glacier river. A peculiar thing is that if invertebrates, which had assimilated old carbon, had been recovered as subfossils and radiocarbon dated, their age had been overestimated by up to 1100 years [29]. Since several pioneer species were herbivores on biofilm or mosses, the present succession did not fit with the 'predator-first' hypothesis. Although pioneer species may be ecologically very different, the pioneer community is surprisingly predictable, both within Norwegian forelands and in the Alps, and several genera are in common [32].

We need to improve our knowledge about the autecology of the individual species to better understand their position and functional role in the succession process. From each species' point of view, colonising the foreland is a question of fulfilling minimum ecological demands. For instance, analyses of gut content were the key to understand the pioneer food web in the present foreland [29, 31]. Experimental studies involving transportation and re-location of species could be rewarding, but would it for the sake of science be ethically acceptable to move species within a 'natural laboratory' that should develop in a natural way?

A negative and special aspect by melting glaciers is that their meltdown will threaten cold-adapted invertebrates which live near glaciers. Especially when it comes to endemic, cold-adapted species, melting glaciers represent an extinction threat, as in certain mountains of the Southern Alps [50].

8. Conclusions

The questions posed in the 'Introduction' section can be answered in the following way:

a. *Comparison between botanical and zoological succession*

- Are there alternative succession patterns for arthropods, in the same way as there are alternative succession patterns for vegetation? Yes, also in animal succession, local conditions like topography and moisture modify the succession pattern. Among both soil-living microarthropods and surface-living macroarthropods, we can distinguish between a 'dry' and a 'moist' succession.

- Is there a strong progressive succession of arthropods on terrain ages of 20–50 years, as in plants? The period of fast colonisation among arthropods was longer in this study, around 80 years. Most species of springtails and beetles had arrived at that age, but species numbers of mites and spiders continued to increase substantially also after 80 years.

- Do animal and botanical successions differ in their early phases? Yes, in the early phase, animal succession may be said to differ from botanical succession. Before higher plants established, or were represented by very few species, a rather rich assemblage of arthropods was present. However, if we include pioneer mosses and terrestrial diatom algae, chlorophyll-based food chains established very early. In addition, several pioneer arthropods were able to use ancient carbon released by the glacier, being independent of primary production.

b. *Questions about zoological succession*

- Do most arthropod species tend to persist after colonising? Yes, but there were exceptions. The occurrence of many rare species makes it difficult to answer the question.

- Is a geo-ecological perspective fruitful and relevant when considering mechanisms of facilitation and inhibition in zoological successions? Yes, since abiotic factors highly influence colonisation and succession pattern.

- Does arthropod succession pattern differ between surface-active macroarthropods and soil-living microarthropods? There were large similarities.

- Is soil fauna succession in *S. herbacea* snow bed vegetation related to the gradual development of an organic layer? Yes, soil fauna succession goes on even after this vegetation type has been permanently established, and species numbers are related to the further development of the soil profile.

c. *Question about methods*

- Are sampling methods, material size and taxonomic resolution critical factors when studying arthropod succession? Yes.

Acknowledgments

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