Primary succession of arthropods (*Coleoptera* and *Araneae*) on a newly exposed glacier foreland at Finse, southern Norway

Anders Thon Bråten & Daniel Flø

Norwegian University of Life Sciences
Department of Ecology and Natural Resource Management (INA)
Master Thesis 60 credits 2009

Ås 15th of June 2009

Anders Thon Bråten

Daniel Flø

Abstract

The succession pattern of surface-active arthropods on newly exposed substrates in pre-glaciated areas was studied for two years in front of the receding Midtdalsbreen glacier snout, which is a part of the Hardangerjøkulen ice cap, Finse, Norway. Midtdalsbreen has receded since 1750, leaving a glacier foreland of 1,1 km at altitudes between 1300 and 1400 meters above sea level. Surface-active arthropods were sampled in a chronosequence (space for time substitution) with pitfall traps at six sites of different age spanning from 3 to 205 years. Twenty pitfall traps were operated at each site. We chose to describe the community structure by ordination. We employed a Detrended Correspondence Analysis (DCA) to find out what the most important environmental gradients are. Unexpectedly and contradictory to the common view on primary succession we found that both spiders and beetles are found very close to, and quickly colonize, the barren ground in front of the glacier snout. The length of the DCA axis tells us that one will not find the same species composition in the beginning of the axis as in the end (i.e. there is a high beta diversity). And this is also true for the chronosequence, since the DCA is a representation of the chronosequence. Vegetation cover and distance are the strongest variables governing the fauna distribution. When we look at how and when the different guilds enter the succession/chronosequence, we see that the numbers of herbivores does not increase, as fast as the predatory beetles and spiders.

Samandrag

Vi studerte korleis suksesjonsmønstra til overflateaktive virvellause dyr forandra seg på nyleg framsmelta mark. Denne studia gjekk over to år framfor Midtdalsbreen, som er ein brearm av Hardangerjøkulen ved Finse, Noreg. Midtdalsbreen har drege seg tilbake sidan 1750 og blottlagt eit område som er 1,1 km langt, som har ei høgde over havet på mellom 1300 og 1400 meter. Vi samla dei overflateaktive virvellause dyra i ein kronosekvens (erstatning av tid med rom) med fallfeller, som vart plassert på seks forskjellige steder og spenner over eit aldersintervall frå 3 til 205 år. På kvar av desse stadene nytta vi 20 fallfeller. Vi nytta ordinasjon for å beskrive samfunnstrukturen. Metoden vi nytta for å finne dei viktigaste miljøfaktorane er kalla Detrended Correspondence Analysis (DCA). Uventa, og i motsetning til vanleg oppfatting av primærsuksesjon, fann vi både edderkoppar og biller heilt inntil breen, kor dei raskt koloniserte den ufruktbare marka. Lengda på DCA aksen fortel oss at vi ikkje vil finne den same artssamansetninga i starten av aksen som i slutten, altså ser vi ein høg betadiversitet. Dette gjeld også for kronosekvensen, sidan DCA aksen er ein representasjon av kronosekvensen. Avstanden og prosenten vegetasjonsdekke er dei viktigaste faktorane som påverkar kva artar ein finn. Når vi ser på korleis og når dei forskjellige lauga trer inn i kronosekvensen, kan ein sjå at mengda herbivore biller ikkje aukar like raskt som mengda predatorbiller og edderkoppar aukar.

1.Introduction

The gradual retreat of alpine glaciers since the little ice age 1750, and the accelerating retreat in the past decade (IPCC 2007) offer a unique opportunity to study primary succession under alpine conditions (Kaufmann & Raffl 2002). This gradual retreat has been well documented in some areas and can thus be regarded as natural chronosequence experiments and model systems for investigating fundamental ecological processes. The primary floral succession has been well documented and described, see Matthews (1992), Vetaas (1997), Raffl et al. (2006). Primary faunal succession is less studied , and little is known about the invertebrate glacier foreland succession, a few systematic studies has been undertaken in the European Alps (Kaufmann 2001; Kaufmann 2002; Kaufmann et al. 2002; Kaufmann & Raffl 2002; Gobbi et al. 2006) and to some extent in the high arctic, Svalbard archipelago (Hodkinson et al. 1998; Hodkinson et al. 2001; Hodkinson et al. 2002; Coulson et al. 2003; Hodkinson & Coulson 2004; Hodkinson et al. 2004) and one in Norway (Vater 2006).

While the costal glaciers in Norway are more or less balancing between melting and growing, the continental glaciers have been melting more or less continuously since the 1960s (Nesje 2004). There is now a great opportunity to study the primary succession also in Norwegian glacier forelands. A suitable place for such studies is the Hardangerjøkulen glacier in the central south Norway. At Finse, pioneer ground from about 1750 and older habitats have been studied earlier with respect to surface-active invertebrates (Hauge et al. 1978; Hågvar et al. 1978). However, surface-active invertebrates in habitats younger than about 250 years have not been studied earlier at Finse. For practical reasons, we have chosen to focus on beetles (*Coleoptera*) and spiders (*Araneae*). A suitable sampling method to catch the mentioned groups is pitfall traps, due to their roaming nature (Greenslade 1964; Leather 2005).

The common view on primary succession in introductory general ecological textbooks (Schowalter 2000; Krebs 2001; Molles 2005) is the early establishment of autotrophs, such as lichens, mosses and higher plants, accumulating nutrients before the heterotrophic community is able to establish itself. Thus it is the autotrophs that initiate the nutrient cycles and the succession (Bardgett et al. 2007).

Introduction

Paradoxically it has been observed that the numbers of predators exceed the numbers of herbivores on glacier foreland (Hodkinson et al. 2001; Hodkinson et al. 2002; Kaufmann & Raffl 2002; Hodkinson et al. 2004; Vater 2006). It was proposed as a general rule by Hodkinson et al. (2002) that: "community assembly by autotrophs is preceded by a largely unrecognized heterotrophic phase that may be instrumental in facilitating the establishment of green plants and consolidating the process of community development". It is to our knowledge many unanswered questions regarding arthropod succession on newly exposed substrates.

In this study we want to see if we find a colonization patterns similar to that recorded in glacier forelands in the Alps and in other Norwegian glacier forelands (Vater 2006). We also want to describe the phenology of the species, and also check whether soil moisture and vegetation cover are important factors explaining the succession. Primarily we test the following hypotheses;

1) The succession pattern of surface-active arthropods on newly exposed substrates in pre-glaciated areas will be related to age and distance from glacier.
2) The degree of vegetation cover will modify the age and distance factors
3) Autochthonous flying species will not be overrepresented in the earliest successional stages and that allochthonous species will be overrepresented in closer vicinity to the glacier as random fallout is more prevalent.
4) The surface-active arthropod community on newly exposed, vegetation free substrate will depend on allochthonous food sources.
5) Changes of species composition through the season due to phenological differences

2 Material and methods

2.1 Study area and sampling sites

This chronosequence study was conducted in front of the receding Midtdalsbreen glacier snout, which is a part of the Hardangerjøkulen ice cap. Geographic position is 60˚ 35`N, 7˚ 28`E; UTM- coordinates are 32V MN 67162 4161 (glacier front). Midtdalsbreen has receded since 1750, leaving a glacier foreland of 1,1 km at altitudes between 1300 and 1400 meter above sea level. The study area is located 4km from Finse alpine research center.

Surface-active arthropods were sampled with pitfall traps at six sites of different age, based on information from Sørlie (2001). Twenty pitfall traps were operated at each site. The sites are numbered 1, 2, 3, 4, 5, and 6 (figure 1) and are dated 3, 38- 40, 62-63, 78-79, 159-160 and 204-205 years respectively.

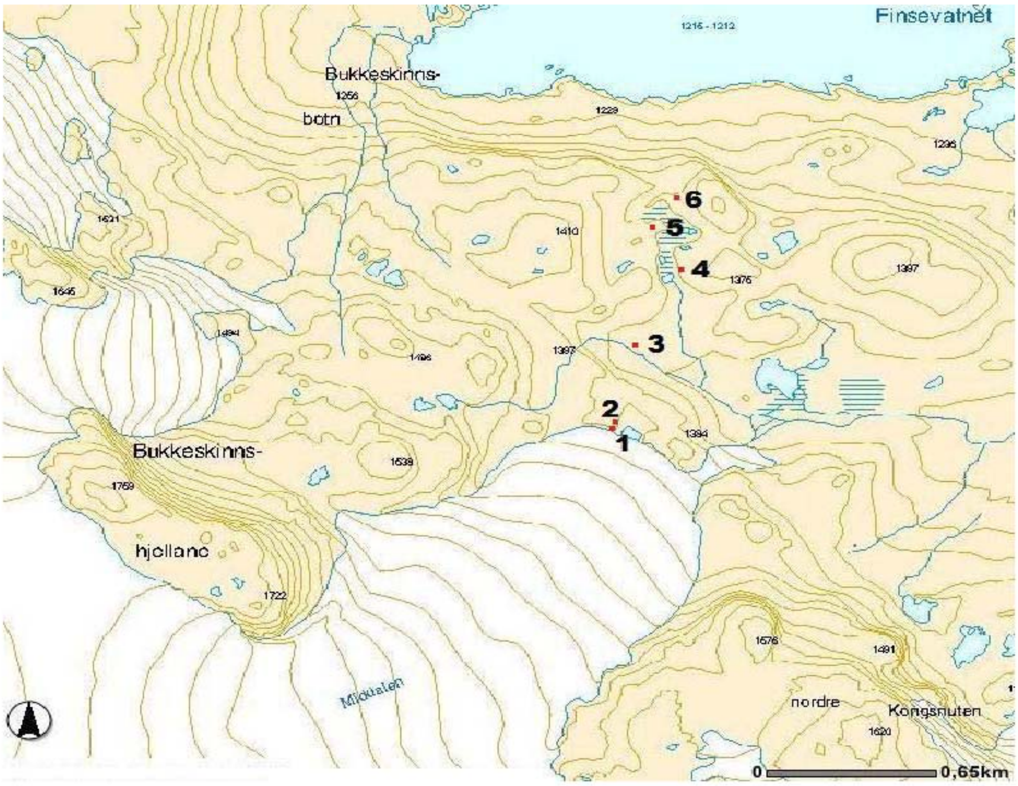


Figure 1. Map of study area showing the position of the six sampling sites, marked with red dots and numbers, number one being closest to the receding Midtdalsbreen glacier snout, the chronosequence stretches towards Finsevatn.

Material and methods

According to Ottesen (1996), soil moisture is the most important ecological factor for habitat choice in alpine, ground-living beetles. Therefore, at a given collection site the twenty pitfall traps were placed in a gradient from dry to moist habitats, in order to cover the highest possible number of species and in this way we also covered the main variation of plant communities at the site. The distance between traps was usually 1-1.5 m. occasionally, traps were placed in two parallel lines, each line with ten traps covering the gradient. The percentage of vegetation cover and the dominant plants were noted in 1 m^2 around each trap.

2.2 Sampling method

In 2007 arthropods were collected during the snow-free season from the 18 June to 15 September. Seventy four traps were put out the 18 June, while the remaining 26 were operational 14 days later due to snow conditions. All traps were left to spend the winter until the next snow free collection period of 2008, from 28 June to 23 August. Twenty more traps were operated in the 2008 season on a newly exposed moraine. The 2008 season was terminated before snowfall to avoid losing samples and traps beneath the snow. Traps were emptied every 14 days. If the condition of a trap was unfavorable, for example flooded or otherwise damaged, this sample was excluded from the statistical analysis. All data were adjusted to catches per 20 functioning traps in each 14 day period.

The traps were plastic cups, consisting of an inner and outer cup. The inner cup, of 6.5 cm was modified with a fine wire mesh bottom, as described by Ottesen (1996). This allowed us to replace the inner cup with a new one at each collection time, without changing the preservation fluid.

The traps were protected from precipitation by a 15 x 15cm plywood roof approximately 3cm above ground, each roof numbered to identify the traps. Each trap contained 1dl 50% ethylene glycol with 2 drops of liquid detergent per liter. All the samples were washed in water before being preserved in glass vials with 70% ethanol. Caution was taken not to spill preservation fluid to the surroundings.

The spiders were identified by Kjetil Åkra (Midt-Troms Museum), and beetles by our supervisor Sigmund Hågvar and Oddvar Hanssen (NINA). Opiliones are represented by only one species at Finse, *Mitopus Morio*.

Pitfall traps are efficient in catching surface-active arthropods like spiders (*Araneae*), springtails (*Collembola*) and beetles (*Coleoptera*). Pitfall traps are surface activity monitors, meaning that catches of a given species depend both on abundance and the degree of activity. Activity is again governed by vegetation density as well as climatic conditions like temperature and moisture (Spence & Niemela 1994).

2.3 Vegetation cover

Site 1 (traps no. 101 -120): Age 3 years. Mean vegetation cover ≈0%. Moraine formed in 2005 according to Atle Nesje, (pers. comm., Univ. of Bergen). The traps were placed in a long line, covering the topographic variation on the fresh, undulating moraine. The nearest m^2 around 18 of the traps was completely free of vegetation, while one individual of *Poa alpina* and a very small moss patch were present near the two other traps, respectively. A third plant species present on the moraine was *Cerastium cerastoides.*

Site 2 (Traps no.1- 20): Age 38-40. Mean vegetation cover 6%. In this nearly flat area, traps were placed in two parallel rows 15m apart, with 10 traps in each row. Only 2-10% of the ground was covered with vegetation. Vegetated patches usually consisted of a mixture of mosses, *Deschampsia alpina, Salix herbacea* and *Saxifraga oppositifolia.* A few small specimens of *Salix glauca* and *S. lanata* occurred in the area.

Site 3 (Trap no 21-40): Age 62-63. Mean vegetation cover 91%. The traps were situated in two parallel rows about three meters apart, each row with 10 traps covering a gradient from a dry sandy ridge to a moist depression with snow bed vegetation. The ridge had 5-30% open sand and gravel, with vegetation dominated by *Rhacomitrium* mosses and *Stereocaulon* lichens. The lowest part was a continuous, wet mat of *Anthelia* mosses. In the medium part, the field layer covered up to 30-70%, being dominated by *Salix herbacea*, small bushes of *Salix glauca* and *S. lanata*, as well as *Empetrum hermaphroditum, Carex lachenalii, Luzula frigida,* and *Festuca vivipara.*

Site 4 (traps no. 41-60): Age 78-79. Mean vegetation cover 80%. In this site, the local variation was covered by three trap lines, about four meters between each. Ten traps were situated in a moist snow bed with continuous vegetation. Various mosses including *Anthelia* sp. covered 60-80% of the ground, the rest being mainly *Salix herbacea*, with some graminoids and other herbs. Small bushes of *Salix lanata* occurred. The remaining ten traps were set in two lines on a rather dry slope with 5-92% open sand and gravel around the traps. Here, *Stereocaulon* lichens and *Rhacomitrium* mosses dominated the vegetation, while there were also some *Festuca vivipara, Empetrum hermaphroditum, Salix herbacea,* and various graminoids.

Site 5 (traps no. 61-80). Age 153-160. Mean vegetation cover 80%. Two rows of traps were situated about three meters apart in a slope covering a gradient from dry, partly open ground to continuous vegetation in the lower part. In the upper half of the gradient, 5-60% of the ground was open sand and gravel, with *Cetraria nivalis*, *Stereocaulon* and *Cladonia* lichens combined with *Empetrum hermaphroditum* as dominant vegetation. In the lowest part, *Salix herbacea, Empetrum hermaphroditum* and *Vaccinium uliginosum* dominated, together with various green mosses. Small *Salix* bushes, mainly *Salix glauca*, occurred throughout the gradient, especially in the lower half.

Site 6 (traps no. 81-100). Age 198-205. Mean vegetation cover 96%. Also here, two rows of traps, 2-3 meters apart, covered a gradient in a slope, with moistest conditions in the bottom. Only about 4% of the ground lacked vegetation, except for some stones. In the uppermost part, a species rich meadow was dominated by graminoids, various weeds and *Empetrum hermaphroditum* in the field layer, combined with *Cladonia* and *Stereocaulon* lichens and various mosses. Most of the gradient, however, was dominated by *Salix herbacea* in combination with several weeds, including graminoids. The two lichen genera remained, but in low cover, around 5-15%.

2.4 Soil moisture

The relative soil moisture was found by collecting soil samples of about 30cm^3 in the upper 3cm layer, about 20 cm from each trap. After weighing, the samples were left to dry at room temperature, and finally dried for 3 hours at 105°, and immediately thereafter weighed again. All stones larger than 2 mm were then removed and weighed to get the exact dry weight of the stone free soil.

The relative soil moisture of each sample was then calculated by subtracting stone-free dry weight from stone-free wet weight, dividing by stone-free wet weight and then multiplying this by 100. To minimize errors the sampling at each site was done in the same day, and after a relatively dry period. If this had been done in a moist period the difference would have been less because the soil would be saturated.

2.3 Data Analysis

Assuming that there are a few underlying environmental factors that determine the distribution of the species along our gradient, we chose to describe the community structure by ordination. We employed a Detrended Correspondence Analysis (DCA) using the program R (R Development Core Team 2008) and the R package Vegan (Oksanen et al. 2008), with default settings. With this DCA analysis we are asking each species, what the most important environmental gradients are. The DCA orders the species along faunistic gradients (DCA-axes) that represent the largest possible difference in species composition. DCA is a more robust method than Principal Components Analysis (PCA) in community ordination, when dealing with long ecological gradients.

Ideally all of our traps would have the same operation time, and we would only have one dataset. Since this was not the case, we had to divide the data into datasets with comparable material. We wanted one dataset to include data from both years, and could then only included trap numbers 1-100, which were operated through both seasons. This analysis would show us differences in phenology through the seasons. In the 2008 season we included a younger site to improve our observation of the pioneer community. Due to difference in time of snowmelt, we only included data from the period when all 120 traps were operated, being from 26 July to 23 August 2008. This analysis did not include phenology. To get both phenology and a description of the pioneer community we made a dataset that included all the data. This would show us if the patterns were different. We know that this could affect the results since the operating times vary.

The beetle data, spider data and beetles and spiders data combined was given this treatment, thus giving us nine different DCA analyses. DCA-1 represents the combined data of spiders and beetles through the whole period, DCA-2 represents the combined data of spiders and beetles but excludes pitfall traps 101-120, DCA-3 represents the combined data of spiders and beetles in the period from 26 July until 23 August 2008 when all traps were operational, DCA-4 represents beetles through the whole period, DCA-5 represents all beetle data but excludes pitfall traps 101-120, DCA-6 represents all beetle data from 26 July until 23 August 2008 when all traps were operational, DCA-7 represents spiders through the whole period, DCA-8 represents all spider data but excludes pitfall traps 101-120, DCA-9 represents all spider data from 26 July until 23 August 2008 when all traps were operational. The datasets were further split in two, one containing the species and the other containing the environmental variables. Rare species appearing less than four times, were excluded from the data set because their excessive effect. A histogram of the species data showed that it was Poisson distributed, as is expected when the data represents counts. We then square rooted the species data conforming it to a normal distribution curve. We initiated the analysis by running a DCA analysis to check if the length of the first DCA-axis was long enough to expect unimodal responses of the species (Jongman et al. 1995). Scree plots from our DCA analysis show that we have two interpretable axes.

The DCA analysis gave us a faunistic beta diversity (changes of species diversity along a gradient) of the sampled terrain at almost four standard deviation units (S.D.-units). Four S.D.-units covers a complete Gaussian response curve (Jongman et al. 1995). We therefore expect that species at opposite ends have different ecological requirements, or alternatively, that sites at opposite ends have no species in common.

We therefore proceeded further with unimodal methods using DCA analysis to avoid the arch-effect and distortion of relative distance between samples (Hill & Gauch 1980).

Our DCA plots were plotted using Bray-Curtis distance, where “Two sites are chosen as endpoints for each axis, and all the other sites are ordinated relative to these endpoints, based upon their similarity to these endpoints”(Palmer 2009).

Our original environmental factors were, Distance from glacier front (*Distance*), mean percentage of vegetation cover (*Vegetation cover*), Collection year (*Year*), day of collection (*Day Number*) and age of soil (*Age Year*). We limited our number of environmental variables to four and ran a forward selection based on Aikaike Information Criterion (AIC), See tables under results.

Three different tables are presented in the results, one displaying S.D-units and eigenvalues, one present the correlation between the environmental variables and one presents the correlation between the environmental variables and the different axes. The correlation explains the degree of relationship between variables or the variables and the axes.

In the results chapter each DCA analysis will be presented in three different DCA plots. The species names are shortened to six letters, See appendix 8 and 9 for full names of taxa and author.

The first plot in each section shows only the species. Overlapping species names has been slightly adjusted to get a clear plot, but each data point is exactly the same as in the following plot which also displays the species but together with the environmental vectors.

In order to test differences in response to soil moisture between beetle species, we decided that a Spearman rank correlation would be the most suitable test since we had a none-parametric response variable. The actual test was conducted on free statistical software (Wessa 2009). Only traps that collected perfectly were used, and only from site 3 and 4 due to most stable collecting conditions there and the best span, with regards to moisture differences.

To enable assessment of the beetle and spider phenology, bar charts were produced to get a visual representation of seasonal distribution. All species occurring with less than 10 individuals was excluded.

3 Results

3.1 Beetles and soil moisture

Because Ottesen (1996) found that soil humidity was more important than vegetation associations in determining beetles distribution we placed our traps in moisture gradients. Ottesen (1996) took five samples within his 47 plots twice to determine his moisture gradients. We did not have the capacity to take this many samples but took one sample juxtaposed each trap. In table 1 we see that the beetle species do not have the same preferences with respect to soil moisture. *Amara quenseli, Byrrhus fasciatus* and *Cymidis vaporariorum* prefer dry habitat around the traps or at least avoiding the traps with high soil moisture. The two first mentioned species have a strong response, while the last one has a somewhat weaker response. *Geogromicus longipes*, *Patrobus sepentrionis* and *Liogluta alpestris* are avoiding traps in dry spots or are drawn to high moisture. The two first mentioned have a strong response while the last one has a weaker response

Table 1. Beetle response to soil moisture, described by Spearman rank correlation. This table shows how soil moisture affects different beetle species at the Midtdalsbreen glacier, Norway 2007-2008. Only beetles from traps with absolutely no errors were selected for this test, non significant results were excluded.

	ß (uncorrected)	*ß* (corrected)	t	2-sided t-value (5%)	1-sided t-value (5%)	P	SE	N
Amara quenseli	-0,72	-0,72	-3,83	2,16	1,77	0,007	38,64	15
Byrrhus fasciatus	-0,73	-0,76	-5,82	2,06	1,71	<0,001	114,72	26
Cymindis vaporariorum	-0,38	-0,40	-2,19	2,06	1,70	0,050	123,64	27
Geodromicus longipes	0,61	0,60	2,87	2,14	1,76	0,017	43,89	16
Liogluta alpestris	0,41	0,39	2,38	2,04	1,69	0,019	184,14	33
Patrobus septentrionis	0,73	0,73	5,95	2,04	1,69	<0,001	173,22	32

3.2 Phenology

As mentioned the pitfall traps register activity level rater then abundance, but in this chapter the amount of a species caught will be referred to as abundance.

Phenology of the beetles:

Acidota crenata: Does not show any particular pattern, just activity in the cold periods. Note the low abundance (figure 2).

Amara alpina: Peaks in July of both years (figure 2).

Amara quenseli: Peaks in the start of the season in both years and decreasing as summer turns into fall (figure 2).

Anthophagus alpines: Shows a top in the start of the summer and decreases rapidly and evenly towards fall (figure 2).

Arpedium quadrum: Is only present in very small numbers, but shows increasing numbers in the end of the 2008 season (figure 2).

Athenta hypnorum: Could be active during the winter or early spring, but also active in July 2008. Note the low abundance (figure 2).

Bembidion hastii: Is showing an increasing presence towards the fall of 2008 (figure 3).

Boreaphilus henninganus: Had a top in the first 2008 collection which also includes winter collections, but also a higher abundance in early July. Note the low abundance (figure 3).

Byrrhus fasciatus: Had a top in the beginning of 2007, which rapidly decrees and a top could not be said to be recorded after this (figure 3).

Cephalocousya nivicola: Had a top in the early season of both years, with the largest top in 2008 which also was a bit earlier (figure 3).

Chrysomela collaris: Was frequently caught in the first trapping interval, but was almost not present at all after this (figure 3).

Curimopsis cyclolepidia: Apparently has a top in July both years (figure 3).

Cymindis vaporariorum: Is most abundant in the start of the seasons, and evenly decreases in numbers, towards the fall. Note the low abundance (figure 4).

Eucnecosum brachypterum: Has a top in July. Note the low abundance (figure 4).

Geodromicus longipes: Has a top in July in both years (figure 4).

Liogluta alpestris: Increases as the 2007 season moves on, and if the first 2008 date is not considered (because of cumulative fall and winter catchments), we can see the same pattern only slightly earlier (figure 4).

Mycetoporus erichsonanus: Occurs in small numbers and few dates, no real pattern (figure 4).

Nebra nivalis: Shows a top in the early 2007 season and declines smoothly after this. In 2008 however there is hard to see a pattern, but have in mind the low abundance (figure 4).

Nebria rufescens: Appears to have a top early in the season. Note the low abundance (figure 5).

Notiophilus aquaticus: Appears to have a top early in the season. Note the low abundance (figure 5).

Omalium caesuin: Occurs in small numbers but seems to have a top towards the fall (figure 5).

Otiorrhynchus nodosus: Seems to have a top in July, but occurs in small numbers (figure 5).

Patrobus septentrionis: Probably peaks in early July both years (figure 5).

Pelophila borealis: Only has a top in early July 2007 and are rarely caught after this. Note the low abundance (figure 5).

Simplocaria metallica: Occurs in small numbers, but seems to have a top in the start of the 2007 season (figure 6).

Tachinus elongates: Has a top in July 2008, but occurs in very few numbers (figure 6).

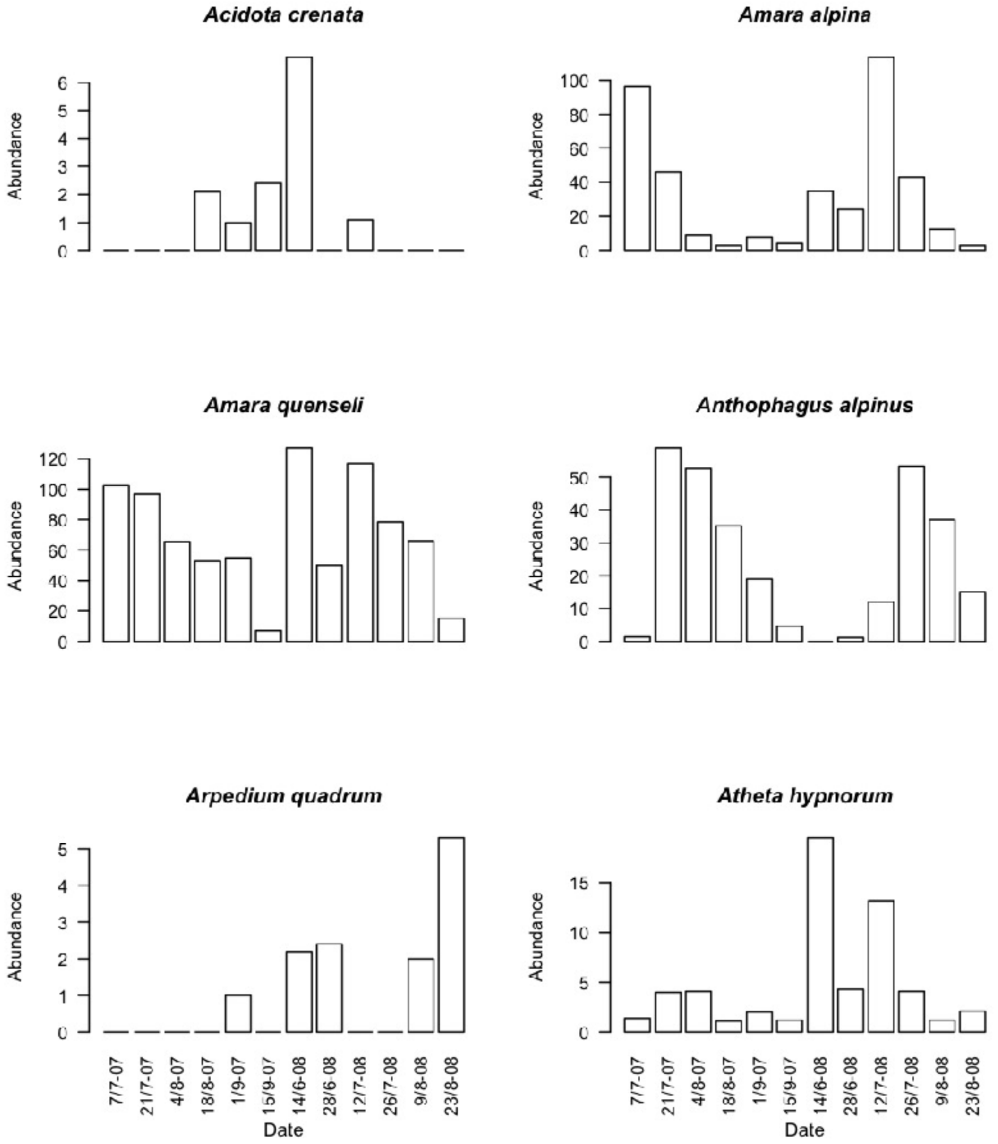


Figure 2. Phenological patterns of beetles shown through the entire collection period. Note that all the dates in 2008 have an extra set of traps placed on the youngest moraine. This figure only shows patterns. One should not compare abundance between the years, only notice how the dates are displaying a pattern or not. Abundance in this figure is adjusted to catches per 20 traps. The first date in 2008 is overestimated because this includes all the individuals caught after the traps were snowbound. Likewise, the 15 September 2007 could be underestimated due to snow covering some of the traps. These dates should not be taken into account.

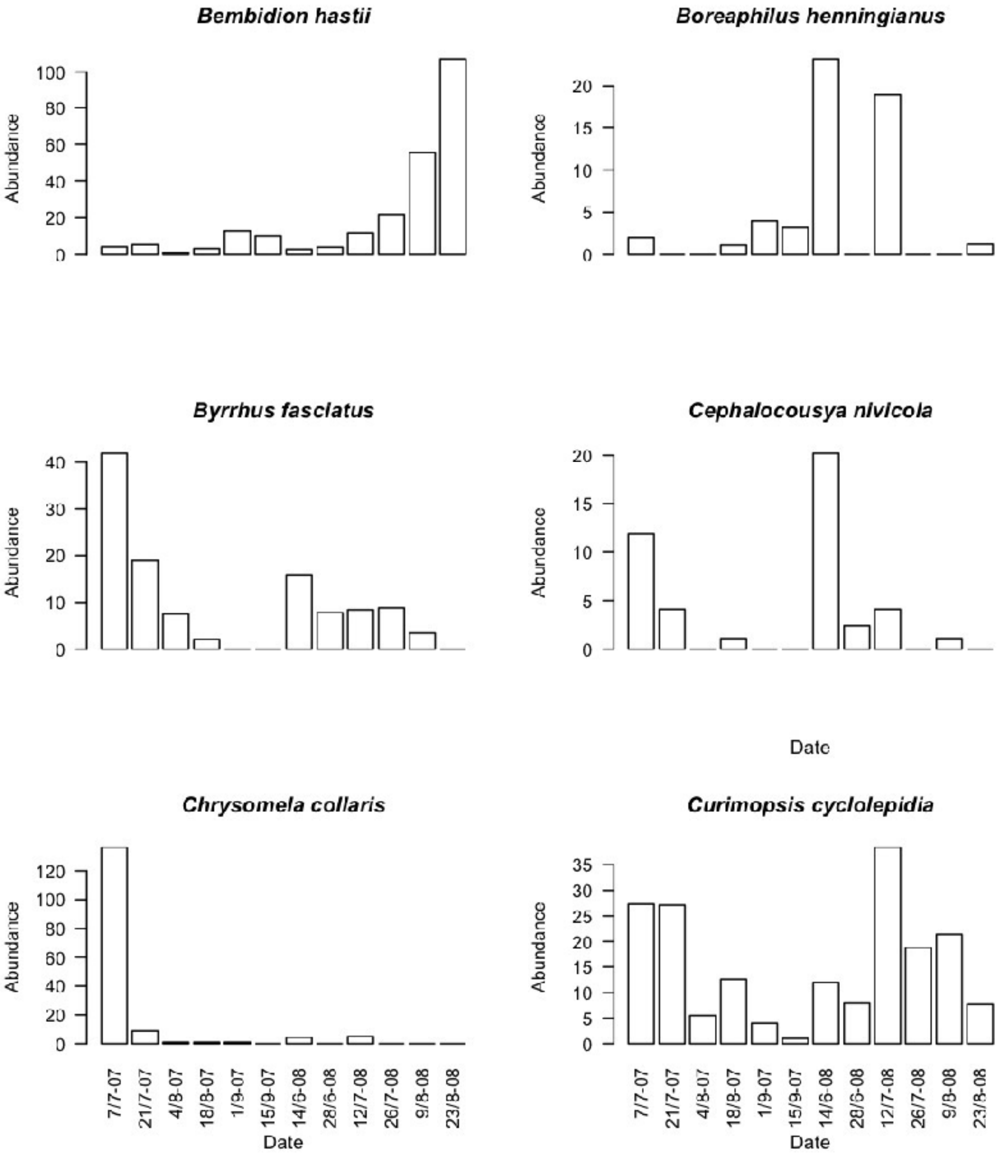


Figure 3. Phenological patterns of beetles shown through the entire collection period. Note that all the dates in 2008 have an extra set of traps placed on the youngest moraine. This figure only shows patterns. One should not compare abundance between the years, only notice how the dates are displaying a pattern or not. Abundance in this figure is adjusted to catches per 20 traps. The first date in 2008 is overestimated because this includes all the individuals caught after the traps were snowbound. Likewise, the 15 September 2007 could be underestimated due to snow covering some of the traps. These dates should not be taken into account.

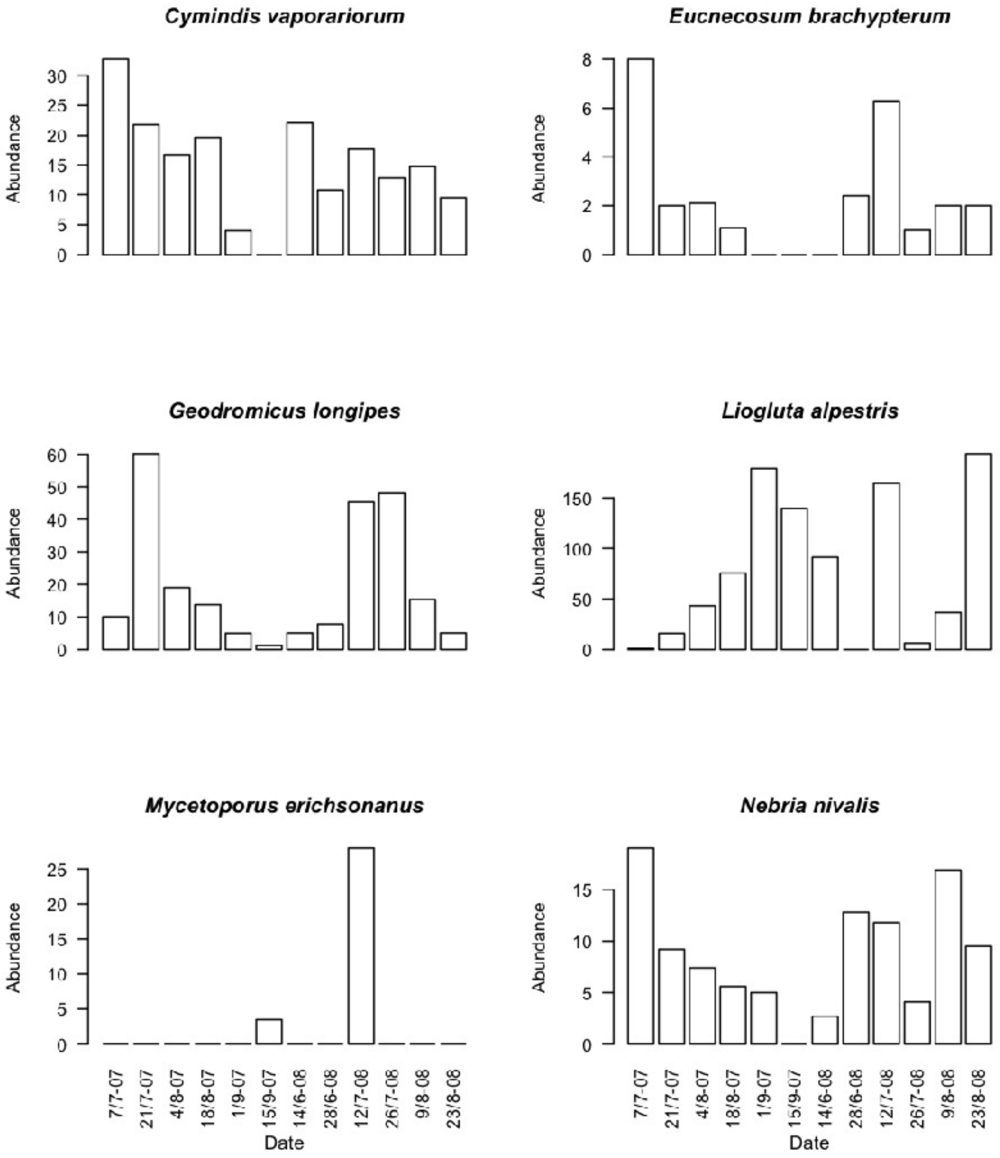


Figure 4. Phenological patterns of beetles shown through the entire collection period. Note that all the dates in 2008 have an extra set of traps placed on the youngest moraine. This figure only shows patterns. One should not compare abundance between the years, only notice how the dates are displaying a pattern or not. Abundance in this figure is adjusted to catches per 20 traps. The first date in 2008 is overestimated because this includes all the individuals caught after the traps were snowbound. Likewise, the 15 September 2007 could be underestimated due to snow covering some of the traps. These dates should not be taken into account.

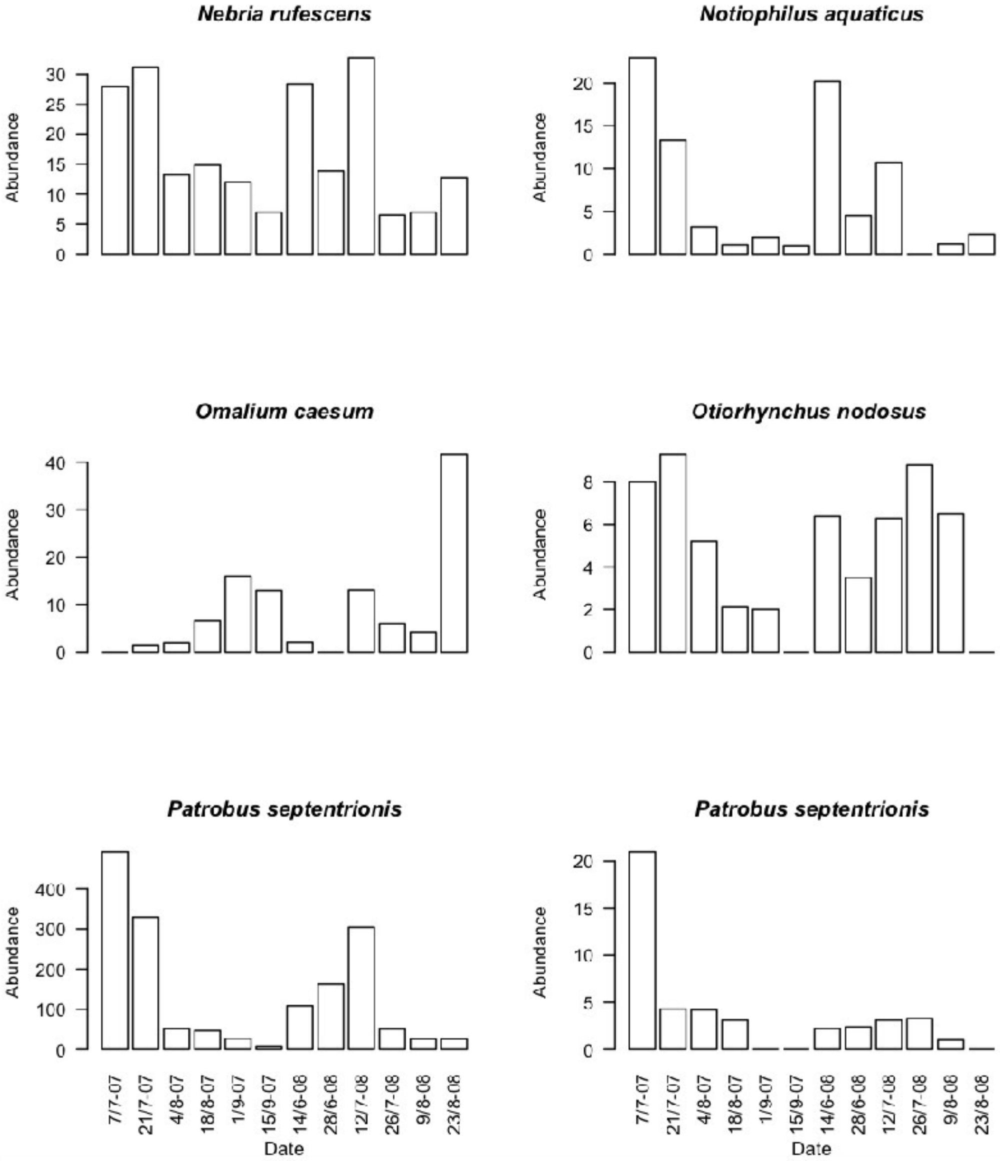


Figure 5. Phenological patterns of beetles shown through the entire collection period. Note that all the dates in 2008 have an extra set of traps placed on the youngest moraine. This figure only shows patterns. One should not compare abundance between the years, only notice how the dates are displaying a pattern or not. Abundance in this figure is adjusted to catches per 20 traps. The first date in 2008 is overestimated because this includes all the individuals caught after the traps were snowbound. Likewise, the 15 September 2007 could be underestimated due to snow covering some of the traps. These dates should not be taken into account.

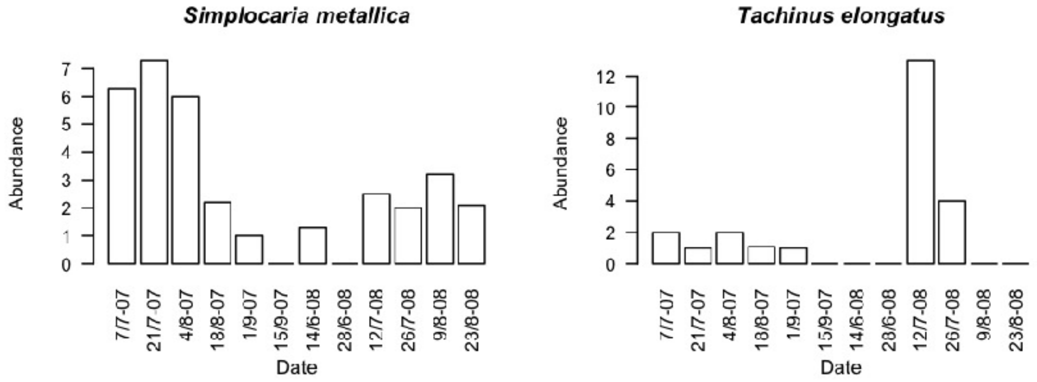


Figure 6. Phenological patterns of beetles shown through the entire collection period. Note that all the dates in 2008 have an extra set of traps placed on the youngest moraine. This figure only shows patterns. One should not compare abundance between the years, only notice how the dates are displaying a pattern or not. Abundance in this figure is adjusted to catches per 20 traps. The first date in 2008 is overestimated because this includes all the individuals caught after the traps were snowbound. Likewise, the 15 September 2007 could be underestimated due to snow covering some of the traps. These dates should not be taken into account.

Phenology of the spiders:

Agyneta nigripes: Has a top in mid June of 2008. Note the low abundance (figure 7).

Arctosa alpigena: Has a top in the start of the season, but decreases quite rapidly towards the fall. Note the low abundance (figure 7).

Bathyphantes gracilis: Has a top in early July in both seasons. Note the low abundance (figure 7).

Collinsia Holmgreni: Has a top in July in both seasons, but twice as many in 2007. Note the low abundance (figure 7).

Erigone arctica: Has a top during the winter period or in early spring (before 14 June). Seems to like it cold and could be winter active. Note the low abundance (figure 7).

Erigone triolensis: Has a top early in the season. Note the low abundance (figure 7).

Hilaria frigid: Has a top early in the season. Note the low abundance (figure 8).

Gnaphosa leporia: Has a top in July, Note the low abundance (figure 8).

Gonatium rubens: Has a top in July in both years, but also a top in the first half of august in 2007. Note the low abundance (figure 8).

Mecynargus morulus: Has a small top in early July. Note the low abundance (figure 8).

Oedothorax retusus: Has a top in early July in 2007, but a much lower appearance in 2008. Note the low abundance (figure 8).

Oreonetides vaginatus: Has a top in early July. Note the low abundance (figure 8).

Ozyptila arctica: Has a top during the winter or early June. Note the low abundance (figure 9).

Pardosa paludicola: Has a top in early July (figure 9).

Pardosa septentrionalis: Has a top during the winter or early June. Note the low abundance (figure 9).

Pardosa trailli: Has a top in early July in 2007, but are more or less increasing towards fall in 2008. Note the low abundance (figure 9).

Pelecopsis mengei: Is very evenly distributed, but has a winter or early June top in 2008. Note the low abundance (figure 9).

Scotinotylus evansi: Has a top in winter or early June of 2008 (figure 9).

Tiso aestivus: Has a small top in early June in both 2007 and 2008, but the biggest top during the winter or early June of 2008 (figure 10).

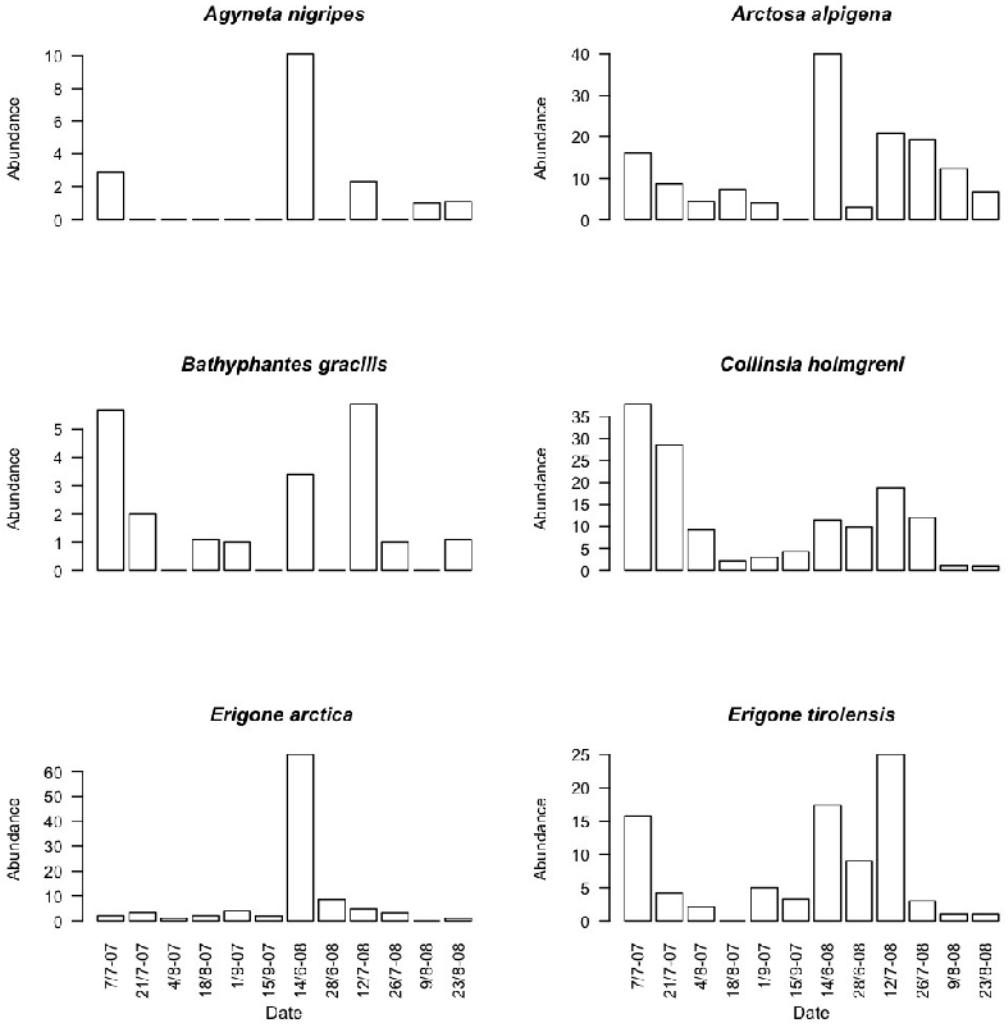


Figure 7. Phenological patterns of spiders shown through the entire collection period. Note that all the dates in 2008 have an extra set of traps placed on the youngest moraine. This figure only shows patterns. One should not compare abundance between the years, only notice how the dates are displaying a pattern or not. Abundance in this figure is adjusted to catches per 20 traps. The first date in 2008 is overestimated because this includes all the individuals caught after the traps were snowbound. Likewise, the 15 September 2007 could be underestimated due to snow covering some of the traps. These dates should not be taken into account.

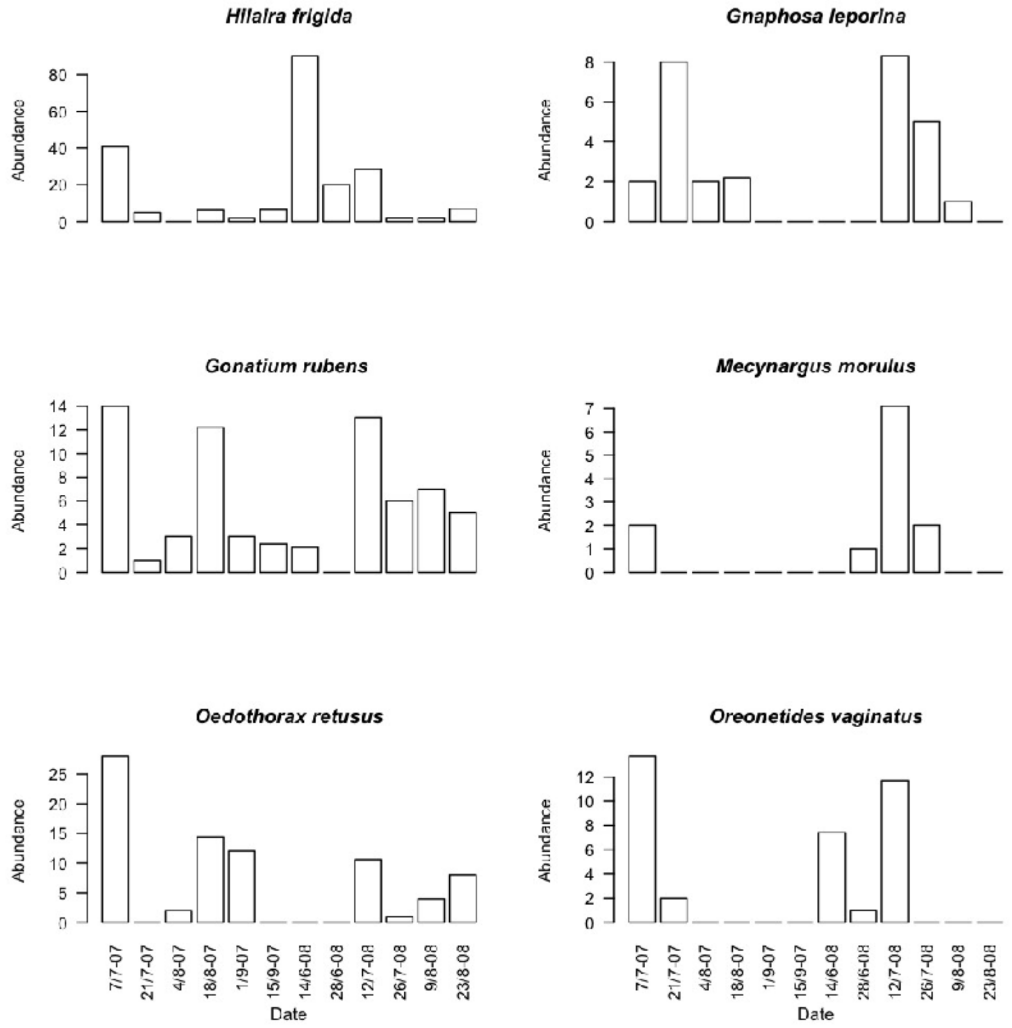


Figure 8. Phenological patterns of spiders shown through the entire collection period. Note that all the dates in 2008 have an extra set of traps placed on the youngest moraine. This figure only shows patterns. One should not compare abundance between the years, only notice how the dates are displaying a pattern or not. Abundance in this figure is adjusted to catches per 20 traps. The first date in 2008 is overestimated because this includes all the individuals caught after the traps were snowbound. Likewise, the 15 September 2007 could be underestimated due to snow covering some of the traps. These dates should not be taken into account.

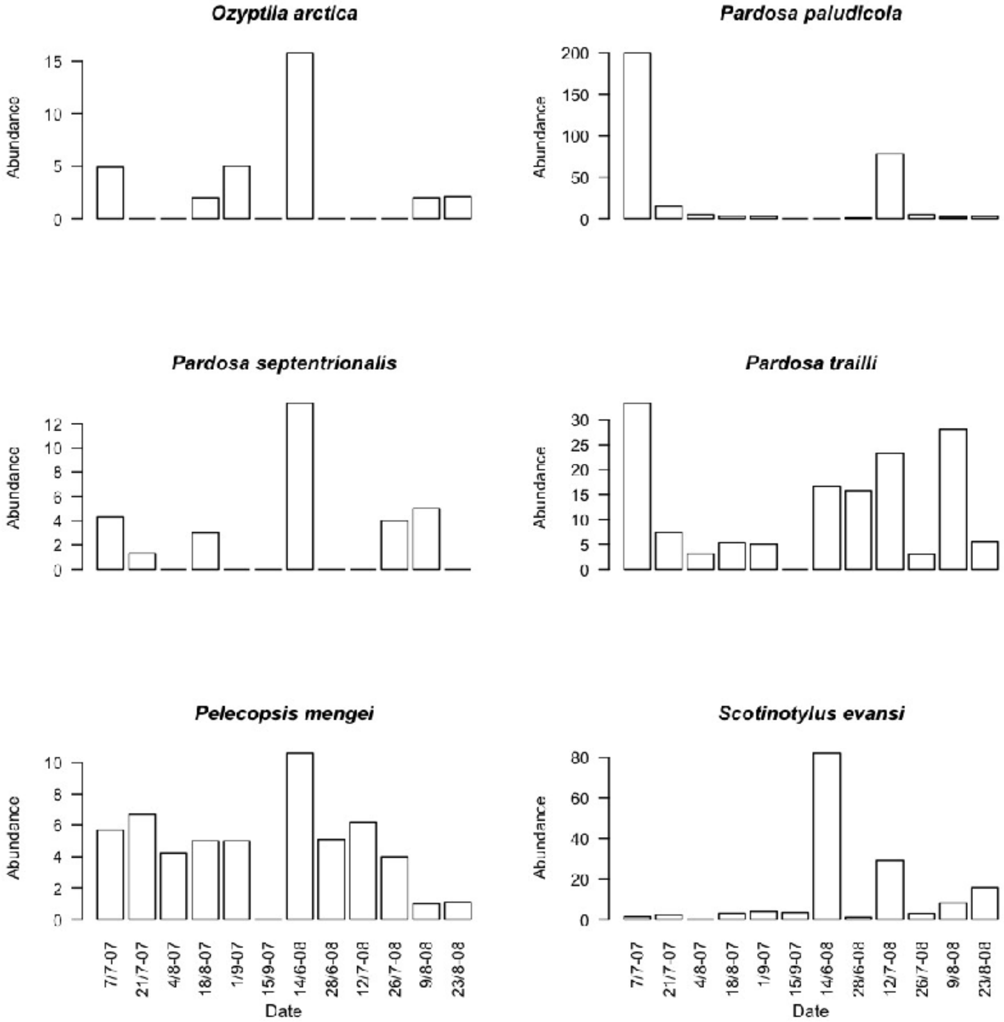


Figure 9. Phenological patterns of spiders shown through the entire collection period. Note that all the dates in 2008 have an extra set of traps placed on the youngest moraine. This figure only shows patterns. One should not compare abundance between the years, only notice how the dates are displaying a pattern or not. Abundance in this figure is adjusted to catches per 20 traps. The first date in 2008 is overestimated because this includes all the individuals caught after the traps were snowbound. Likewise, the 15 September 2007 could be underestimated due to snow covering some of the traps. These dates should not be taken into account.

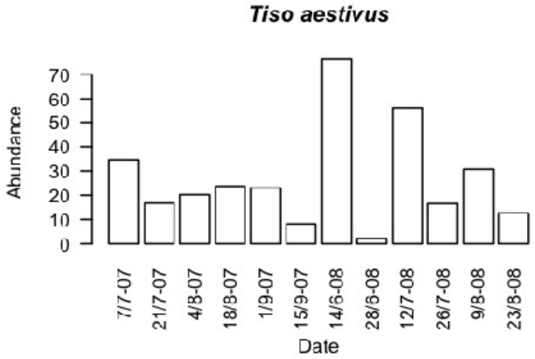


Figure 10. Phenological patterns of spiders shown through the entire collection period. Note that all the dates in 2008 have an extra set of traps placed on the youngest moraine. This figure only shows patterns. One should not compare abundance between the years, only notice how the dates are displaying a pattern or not. Abundance in this figure is adjusted to catches per 20 traps. The first date in 2008 is overestimated because this includes all the individuals caught after the traps were snowbound. Likewise, the 15 September 2007 could be underestimated due to snow covering some of the traps. These dates should not be taken into account.

3.3.1 Beetles and spiders combined

3.3.1.1. DCA-1: Total material

Table 2 shows the axes lengths in S.D.-units for the combined data plots of spiders and beetles. The axes lengths indicate a complete species turnover. The eigenvalues expresses the variation in the data of each axis.

Table 2. SD-units and eigenvalues for DCA axes one and two for DCA-1-3

	DCA-1		DCA-2		DCA-3	
Axis	DCA1	DCA2	DCA1	DCA2	DCA1	DCA2
Eigenvalues	0.47	0.21	0.43	0.20	0.63	0.27
Axis lengths	3.74	2.54	4.00	2.60	3.88	2.14

According to our scree plot we have two interpretable axes. Forward selection based on AIC for the DCA-1 data gave us the following model vegetation cover, age year, day number and distance. The best model explains 40% of the variance. Correlation among the environmental variables for DCA-1 is shown in table 3.

Table 3. Correlation among the environmental variables for DCA-1

	Year	Day Number	Age Year	Distance	Vegetation cover
Year		-0.35	-0.15	-0.15	-0.14
Day Number			0.09	0.06	0.03
Age Year				0.90	0.68
Distance					0.85
Vegetation cover					

The distance, age year and vegetation cover vectors are correlated at -0.99, -0.97 and -0.97 along DCA axis one respectively. The year vector is correlated along DCA axis two at 0.92. All vectors are significant (<0.05) except for year and day number (0.55 and 0.56).

The correlation between the environmental variables and the different axes for the combined data plots of spiders and beetles for all six figures DCA-1- DCA-3 (figure 11,12,13,14,15 and 16) are shown in table 4.

Table 4. Correlation between the environmental variables and different axes for DCA-1-3.

	DCA-1		DCA-2		DCA-3	
Axis	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
Age Year	-0.82	0.18	-0.77	0.19	-0.87	-0.05
Distance	-0.92	0.17	-0.90	0.16	-0.95	-0.01
Vegetation cover	-0.94	0.06	-0.92	-0.01	-0.94	-0.05
Day Number	-0.09	-0.03	-0.10	0.02	-0.02	-0.13
Year	0.15	0.07	0.00	0.12	0	0

In the DCA-1 plots, figure 11 and 12, nine species, five spiders and four beetles are ordinate along DCA axes one with values higher than one *Bembidion hastii, Simplocaria metallica, Collinsia holmgreni, Erigone tirolensis, Nebria nivalis, Pardosa trailli, Hilaira frigida, Erigone arctica* and *Amara alpina* in descending order respectively (see appendix 2). We regard these as pioneer species, since they are negatively related with all significant vectors. All are believed to be predators except for one, *Simplocaria metallica* (see appendix 8). The rest of the species are spared out along DCA axis two.

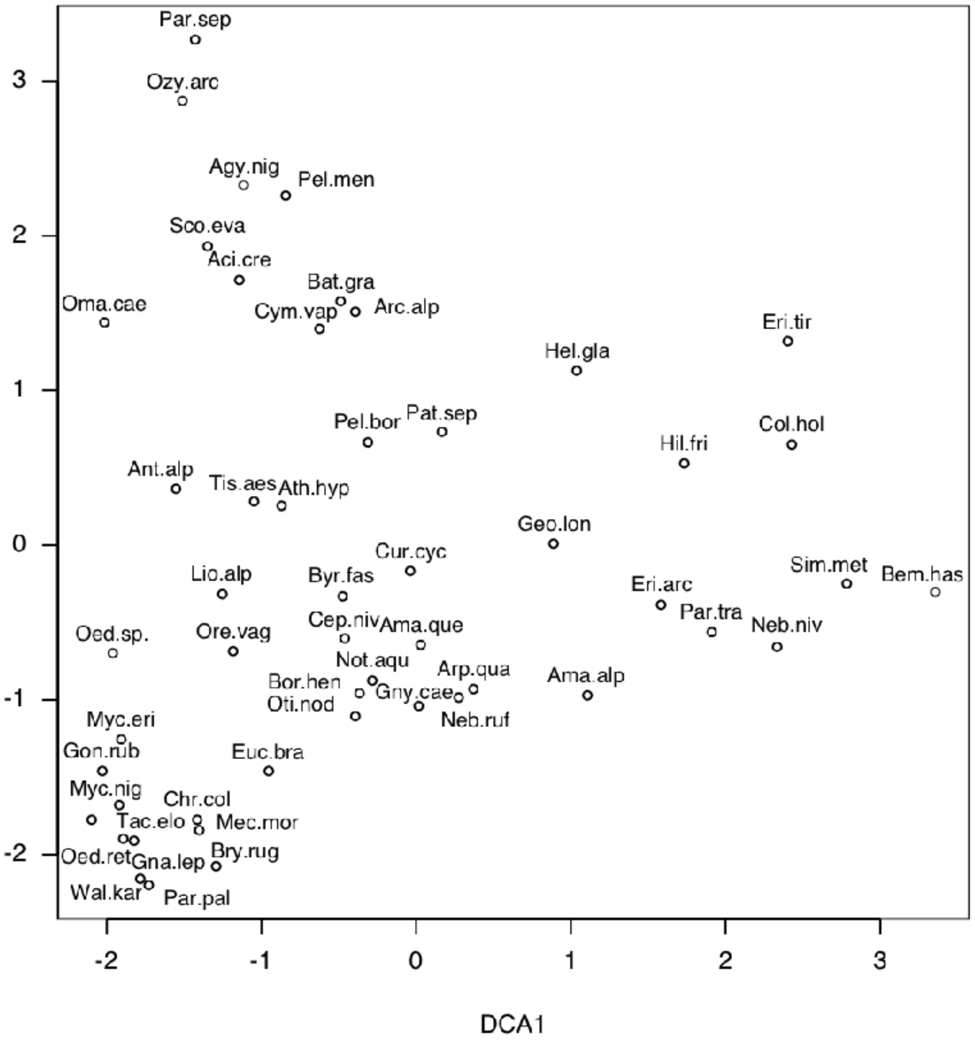


Figure 11. DCA plot of the first two axes of DCA-1, showing the ecological distence between the different beetle and spiders. DCA axis one is best explained by distance from glacier snout, age of the soil and vegetation cover, respectively. Values increase from right to left.

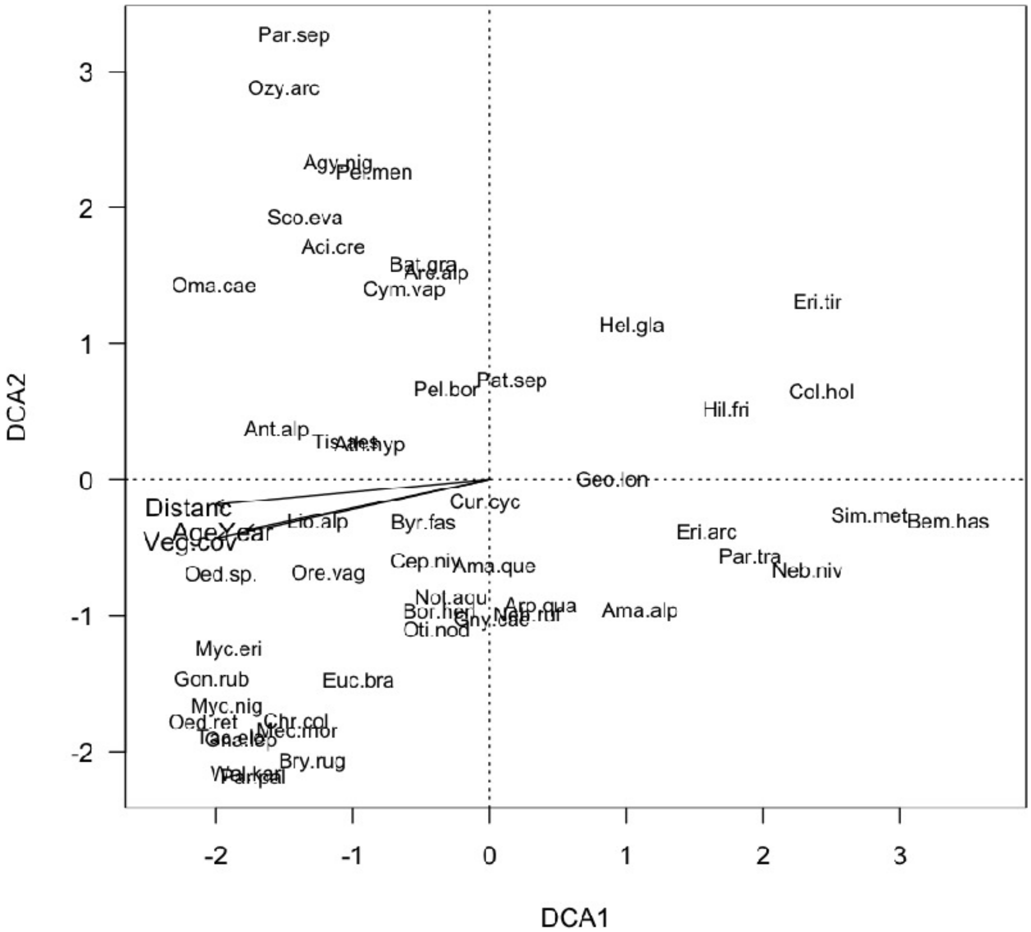


Figure 12. DCA biplot of the first two axes of DCA-1, showing the ecological distance between beetles and spiders, and also environmental gradient vectors. DCA axis one is well explained by distance from glacier, age of soil and vegetation cover, respectively. Values increase from right to left.

3.3.1.2 DCA-2: Total material excluding pitfall traps 101-120

For the DCA-2 ordination forward selection based on AIC gave us the following model vegetation cover, age year, day number, and distance. The best model explains 41% of the variance. Correlation among the environmental variables for DCA-2 is shown in table 5.

Table 5. Correlation among the environmental variables for DCA-2

	Year	Day Number	Age Year	Distance	Vegetation cover
Year		-0.36	-0.04	-0.03	-0.01
Day Number			0.08	0.05	0.01
Age Year				0.88	0.59
Distance					0.81
Vegetation cover					

The distance, age year, vegetation cover and day number vectors are correlated at -0.99, -0.99, -0.97 and -0.93 along DCA axis one respectively. The year vector is correlated along DCA axis two at 0.99. All vectors are significant (<0.05) except for year and day number (0.65 and 0.42).

In the DCA-2 plots, figure 13 and 14, five spiders and four beetles are ordinate along DCA axis one with values higher than one *Bembidion hastii, Simplocaria metallica, Collinsia holmgreni, Erigone tirolensis, Nebria nivalis, Pardosa trailli, Hilaira frigida, Erigone arctica* and *Amara alpina* in descending order respectively (see appendix 2). We regard these as pioneer species, since they are negatively related with all significant vectors. All are believed to be predators except for one, *Simplocaria metallica* (see appendix 8). The rest of the species are spared out along DCA axes two. Figure 13 and 14 are almost identical to figure 11 and 12 except for small adjustments, the species are moved further up the positive end of DCA axes two (see appendix 2).

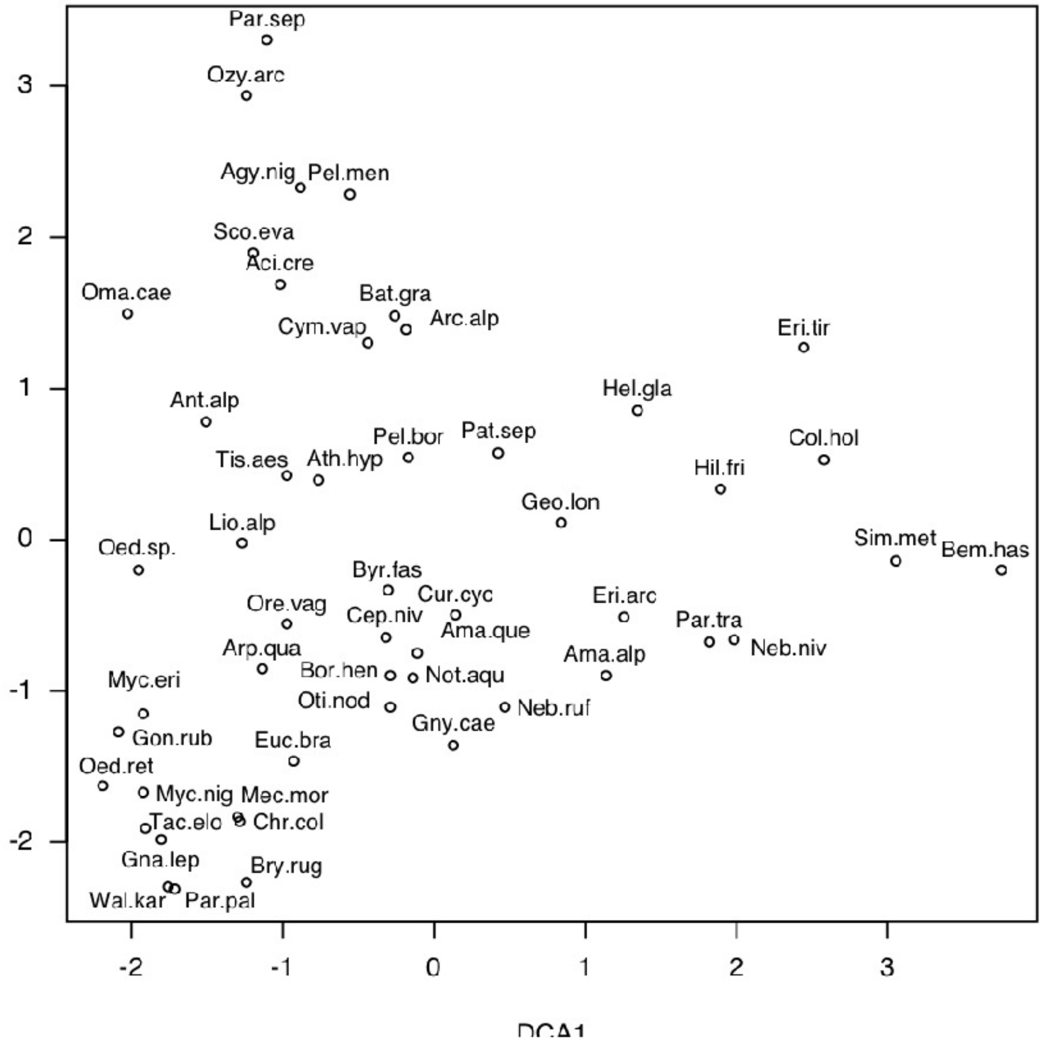


Figure 13. DCA plot of the first two axes of DCA-2, showing the ecological distance between different species of beetles and spiders. DCA axis one is best explained by distance from glacier snout, age of soil and vegetation cover, respectively. Values increase from right to left.

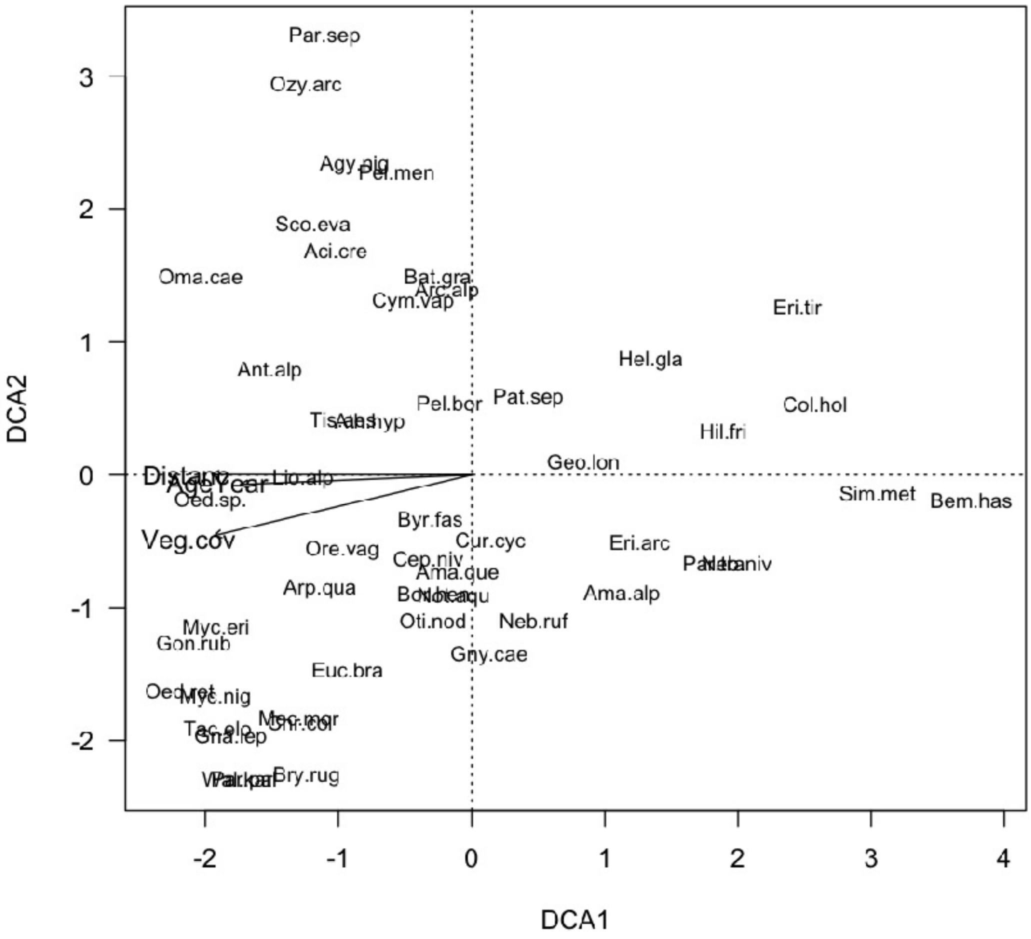


Figure 14. DCA biplot of the first two axes of DCA-2, showing the ecological distance between different species of beetles and spiders also including environmental gradient vectors. DCA axis one is best explained by distance from glacier snout, age of soil and vegetation cover, respectively. Values increase from right to left.

3.3.1.3 DCA-3: Summer catches (simultaneous sampling in the complete gradient)

For the DCA-3 ordination forward selection based on AIC gave us the following model vegetation cover, age year and day number. The best model explains 51% of the variance. Correlation among the environmental variables for DCA-3 is shown in table 6.

Table 6. Correlation among the environmental variables for DCA-3

	Day Number	Age Year	Distance	Vegetation cover
Day Number	1	0.00	0.00	0.00
Age Year	0	1.00	0.92	0.74
Distance	0	0.92	1.00	0.87
Vegetation cover	0	0.74	0.87	1.00

The vegetation cover, distance and age year vectors are correlated at -0.96, -0.93 and -0.84 along DCA axis one respectively. The day number vector is correlated along DCA axis two at 0.99. All vectors are significant (<0.05) except for day number (0.78).

In the DCA-3 plots figure 15 and 16, nine species are ordinate along DCA axis one with values higher than one *Bembidion hastii, Simplocaria metallica, Nebria nivalis, Erigone arctica, Collinsia holmgreni, Hilaira frigida, Erigone tirolensis, Pardosa trailli* and *Geodromicus longipes* in descending order respectively (see appendix 2).

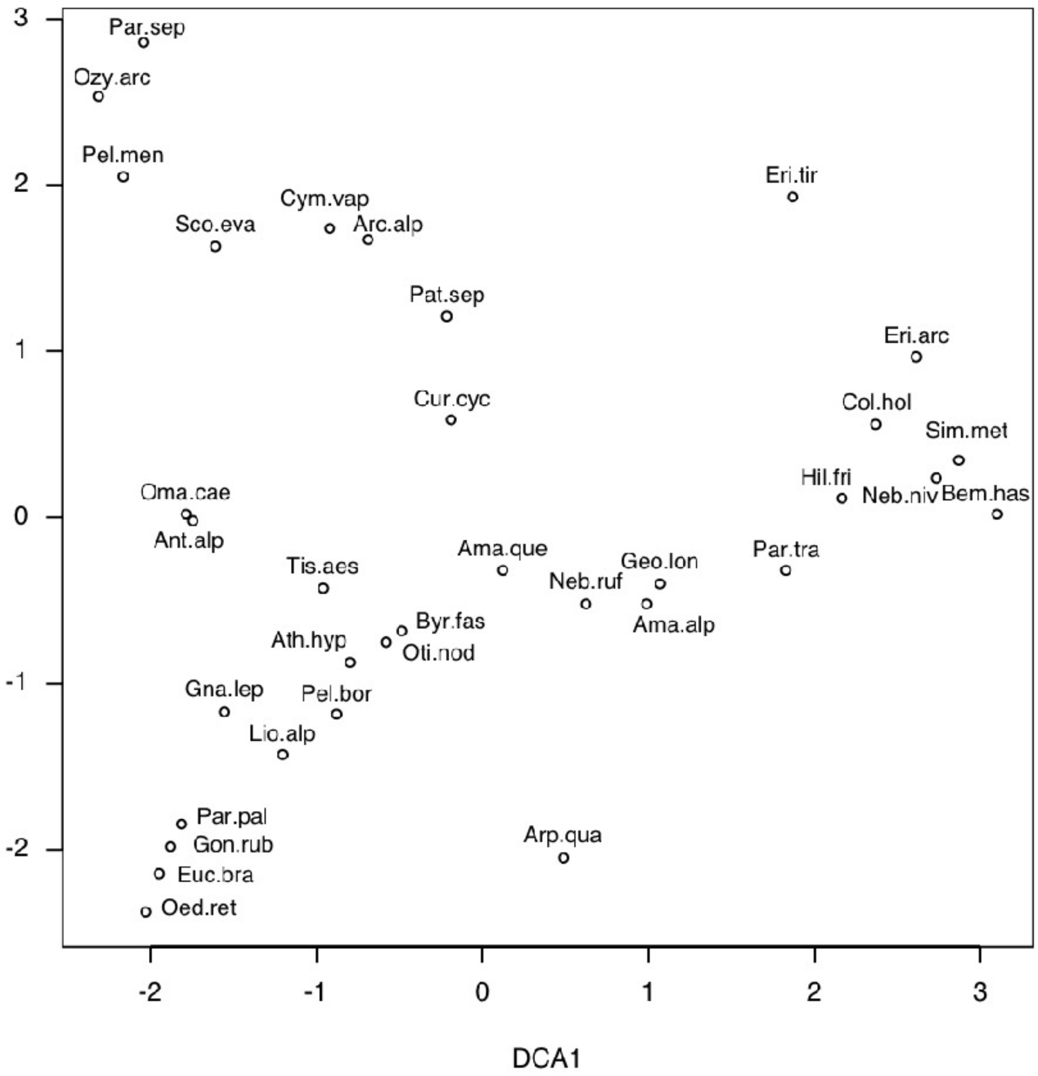


Figure 15. DCA plot of the first two axes of DCA-3, showing the ecological distance between different species of beetles and spiders. DCA axis one is best explained by vegetation cover, distance from glacier snout and age of the soil, respectively. Values increase from right to left.

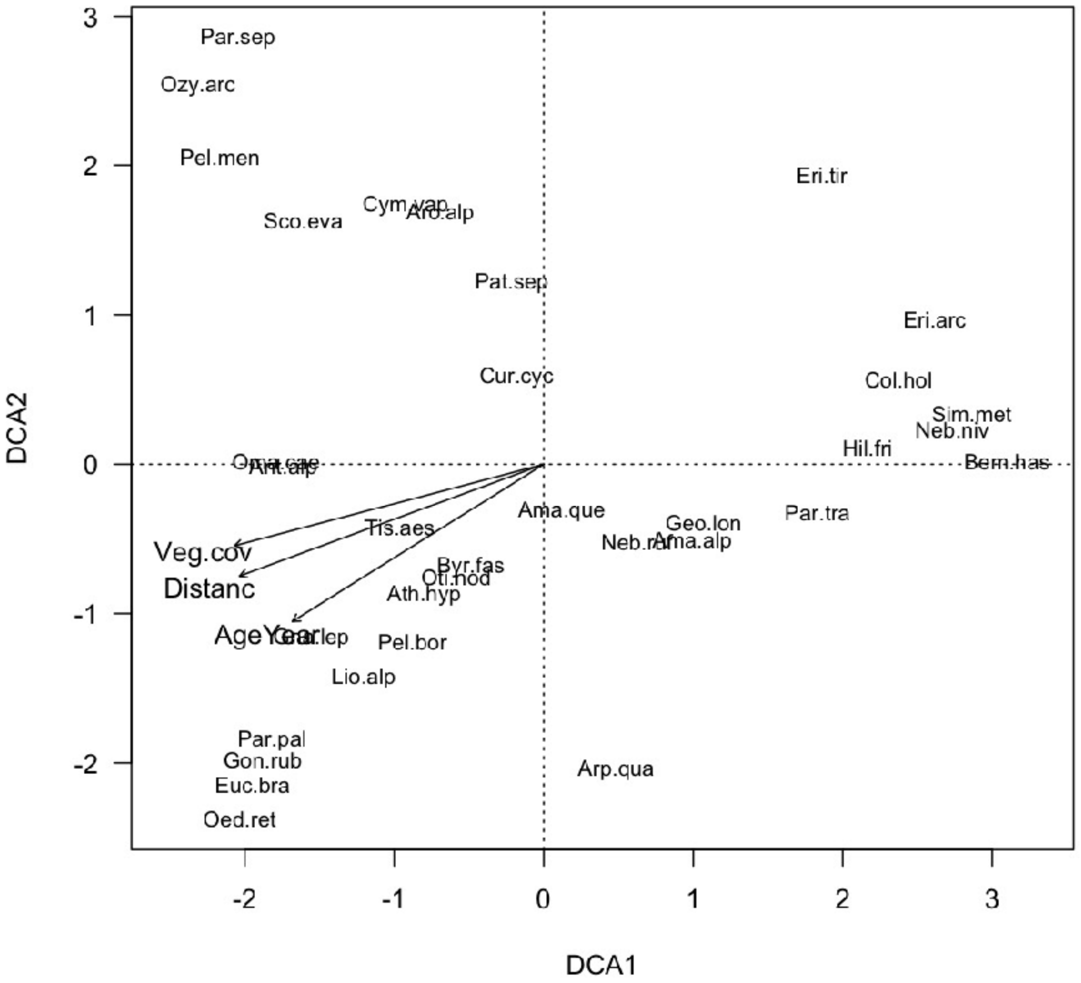


Figure 16. DCA biplot of the first two axes of DCA-3, showing the ecological distance between species of beetles and spiders. DCA axis one is best explained by vegetation cover, distance from glacier snout and age of soil, respectively. Values increase from right to left.

3.3.2 Beetles

3.3.2.1 DCA-4: Total beetle material

The axis lengths in S.D.-units for the beetle plots DCA-4 – DCA-6 (figure 17, 18, 19, 20, 21 and 22) are shown in table 7 and indicate a complete species turnover.

Table 7. S.D.-units and eigenvalues for DCA axes one and two for the beetle plots DCA-4-6

	DCA-4		DCA-5		DCA-6	
Axis	DCA1	DCA2	DCA1	DCA2	DCA1	DCA2
Eigenvalues	0.42	0.20	0.35	0.21	0.60	0.18
Axes lengths	3.97	2.29	4.05	2.07	3.73	1.99

Forward selection based on AIC for the DCA-4 data gave us the following model vegetation cover, age year and day number. The best model explains 37% of the variance. Correlation among the environmental variables for DCA-4 is shown table 8.

Table 8. Correlation among the environmental variables for DCA-4

	Day Number	Age Year	Distance	Vegetation cover
Year	-0.35	-0.15	-0.15	-0.14
Day Number		0.09	0.06	0.03
Age Year			0.90	0.68
Distance				0.85

The vegetation cover and distance vectors are correlated at -0.99 and -0.85 DCA axis one respectively. The day number, year and age year vector is correlated along DCA axis two at -0.98, -0.94 and 0.75. All vectors are significant (<0.05) except for year (0.33).

The correlation between the environmental variables and the different axes for the combined data plots of spiders and beetles for all six figures DCA-4- DCA-6 (figure 17, 18, 19, 20, 21 and 22) are shown in table 9.

Table 9. Correlation between the environmental variables and the different axes DCA-4-6

	DCA-4		DCA-5		DCA-6	
Axis	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
Age Year	-0.75	0.46	0.67	0.62	-0.84	-0.33
Distance	-0.88	0.26	-0.85	0.36	-0.94	-0.23
Vegetation cover	-0.91	-0.02	-0.89	-0.04	-0.93	-0.07
Day Number	-0.05	-0.39	-0.08	-0.28	-0.03	0.52
Year	0.13	-0.01	-0.03	0.01	-	-

The DCA-4 plots shows two distinct groups separated along the DCA axis one. The beetles are separated in two distinct groups separated along the DCA axis one. The pioneer species *Bembidion hastii, Simplocaria metallica, Nebria nivalis, Amara alpina, Helophorus glacialis, Geodromicus longipes* and *Arpedium quadrum* are grouped in the far positive end of the axis negatively correlated with vegetation cover, distance and age year. The other extremity represents the latest arrivals in the primary succession. The rest is spread out along DCA axes two and primarily affected by the variable day number.

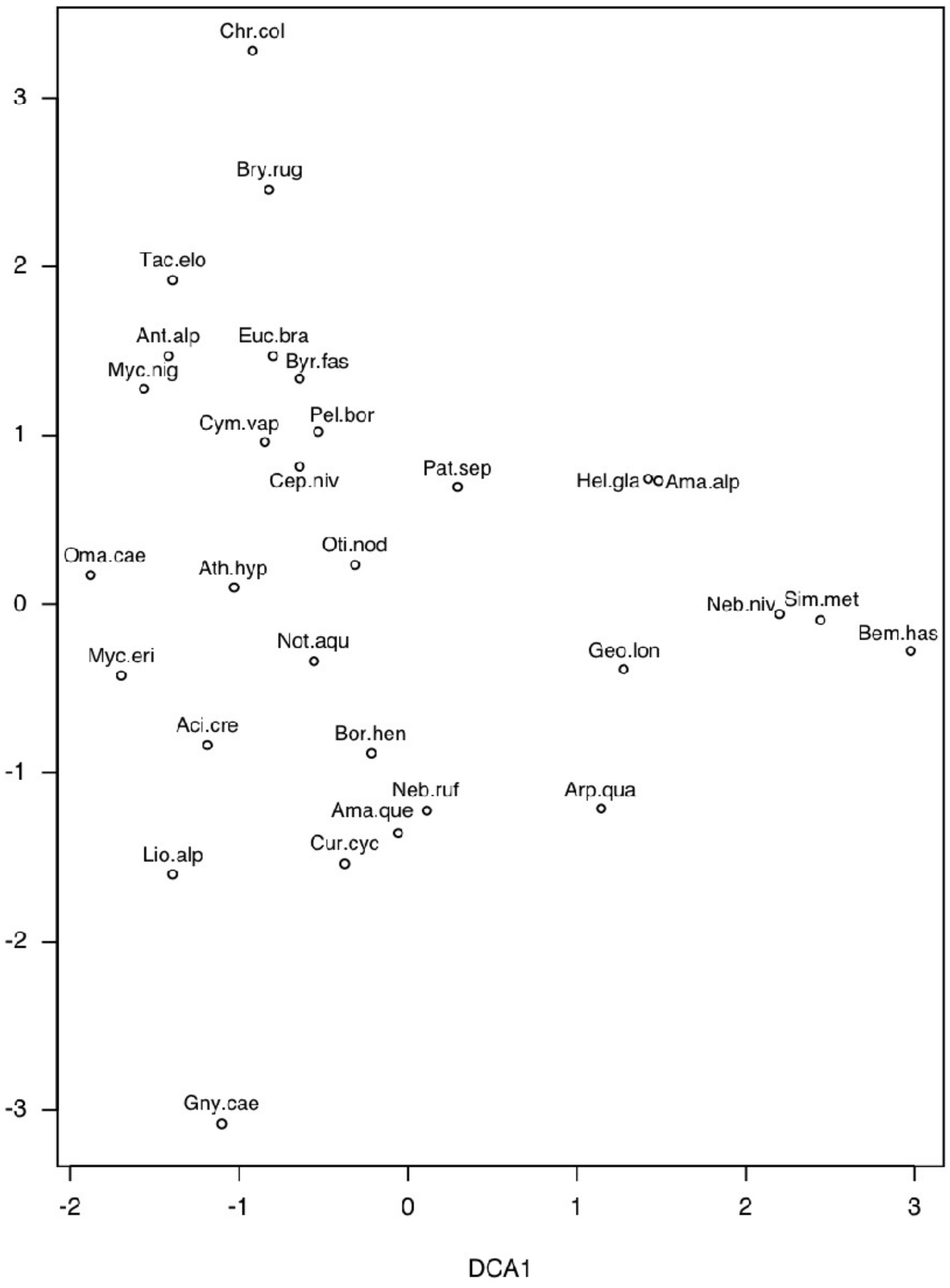


Figure 17. DCA plot of the first two axes of DCA-4, showing the ecological distance between the different beetle species. DCA axis one is highly explained by vegetation cover. Values increase from left to right. DCA axis two is explained by seasonal differences with spring on top and autumn towards bottom.

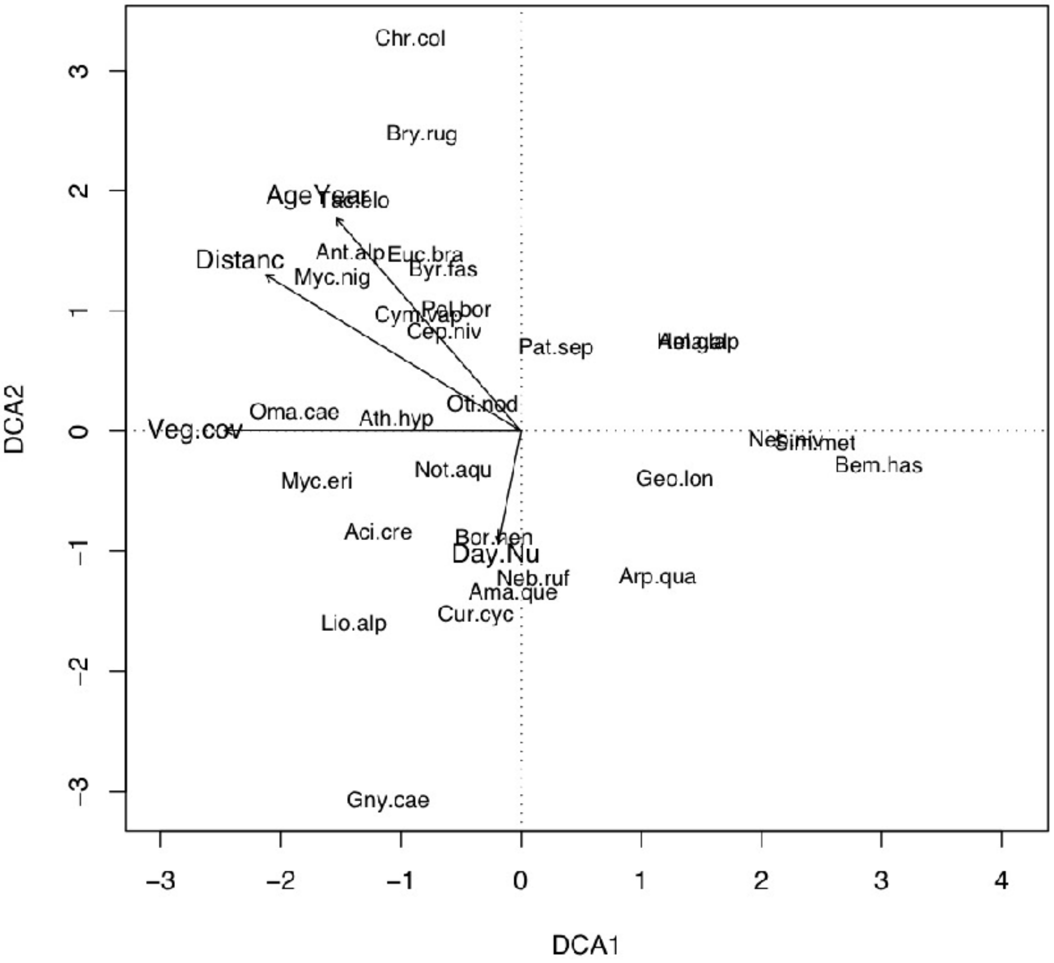


Figure 18. DCA biplot of the first two axes of DCA-4, showing the ecological distance between the beetles as well as environmental gradient vectors. Vegetation cover is the strongest explanatory vector. Values increase from right to left. Seasonal differences are shown along DCA axis two, with spring on top and autumn towards the bottom.

3.3.2.2 DCA-5: Total beetle material excluding pitfall traps 101-120

Forward selection based on AIC for the DCA-5 data gave us the following model vegetation cover, age year, day number, and distance. The best model explains 38% of the variance. Correlation among the environmental variables for DCA-5 is shown in table 10.

Table 10. Correlation among the environmental variables for DCA-5

	Day Number	Age Year	Distance	Veg.cov
Year	-0.36	-0.04	-0.03	-0.01
Day.Nu		0.08	0.05	0.01
AgeYear			0.88	0.59
Distanc				0.81

The vegetation cover, Distance and Age Year vectors correlated at -1.00, -0.78 and 0.55 along DCA axis one respectively. All vectors are significant (<0.05). The correlation between the environmental variables and the different axes are shown in table 9.

In the DCA-5 plots (figure 19 and 20) *Bembidion hastii, Simplocaria metallica, Nebria nivalis, Helophorus glacialis, Amara alpina,* and *Geodromicus longipes* are still pioneer species and negatively correlated with vegetation cover.

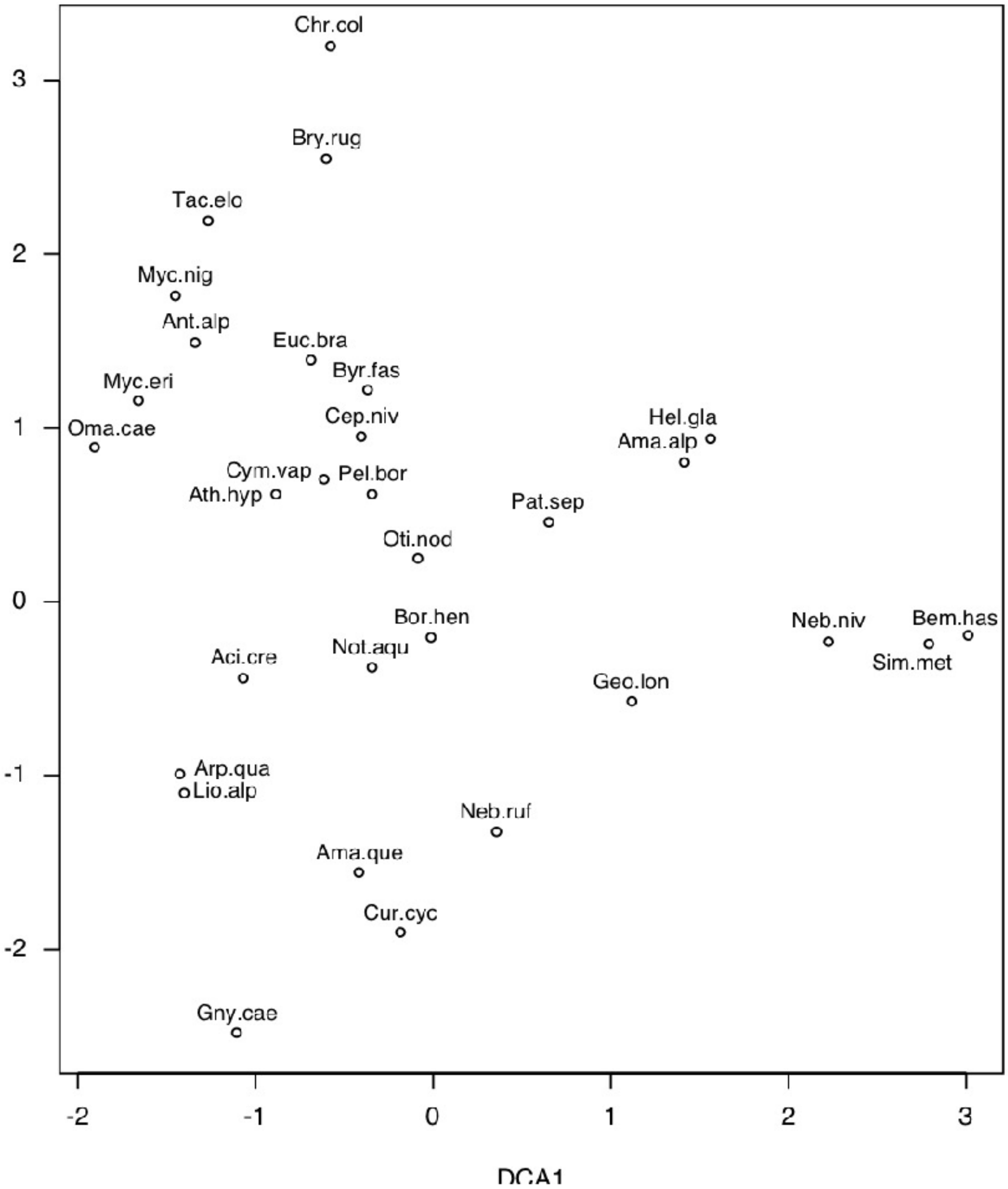


Figure 19. DCA plot of the first two axes of DCA-5, showing the ecological distance between the different beetle species. DCA axis one is highly aligned with vegetation cover, but also to some degree with distance from glacier snout and age of the soil. Values increase from right to left.

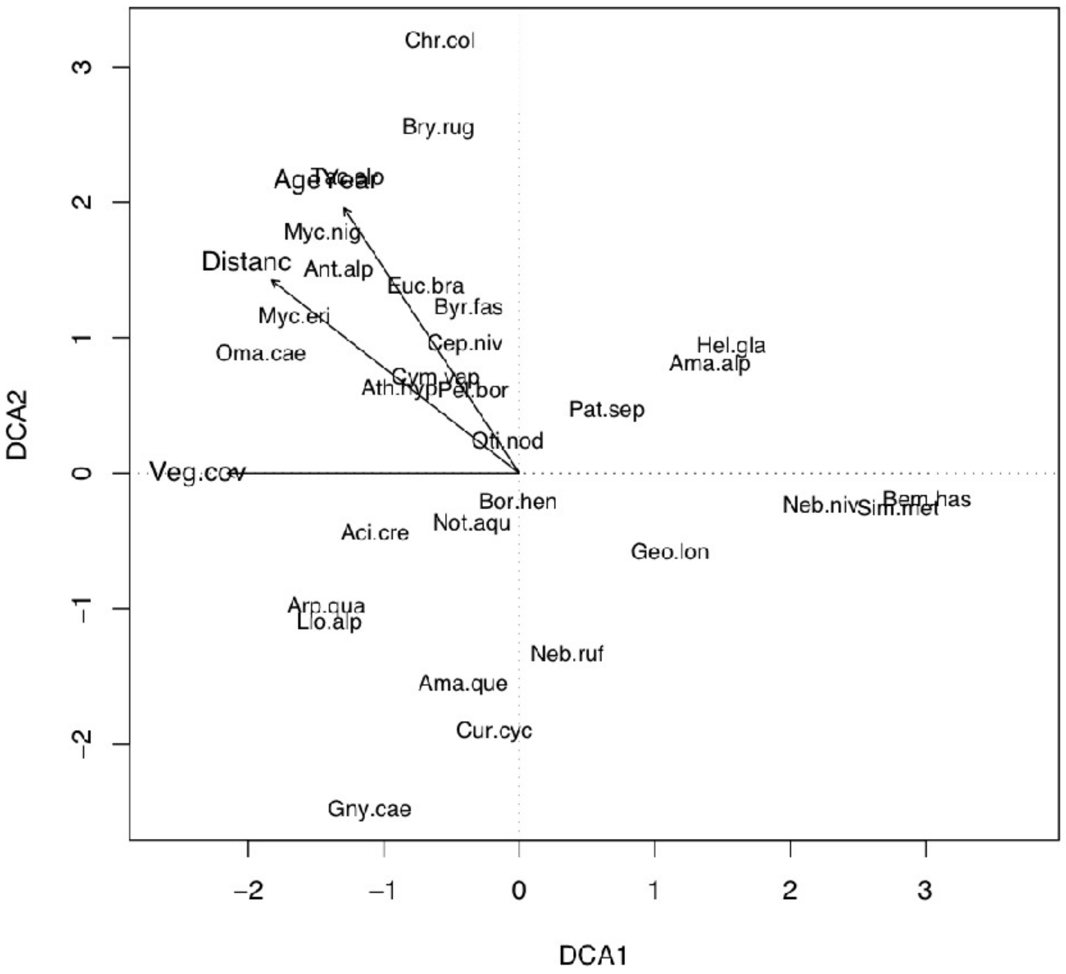


Figure 20. DCA biplot of the first two axes of DCA-5, showing the ecological distance between the different beetle species and also environment gradient vectors. DCA axis one is highly explained by vegetation cover, but to some degree with distances from glacier snout and age of soil. Values increase from right to left.

3.3.2.3 DCA-6: Beetle summer catches (simultaneous sampling in the complete gradient)

Forward selection gave us the model vegetation cover, age year and day number and the best model explains 52% of the variation. Correlation among the environmental variables for DCA-6 is shown in table 11.

Table 11. Correlation among the environmental variables for DCA-6

	Day.Nu	AgeYear	Distanc	Veg.cov
Day.Nu		0.00	0.00	0.00
AgeYear			0.92	0.74
Distanc				0.87

The vegetation cover, distance and age year vectors are correlated at -0.99, -0.97 and -0.89 along DCA axis one respectively. The day number vector is correlated along DCA axis two at 0.99. All vectors are significant (<0.05).

In the DCA-6 plots (figure 21 and 22) *Bembidion hastii, Simplocaria metallica, Nebria nivalis, Amara alpina,* and *Geodromicus longipes* are the pioneer species.

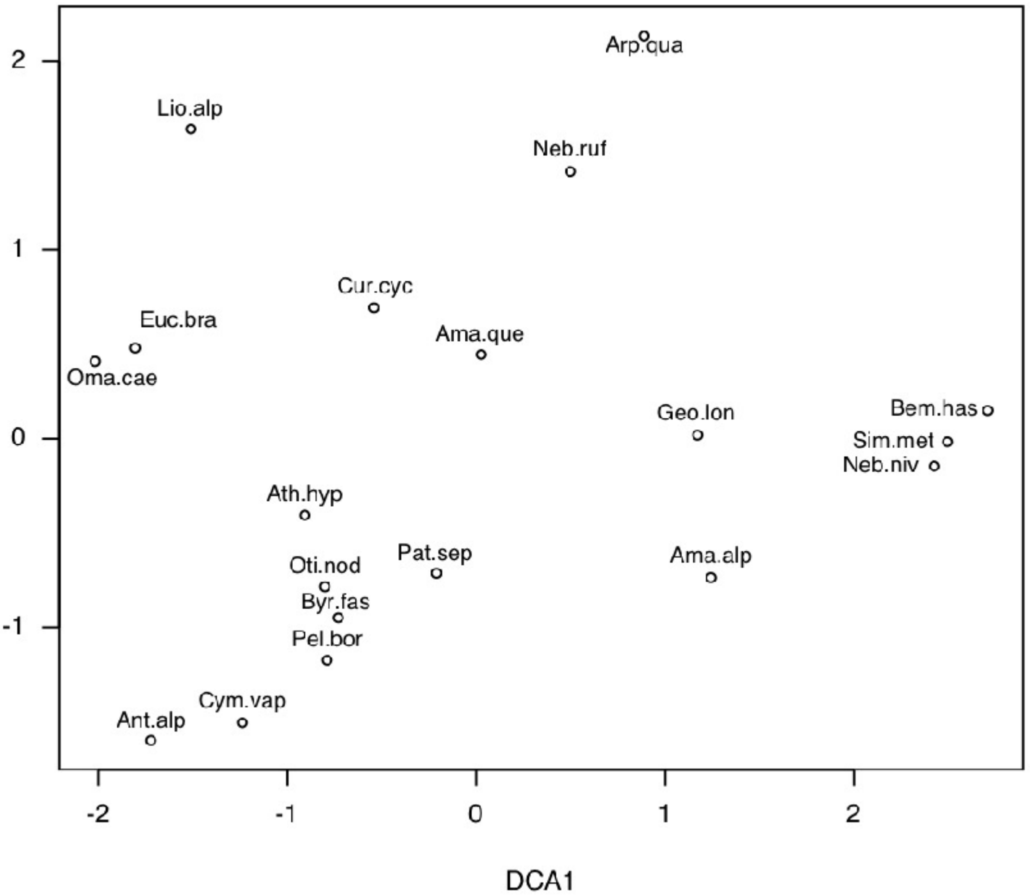


Figure 21. DCA plot the first two axes of DCA-6, showing the ecological distance between different beetle species. DCA axis one is best explained by vegetation cover, closely followed by distance from glacier snout and age of soil. Values increase from right to left. DCA axis two is highly explained by time in season, with spring towards bottom and autumn at the top.

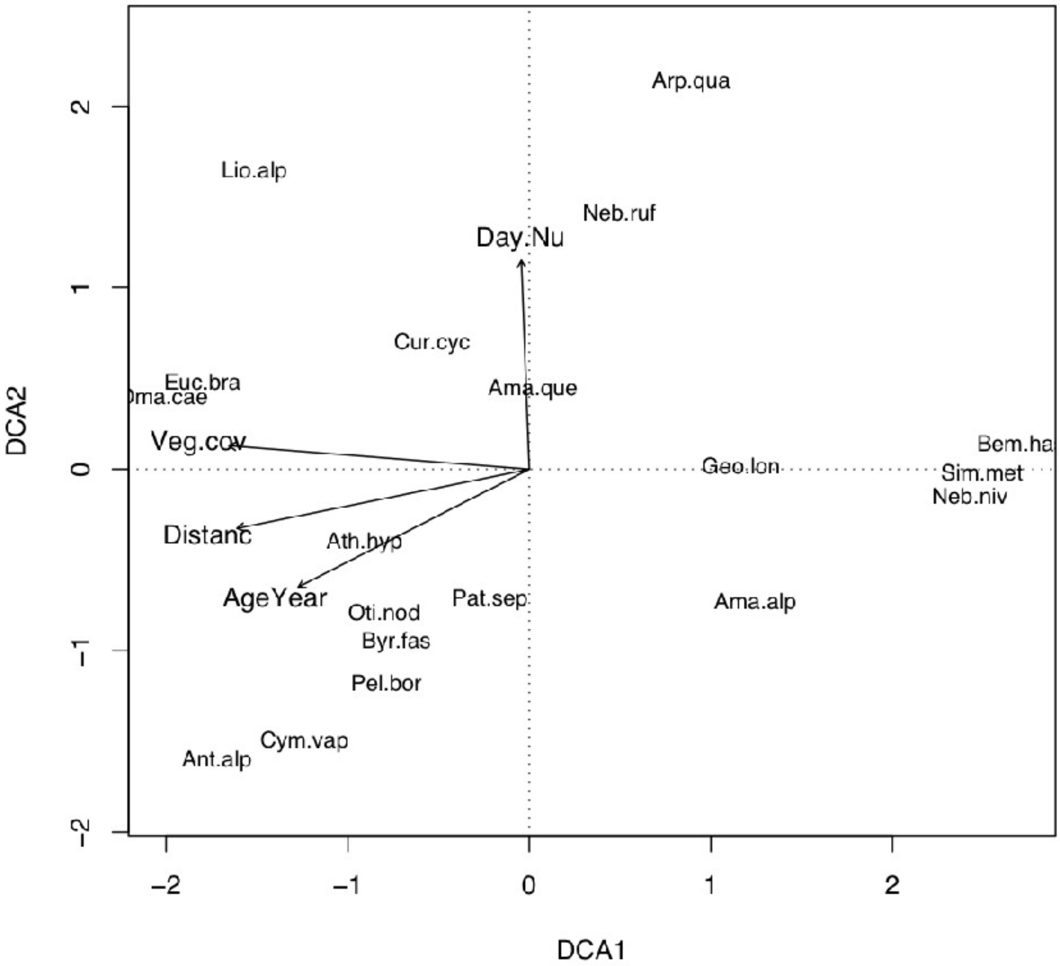


Figure 22. DCA biplot of the first two axes of DCA-6, showing the ecological distance between beetles, and also environmental gradient vectors. DCA axis one is best explained by vegetation cover, with distance from glacier snout and age of soil, respectively. Values increase from right to left. DCA axis two is almost perfectly explained by season, with spring being at the bottom and autumn at the top.

3.3.3 Spiders

3.3.3.1 DCA-7: Total spider material

Table 12 shows the axes lengths in S.D.-units for the spider plots (figure 23, 24, 25, 26, 27 and 28) which also indicate a complete species turnover.

Table 12. S.D.-units and eigenvalues for DCA axes one and two for the spider plots DCA-7-9

	DCA-7		DCA-8		DCA-9	
Axis	DCA1	DCA2	DCA1	DCA2	DCA1	DCA2
Eigenvalues	0.59	0.27	0.57	0.27	0.69	0.41
Axis lengths	3.87	2.78	3.77	2.14	3.77	2.02

Forward selection based on AIC for the DCA-7 data gave us the following model vegetation cover, age year, day number and distance. The best model explains 32% of the variance. Correlation among the environmental variables for DCA-7 is shown in table 13.

Table 13. Correlation among the environmental variables for DCA-7

	Year	Day.Nu	AgeYear	Distanc	Veg.cov
Year		-0.35	-0.15	-0.15	-0.14
Day.Nu			0.09	0.06	0.03
AgeYear				0.90	0.68
Distanc					0.85

The distance, year, vegetation cover and age year vectors are correlated at 0.99, -0.92, 0.85 and 0.84 along DCA axis one respectively. The day number vector is correlated along DCA axis two at 0.92. All vectors are significant (<0.05) except for year and day number (0.28 and 0.78).

The correlation between the environmental variables and the different axes for the spider plots for all six figures DCA-7- DCA-9 (figure 23, 24, 25, 26, 27 and 28) are shown in table 14.

Table 14. Correlation between the environmental variables and the different axes for DCA-7-9

	DCA-7		DCA-8		DCA-9	
	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
Age.Year	0.84	-0.33	0.82	-0.30	-0.85	-0.39
Distanc	0.80	-0.09	0.76	-0.02	-0.85	0.49
Vegetation cover	0.79	0.20	0.76	0.35	-0.85	0.49
Day Number	0.12	0.15	-0.08	0.11	-0.10	-0.17
Year	-0.05	-0.04	-0.03	-0.09		

In figure 23 and 24 *Erigone tirolensis, Collinsia holmgreni, Pardosa trailli and Erigone arctica* are the pioneer species.

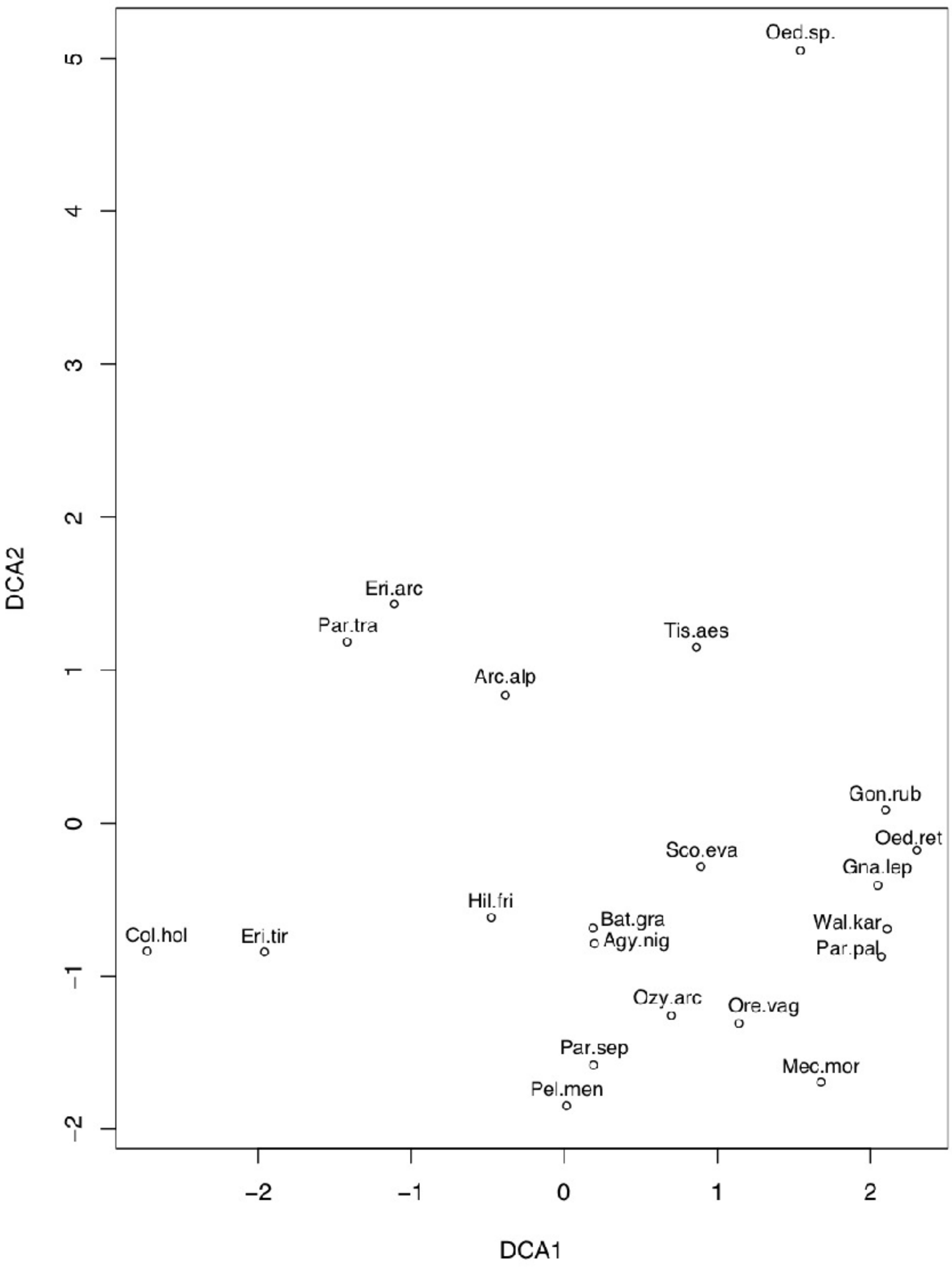


Figure 23. DCA plot of the first two axes of DCA-7, showing the ecological distance between spider species. DCA axis one is best explained by distance form glacier snout with vegetation cover and age of soil, respectively. Values increase from left to right.

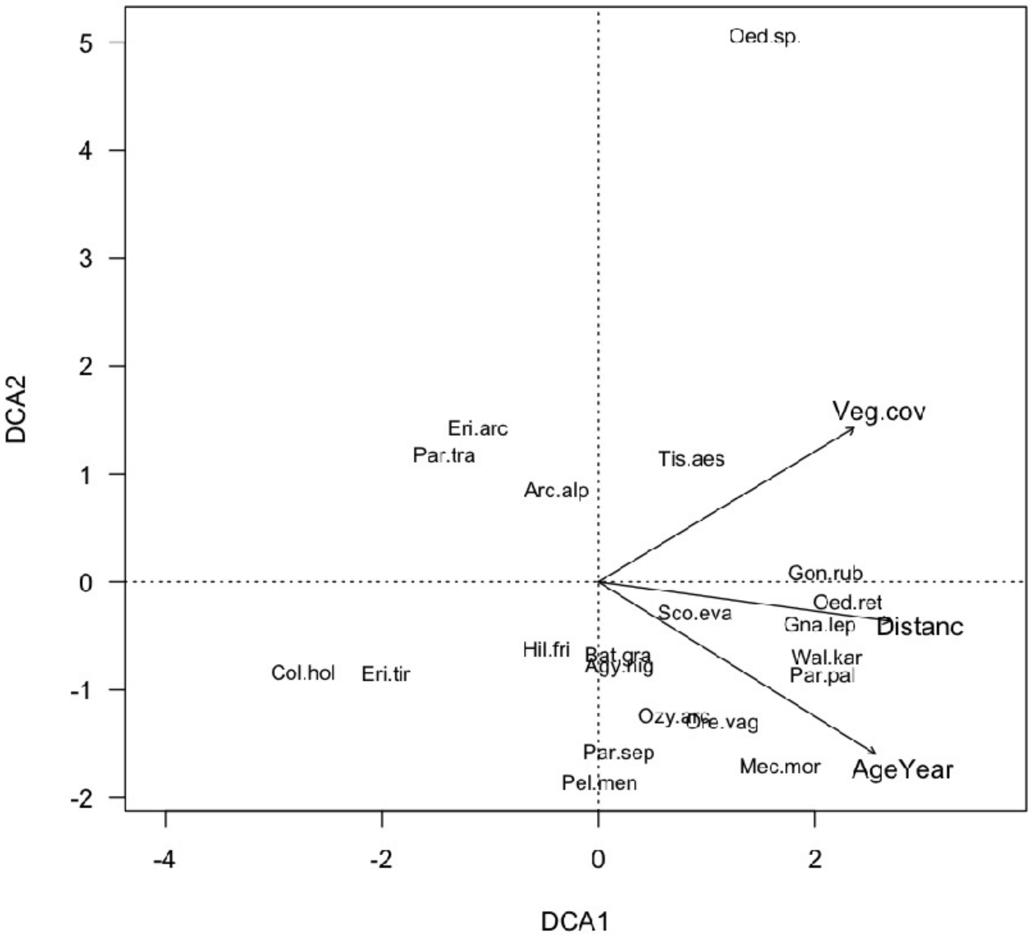
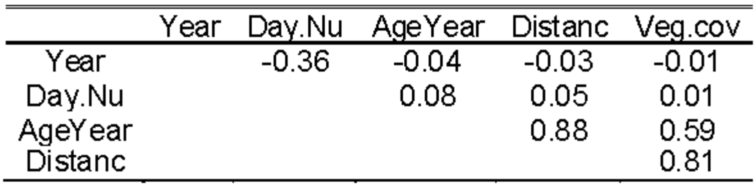


Figure 24. DCA biplot of the first two axes of DCA-7, showing the ecological distance between spider species and also including environmental gradient vectors. DCA axis one is best explained by distance from the glacier snout, followed by vegetation cover and age of soil. Values increase from left to right.

3.3.3.2 DCA-8: Total spider material excluding pitfall traps 101-120

Forward selection based on AIC for the DCA-8 data gave us the following model vegetation cover, age year, day number and distance. The best model explains 34% of the variance. Correlation among the environmental variables for DCA-8 is shown in table 15.

Table 15. Correlation among the environmental variables for DCA-8



	Year	Day.Nu	AgeYear	Distanc	Veg.cov
Year		-0.36	-0.04	-0.03	-0.01
Day.Nu			0.08	0.05	0.01
AgeYear				0.88	0.59
Distanc					0.81

The distance, age year and vegetation cover vectors are correlated at 0.99, 0.85 and 0.82 along DCA axis one respectively. The day number and year vectors are correlated along DCA axis two at 0.92 and -0.81. All vectors are significant (<0.05) except for year and day number (0.85 and 0.28).

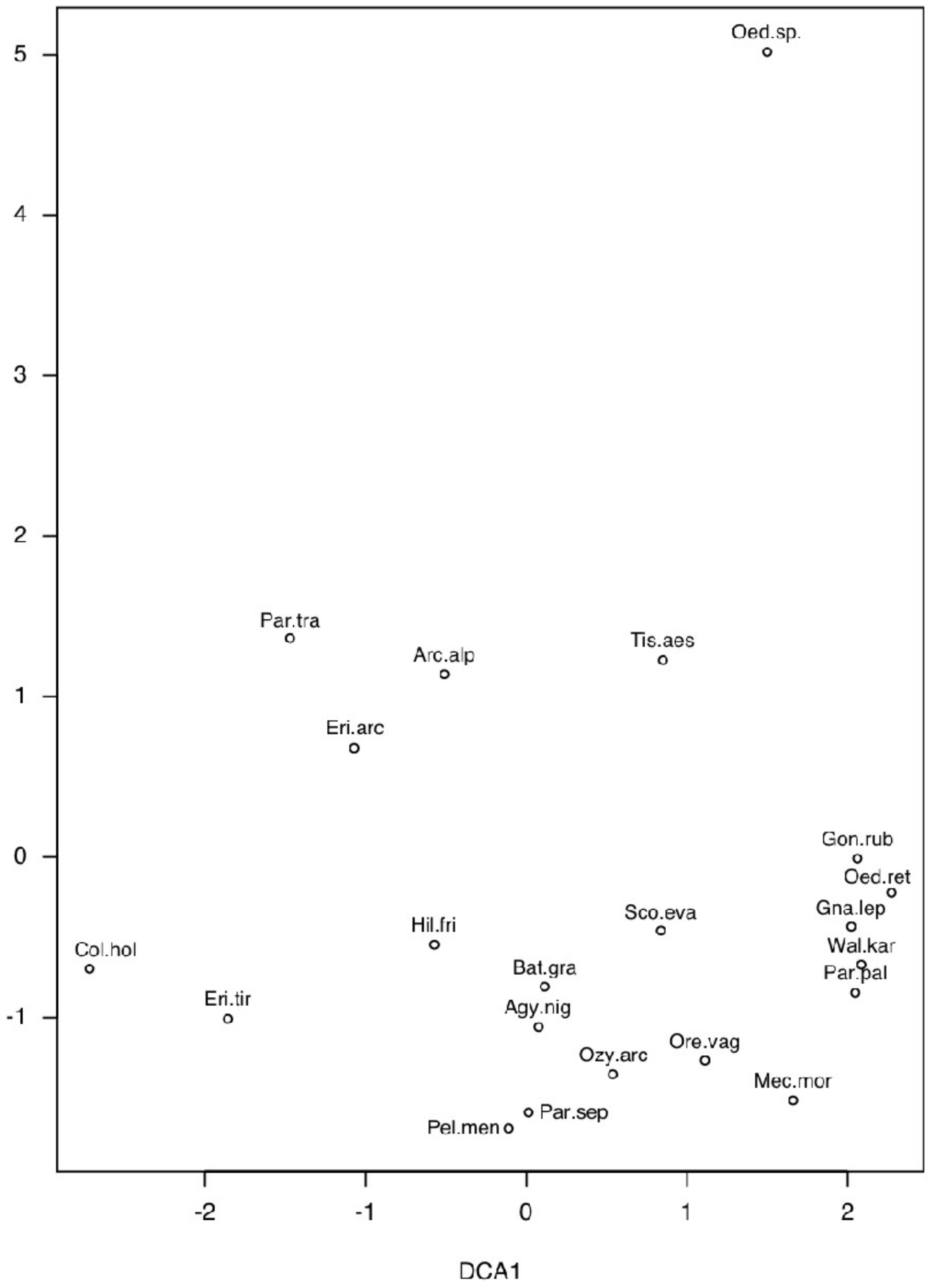


Figure 25. DCA plot of the first two axes of DCA-8, showing the ecological distance between spider species. DCA axis one is highly explained by distance from glacier. Values increase from left to right.

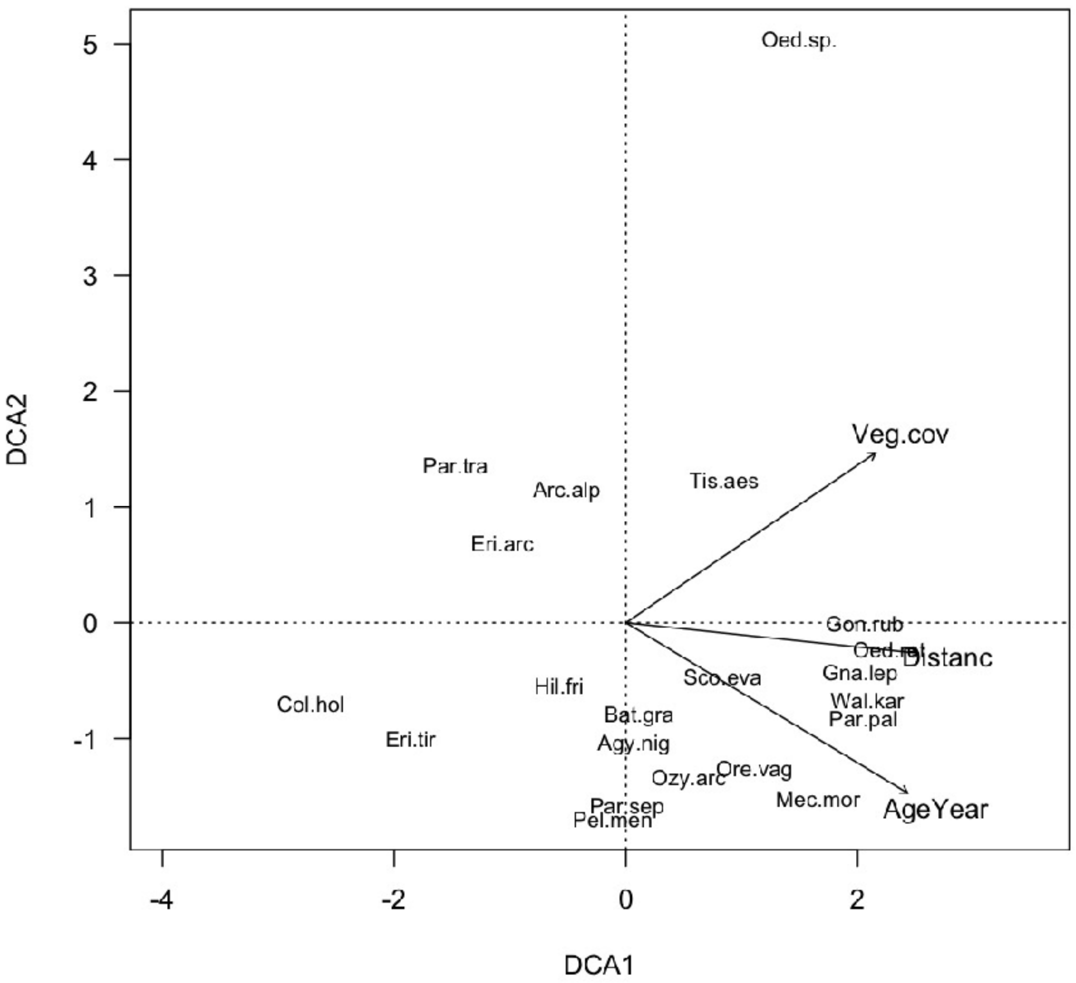


Figure 26. DCA biplot of the first two axes of DCA-8, showing the ecological distance between spider species and also environmental gradient vectors. DCA axis one is explained by the distance from glacier snout. Values increase from left to right.

3.3.3.3 DCA-9: Spider summer catches (simultaneous sampling in the complete gradient)

For the DCA-9 (figure 27 and 28) ordination forward selection based on AIC gave us the vegetation cover variable as the only explaining variable. This variable explains 28% of the variance. Correlation among the environmental variables for DCA-9 is shown in table 16.

Table 16. Correlation among the environmental variables for DCA-9

	Day.Nu	AgeYear	Distanc	Veg.cov
Day.Nu		0.00	0.00	0.00
AgeYear			0.92	0.74
Distanc				0.87

The age year, distance and vegetation cover vectors are correlated at -0.99, -0.89 and -0.87 along DCA axis one respectively. The day number vector is correlated along DCA axis two at 0.93. All vectors are significant (<0.05) except for day number (0.46).

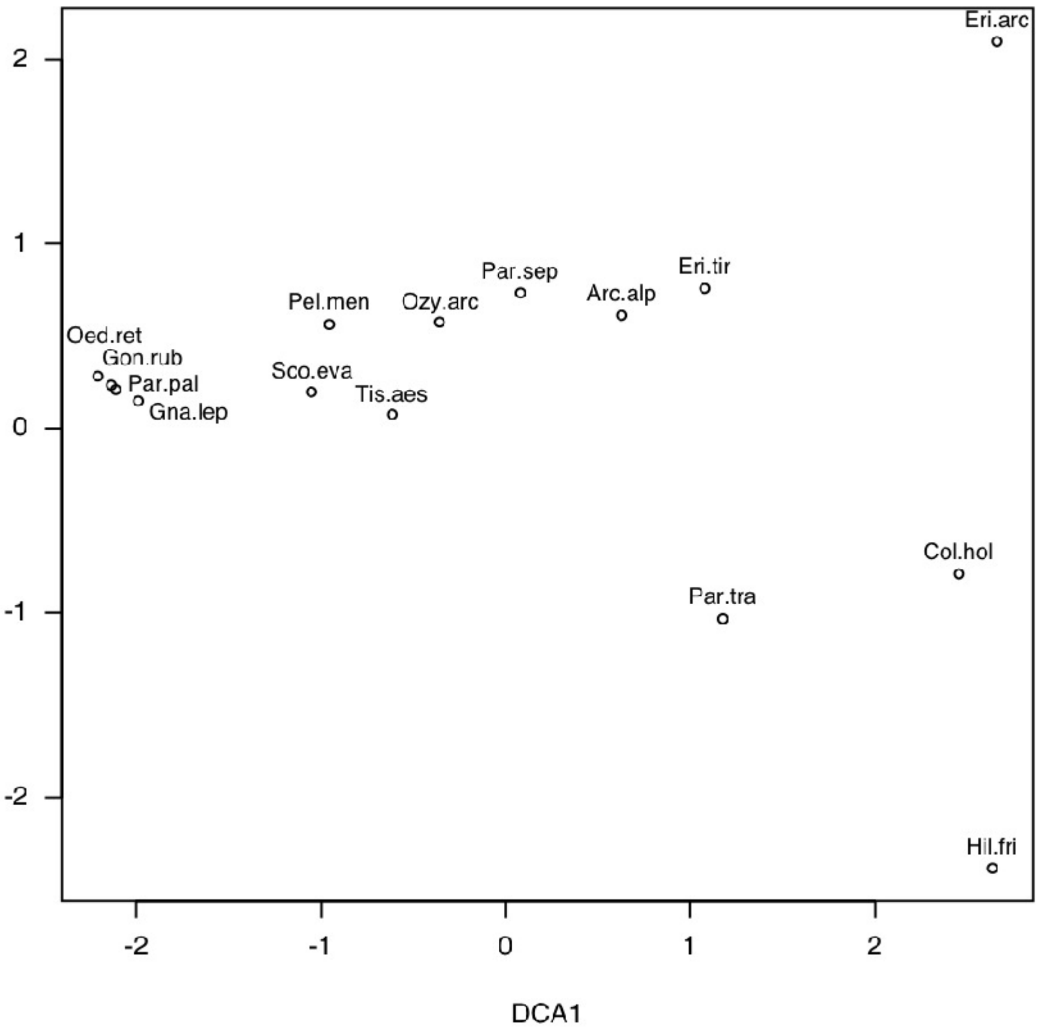


Figure 27. DCA plot of the first two axes of DCA-9, showing the ecological distance between spider species. DCA axis one is highly explained by age of soil. Values increase from right to left

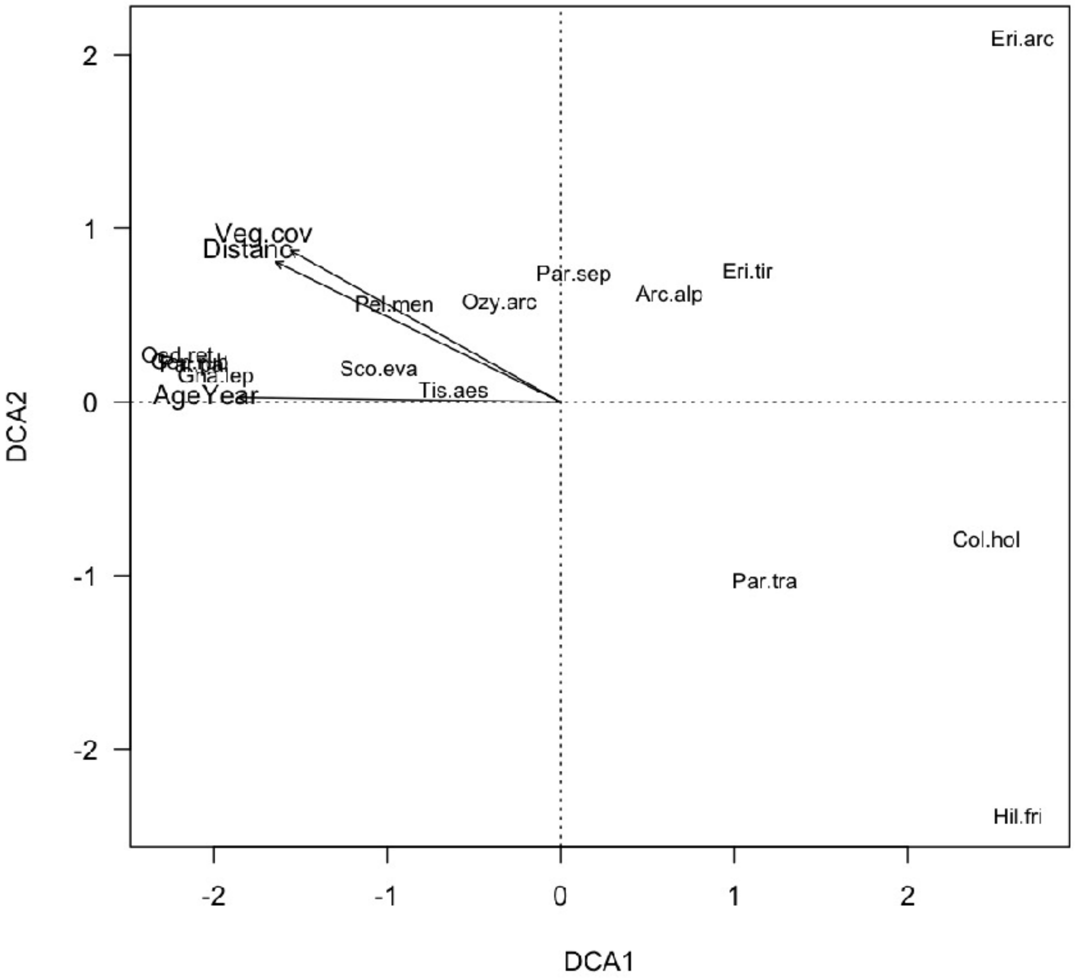


Figure 28. DCA biplot of the first two axes of DCA-9, showing the ecological distance between the spider species and also environmental gradient vectors. DCA axis one is highly explained by age of soil. Values increase from right to left.

4 Discussions

4.1 Discussion on methodology

4.1.1 The chronosequence method (Space for time substitution)

A chronosequence, also called space-for-time substitution, is a set of plots with different ages which are assumed to represent different developmental stages in succession (Walker & Del Moral 2003). One assumes that “important events and processes are independent of space and time” (Pickett 1987). Each set of plots differs only in age and the effects of abiotic and biotic factors are identical. In our chronosequence the conditions have probably varied over the long time scale involved. We do not have any information on the climatic history between 1750 and 1933. In 1934 the glacier made an extensive retreat (Sørlie 2001). It is likely that the temperature was lower, and that the boundary areas were different in composition and abundance from present in a period after 1750. However we are not aware of any major shifts since 1934 until present. The most important assumption of chronosequence is therefore one of fallacy. The sites have not traced the same history. We do have reliable dating of sites and frequent emptying of pitfall traps through two complete seasons and there is no lateral vegetation. In this study we seek general patterns in community structure and believe that these can still be revealed here. The use of chronosequence studies has been criticized by Johnson & Miyanishi (2008). Both Hodkinson et al. (2004) and Kaufmann & Raffl (2002) has noted problems in the use of chronosequence studies but chronosequence study is the best option when your time is limited. We would recommend a joint chronosequence, long-term study to ensure the complete picture in the future.

4.1.2 Pitfall trapping: Advantages and drawbacks

Pitfall traps are often used during extensive sampling of surface-active arthropods. Pitfall traps are inexpensive, enquire little effort and are easy to operate. But there are several issues that need to be addressed when using pitfall traps. Pitfall traps are surface activity monitors and several factors will affect catches. The species locomotive abilities (Greenslade 1964), general behavior, seasonal changes in behavior (i.e. mating behavior) and abundance can affect catches. Furthermore, variation in vegetation density and structure around a trap can have species-specific effects on locomotive speed and can therefore affect catches (Topping & Sunderland 1992). Horizontally moving species are more likely to get caught than species actively moving in three-dimensional vegetation space. We do not consider this as a large problem because of the scarce and short vegetation in the alpine environment. All invertebrates live close to the ground (Ottesen 1996) but the soil fauna and species living in the vegetation could be underrepresented (Kaufmann & Raffl 2002). It has been suggested that pitfall trappings should be viewed as a activity-abundance measurement since the "rate of capture is proportional to the interaction between their abundance and activity" (Leather 2005). A highly abundant low activity species will be underestimated compared to a low abundant highly active species. This is important in this study since some of the focus is on predators. Both spiders and most predatory beetles are highly surface-active and can be overrepresented, but we believe that most species will be represented at frequencies close to their true relative abundance. Abiotic factors like temperature and humidity are the most important factors in this environment. The temperature can fluctuate extremely, and so can the precipitation and melt water, saturating the soil. This is one of the reasons why the traps were placed in moisture gradients along moraine ridges, to capture the differences in moisture and temperature preferences.

We used plywood lids for our traps although it may alter the microclimate close to the trap (Leather 2005). It is proposed that transparent roofs minimize the influence, but (Phillips & Cobb (2005) found that lid transparency had no effect compared to opaque lids on beetles in open areas.

Regarding the trapping fluid, ethylene glycol, it is not to our knowledge reported as a repellent but can attract some invertebrates (Leather 2005).

4.1.3 Beetles and soil moisture

Studies have found that moisture and soil humidity is an important factor in explaining local distribution of beetles (Ottesen 1996) and faunistic distribution in general, (Kaufmann 2001). Since this was known we decided to place our traps in a gradient from dry to wet soil at each site. We would still cover most of the arthropod fauna, independently of their habitat moisture preferences, and get a more general picture of the arthropod succession at the glacier foreland. We also tested how different species was represented in different soil moisture levels just to show that there are different preferences between the species also at the Midtdalsbreen glacier.

We found that *Byrrhus fasciatus* and *Cymindis vaporariorum* preferred dry habitat. Thus we are concurring with Ottesen (1996) that found that Byrrhus sp. and *Cymindis vaporariorum* both preferred habitat with a soil moisture less than 44%. Lindroth (1961) also says that *Cymindis vaporariorum* is found on dry moraines. We could not find anything about what moisture preferences *Amara quenseli have*.

Ottesen (1996) found that *Geodromicus longipes, Liogluta alpestris* and *Patrobus septentrionis* all preferred soil moisture 44-75%, this supports our findings which suggest a preference for high levels of soil moisture. Lindroth (1961; 1985) also supports our results with regards to *Patrobus septentrionis* moisture preferences.

4.1.4 Phenology

The main reason for including phenology in this study was to make sure that we had made it possible to catch all the different species. Since Ottesen (1996) and Østbye & Hågvar (1996) have shown that the species are active in different periods of the season, we now know that we would risk losing data if we had a less frequent emptying schedule. Unfortunately many species were caught in so few numbers that it is difficult to say anything certain about their phenology.

Since the main goal of this study was to describe primary succession, we have chosen to focus on the species we consider to be pioneer species, that is, species found in the two youngest sites. Some of these species occurs in very small numbers and therefore it is impossible to say anything about their phenological patterns.

Phenology result beetles:

Amara alpina: We found that *Amara alpina* had a peak in abundance in July. Lindroth (1986) states that imagines are mainly occurring in July due to breeding activity. Østbye & Hågvar (1996) conducted a survey over three years and found a peak in the abundance in July. Ottesen (1996) found that the top was even earlier, in May, June and first half of July. However that time period only consists of two collections, so we find it likely that the top is closer to late June than early May.

Amara quenseli: We found that *Amara quenseli* had a peak in abundance in early July, decreasing towards the fall. Thus our results could be explained by the fact that imagines are emerging in June/July and mating activity increases towards the fall, in accordance with Lindroth (1986).

Bembidion hastii: Is more frequent in 2008 than in 2007. This could probably be because we had a site even closer to the glacier snout in 2008, but it could also be other factors causing this. We found that *Bembidion hastii* increases quite rapidly towards the fall of 2008. According to Lindroth (1985) *Bembidion hastii* breed form July to September, this fits well with our findings.

Geodromicus longipes: We found that *Geodromicus longipes* had a top in late July of both 2007 and 2008. This is the same results as Ottesen (1996), although his top seems to also include August to some degree. However we caught a higher number both seasons, separately.

Patrobus septentrionis: We found a rather large top in July both years and Lindroth (1985) says that the beetles are emerging in June to August, which could explain our results. Ottesen (1996) found that *Patrobus septentrionis* had a top in the May and June period, with reduction to almost half the amount in the first half of July.

It should be noted that Ottesen (1996) trapping site is facing south, whereas our trapping sites were facing north which implies that the snow is melting much earlier at his sites compared to ours. This difference could be as large as at least one and a half month (pers. obs.). That could explain why we find differences in the phenology, although there are a lot of similarities.

Unfortunately most of the species occurred in small numbers. However we will try to explain what we see in figure 7, 8, 9 and 10, but this is just our personal interpretation of the figures and should not be regarded as any more than that.

It seems like some of the species could be thriving in or preferring cold conditions, since they have the highest activity in the coldest period. *Agyneta nigripes, Arctosa alpigena, Erigone arctica, Hilaria frigida, Ozyptila arctica, Pardosa septentrionalis, Pelecopsis mengei* and *Tiso aestivus* would be put in this group. All the previously mentioned species peak in the coldest period. If we compare our phenology with other studies done at Finse (Hauge et al. 1978; Hauge & Ottesen 2002) we find similarities but also some differences.

Phenology result spiders:

Arctosa alpigena: Have the same pattern in our and Hauge et al.(1978) study but, only in two of the three years they conducted their study. Hauge & Ottesen (2002) also has a top in the very beginning of the season, which probably indicates spring activity and not necessarily activity in the whole winter period.

Collinsia holmgreni: Show a clear peak in early July 2007 in our data. Hauge et al. (1978) and Hauge & Ottesens (2002) studies have the same pattern, our 2008 results is not supported. So it is more likely that the 2007 top is a more correct description of the actual phenology.

Erigone arctica: Is found in very small numbers in Hauge & Ottesen (2002) but has a top at the end of the season. We however found a top during winter and early June 2008, but almost no individuals in the other periods. If we combine these two studies we could suggest that *Erigone arctica* is active in winter or at least cold periods.

Erigone tirolensis: Have the same pattern in our and Hauge et al. (1978) study, with a top early in the season, drop in mid season and a small increase at the end of the season. There are too few individuals to actually conclude.

Hilaria frigid: Is an early species, but since our first collection in 2008 contains so many individuals it could be that this species is late fall or winter active which have been suggested by Hauge et al. (1978). Hauge & Ottesen (2002) also found a huge top in the earliest period (6 May to 29 June).

Pardosa paludicola: Occurs in large numbers in early July both years and almost no individuals in the rest of the season. The reason for the smaller top in 2008 could be that we drained the area for individuals in 2007, but more likely it is natural fluctuations in the population or different abiotic conditions.

Scotinotlus evansi: Have a relatively large top in winter, early June 2008. Since we did not collected as early as in 2007, we cannot say that this is a real top at that time. (Hauge & Ottesen (2002) found a small top in their latest period (29 August to 16 September), but collected few individuals.

Tiso aestivus: Have a large top during winter, early June 2008, but also a top in early July, and a small increase in August. Hauge et al. (1978) did however only find the August increase, we guess this is because the small number of individuals caught (only 41 individuals in a three year period). In Hauge & Ottesen (2002) the number of individuals is much higher, and they found tops in the beginning and middle of the season.

4.2 Main conclusions

Unexpectedly and contradictory to the common view on primary succession we found that both spiders and beetles are found very close to, and quickly colonize, the barren ground in front of the glacier snout. In addition there were a few species that occurred in high numbers, and this was also quite unexpected. Our result tells us that the pioneer species colonize rapidly after the grounds are exposed, that is, some species are very bound to open areas. The number of species increase throughout the chronosequence as expected. However the beetles and spiders do not show the same patterns or rate of increase, as seen in figure 29.

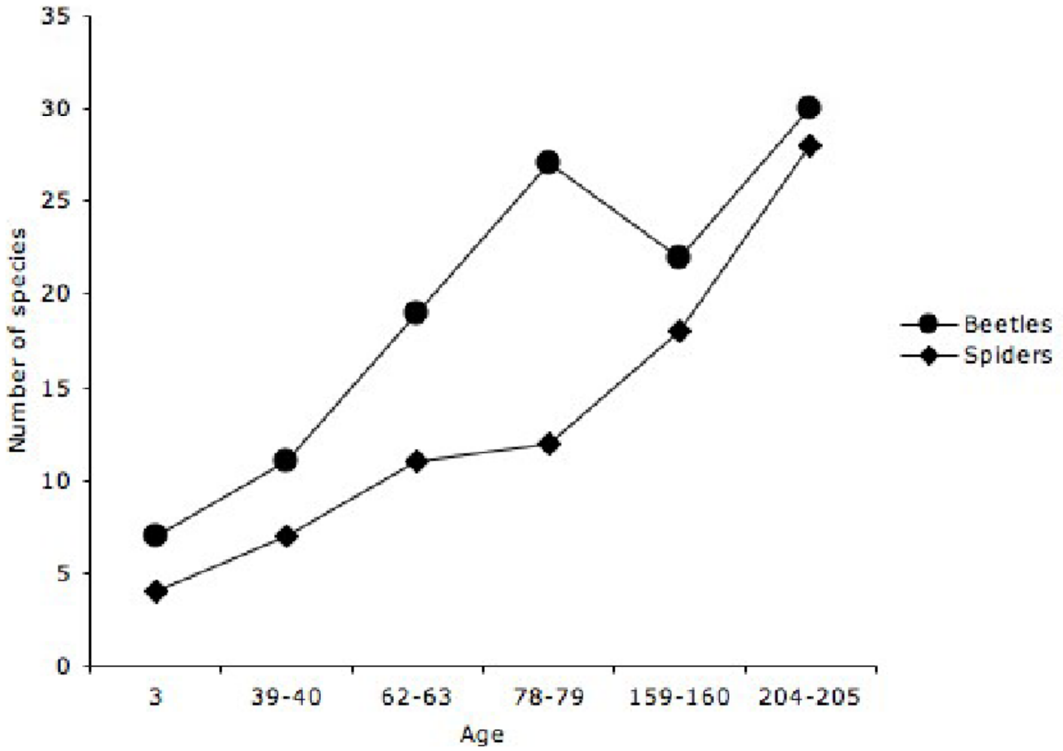


Figure 29. Shows how the numbers of species increase through the chronosequence at the Midtdalsbreen glacier, both seasons combined. Site number 1 represents trap number 101-120, site number 2 represents trap number 1-20, site number 3 represents 21-40, site number 4 represents 41-60, site number 5 represents trap number 61-80 and site number 6 represents 81-100. Beetles represented by filled circles and filled squares represent spiders.

When we look at how and when the different guilds enter the succession/chronosequence (figure 30). We see that the numbers of herbivores does not increase as fast as the predatory beetles and spiders. At the end of our chronosequence it seems even to be fewer herbivorous species than at site 4, the herbivores does not dominate at any point. This could of course happen later on in the succession, at a point not included in our study. We did find one herbivore at site 1, which is barren, the moss eating *Simplocaria metallica*. There could be several factors, not taken into account, which could influence the results. Maybe we have not been able to place the traps in a way that makes them truly comparable. Abiotic conditions can have different effect at different sites. Although there are a lot of possible explanations for the outcome of our results, we do believe that the general patterns are reliable, since many of the features are consistent with the studies of (Kaufmann 2001, Kaufmann et al. 2002, Kaufmann & Raffl 2002, Hodkinson et al. 2004, Gobbi et al. 2006, Vater 2006).

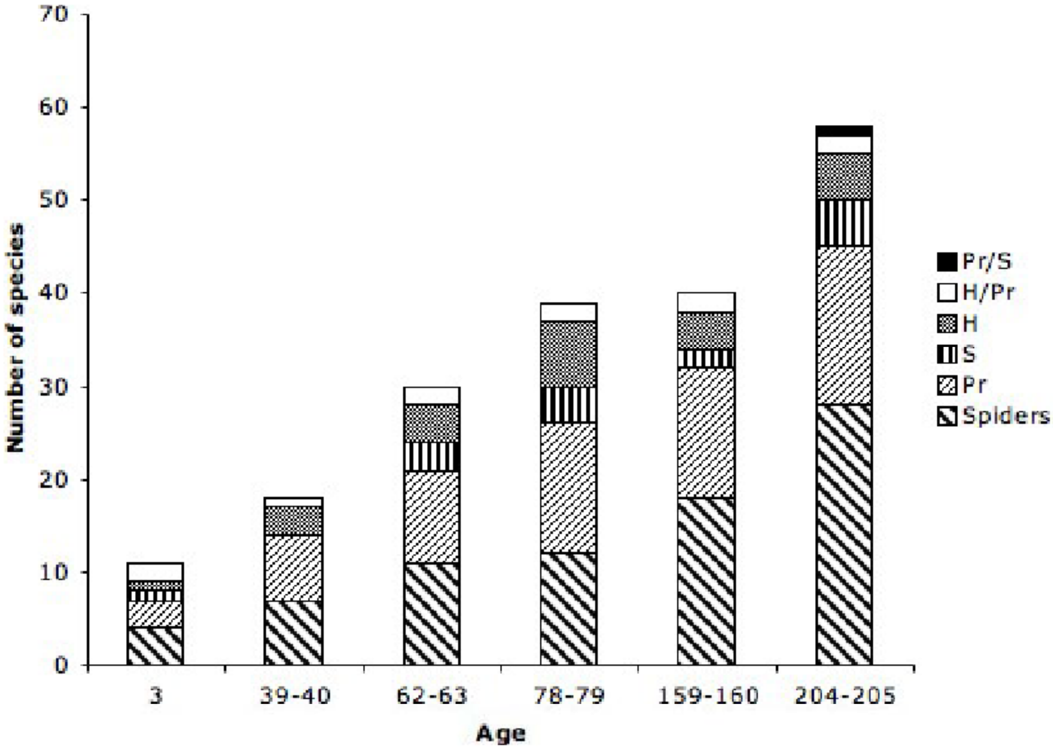


Figure 30. A stacked column plot showing how the numbers of species in each guild are increasing through the chronosequence at the Midtdalsbreen glacier, with both seasons combined. Site number 1 represents trap number 101-120, site number 2 represents trap number 1-20, site number 3 represents 21-40, site number 4 represents 41-60, site number 5 represents trap number 61-80 and site number 6 represents 81-100. Pr/S = predatory/saprophagous beetles, H/Pr = herbivorous/predatory beetles, H = herbivorous beetles, Pr = predatory beetles and Spiders = all spiders are predaceous.

4.3 Succession patterns: explanations and comparisons

4.3.1 The DCA picture

A strictly statistical interpretation of DCA analysis is not possible so we will here give an ecological interpretation of the plots.

Our main prediction that; the succession pattern of surface-active arthropods will be related to age and distance from glacier snout is supported by the DCA analysis. The length of the DCA axis tells us that one will not find the same species composition in the beginning of the axis as in the end (i.e. there is a high beta diversity). And this is also true for the chronosequence, since the DCA is a representation of the chronosequence. There is a relation between the distance variable and time since deglaciation. This can be confirmed by visual inspection and comparisons of our tables. And by so doing we separate the pioneer species. In DCA-1 plot the DCA axis one contains all significant environmental variables. The variables are highly intercorrelated and difficult to separate. This is due to the properties of glacier foreland where time is an overriding factor (Hågvar et al. 2009). In the DCA-1 plot the day number variable is not significant, but a visual inspection and comparison with the other plots and the phenology data could suggest that the phenology is spread out along DCA axis two with early dates on top and later dates in the bottom end. We view this plot as the most important since it includes both beetles and spiders. The other plots were produced to reveal inconsistency in the data collection, because the traps were not operated simultaneously and that the number of traps increased from 2007 to 2008.

In the DCA-4 plot vegetation cover is the strongest variable governing the fauna distribution. This could be due to the fact that vegetation cover does not increase linearly with time and distance but has a bimodal distribution. This could imply that the beetles have vegetation preferences or other factors governing vegetation cover e.g. moisture or snow melt. The pitfall traps were placed in a moisture and vegetation gradient. Most of the beetles are predators and it is therefore possible that its moisture disguised as vegetation cover that governs the beetles. In this plot the variable Day number is significant and the distribution along DCA axis two is due to phenological differences.

In the spider plot DCA-7 the axis increases from left to right and consequently the four pioneer species are located at the left side. In this plot, distance is again the strongest variable that is typical for glacier foreland. Oed.sp. is situated in the upper right corner of the plot. The reason for this extreme observation, is because of few observations and because all observation are at the same locality the same year.

We believe that the DCA-1 plot is a good representation of the species composition along the chronosequence. The same species always turn out as pioneers and the same general patterns are shared. DCA axis two scatters the species more, the further you move from the glacier snout. In the DCA plots it can look like the beetles have stronger preferences for vegetation cover compared to spiders. But as mentioned this could be connected to moisture preferences not necessarily vegetation preferences.

4.3.2 The pioneer community: The predators first, a paradox (explained?)

The amount of spider species increase almost linearly through the chronosequence while the amount of beetle species decreases at 159-160 years and then increases again towards 204-205 years (figure 29). This small reduction in species is probably due to the location of the site aged 159-160 years. Being placed on a peninsula surrounded by bog and water the catches of these pitfall traps were probably affected.

The first species among the beetles to establish on the three year old barren moraine was *Bembidion hastii, Simplocaria metallica, Nebria nivalis, Geodromicus longipes, Amara alpina* and *Patrobus septentrionis* and among the spiders *Collinsia holmgreni, Erigone tirolensis, Pardosa trailli* and *Erigone arctica.* These species has established independently of vascular plants and are all, except for *Simplocaria metallica,* predators.

At 39-40 years only two more species has entered the DCA plots. The beetle *Helophorus glacialis,* which is an herbivore and the spider *Hilaira frigida.* Three other predators; *Oxypoda annularis, Boreaphilus henningianus, Nebria rufescens* and one species believed to be a herbivore*, Otiorhynchus nodosus* are also registered at this location, but with an low abundance and a higher abundance elsewhere and is therefore ordinated lower along the DCA axes, and is consequently not regarded as pioneer species.

From site 2 to 3 the number of species increases with 40%, which is the highest increase between sites. The increase from site three to four is 23%, four to five 2.5% and five to six 31% respectively.

There are surprisingly few herbivores compared to predators through the gradient (figure 30). A higher increase of herbivores, closer to that of predators was expected as vegetation cover, distance and age of soil increased. It is here possible that herbivores are underrepresented in the pitfall traps as earlier discussed. The nourishment preferences of some of the beetles are uncertain some could be omnivorous or belong to different trophic levels than stated. We do not have data on the floral diversity of the area but the low diversity of herbivorous beetles could reflect a low floral diversity. Or the herbivores colonize later along the chronosequence than predators.

Pioneer species will have certain preferences and/or abilities. In the alpine zone some form of cryo-strategy is needed and we will only refer to this as cold-hardiness. Some species must have barren ground and/or high disturbance areas like riversides and snow-beds. Regarding food preferences for our pioneer species we will for simplicity only differ between two strategies, the generalist who forages for anything that might appear in its proximity, and the specialist who searches for a specific meal. It is also important for these species to be good dispersers since their environment is disturbed regularly. We also believe that some of these species will be weak competitors and therefore have filled a niche where competition is avoided in time and space.

The pioneer species *Bembidion hastii* prefers barren ground with rocks and sand and is often found in close proximity to the water edge also along the seashore (Lindroth 1961; Lindroth 1985). A good disperser and a generalist. *Simplocaria metallica* is a cold-hardy boreo-alpine species (Strand 1969) which also has been found in rich vegetation under a nesting cliff on Svalbard (Hågvar 1969). This species was found near mosses on Svalbard and according to Ottesen (1996) it feeds on mosses. It can look like *Simplocaria metallica* is a competition weak cold-hardy moss specialist with good dispersal abilities. *Nebria nivalis* is a typical alpine species often found foraging at the edge of snowfields and at the edge of brooks and even at the seashores (Lindroth 1961). This must be a cold-hardy species that likes barren ground and is a good disperser. *Geodromicus longipes* prefers alpine habitats often found under rocks, moss and detritus. Also found along the seashore and the edge of brooks, in dry and wet places prefers sand and gravel. Often appears in large numbers (Palm 1948). *Amara* *alpina* a characteristic alpine zone inhabitant which occurs on poor mountain ground with uncontinuous dwarf-shrub heats and meadows (Lindroth 1986). Likely a cold hardy generalist with some preferences for vegetation. *Patrobus septentrionis* prefers wet habitats like marshes and meadows, often found close to or hunting on snow. Also found in moist places in the upper conifer region in *Carex* vegetation and along rivers (Lindroth 1985). Most likely a generalist since it frequently hunts on snow, cold-hardy and a good disperser. *Collinsia holmgreni* "Is an alpine species often found in alpine heath-lands" (Aakra 2009) *Collinsia holmgreni* is the most numerous spider at site aged 39-40 and therefore ordinate at the extreme edge of the plot and considered a pioneer species though it does appear through the whole gradient. *Collinsia holmgreni* must have some preferences for barren habitats. *Erigone tirolensis* "Is typical on almost vegetation free pioneer grounder of both sand and gravel and can be found along rivers and even the seashore" (Palmgren 1976). "Similar habitat preferences to *Erigone arctica* but will probably be found in more vegetation rich areas" (Aakra 2009). *Pardosa trailli* has been described as typical for "habitats with rock debris situated above the timberline" (Kronestedt 2004). "The most important criteria for this species seem to be barren ground with rocks and gravel" (Aakra 2009). *Erigone arctica* "Is typical on almost vegetation free pioneer grounder of both sand and gravel along rivers and even the seashore" (Palmgren 1976). "In alpine areas it will typically be found on barren ground with scarce vegetation" (Aakra 2009). *Hilaira frigida* "The taxonomical status of this species is uncertain. This is probably a closely related species dissimilar to *Hilaira frigida*" (Aakra 2009). "*Hilaira frigida* can be found in several habitats both with and without vegetation" (Palmgren 1975).

The paradox is here evident. All of the species mentioned above are believed to be predators except for *Simplocaria metallica.* And this has implications for our view on succession, and many questions arise here. For this to be a prevailing community and not a sink, this habitat need some form of energy input. Several sources are possible. Allochthonous energy flows between systems (Polis et al. 1997) with wind as a vector. This has been called the aeolian subsidization hypothesis (Hawes 2008). Aeolian arthropods and/or detritus have been suggested as a source of energy input (Hodkinson et al. 2001, Kaufmann 2001, Hodkinson et al. 2002, Hodkinson et al. 2004). Enormous amounts of insects are willing or unwillingly airborne at any given time (Chapman et al. 2003). Anabatic winds that cool down when approaching glaciers deposit their stowaways on or nearby the glaciers. Hodkinson et al.

(2002) summarizes attempts to estimate “quantitative inputs of organic matter and nutrients” and concludes that the inputs are “sufficient to sustain newly established food webs”.

Another possible food source is the epigean and endogen acari and collembolan soil fauna. The location of Hågvar et al. (2009) sites 2 and 3, aged 33 and 34 years respectively are practically similar to our location. In this study on soil mites Hågvar et al. (2009) registered three species of oribatei mites in his zone-A (32-48 years) with a total density of 25.900 m^2. The occurrence of other mite groups in this zone was 33.100 m^2. According to Hågvar et al. (2009) oribatei mites are some of the earliest pioneer species of barren glacier foreland and that this also is true for Svalbard, and on the island of Surtsey (Gjelstrup 2000). Kaufmann et al. (2002) and Skubala & Gulvik (2005) has also reported that mites are early colonizers of barren ground.

Collembola has also been found in < 40 year old post coal mining successions (Frouz et al. 2001) and on the island of Surtsey after 10 years (Sigurðardóttir 2002). Kaufmann (2001) says that “Some epigean Collembola were caught in the pitfall traps” on barren moraine. Hodkinson et al. (2004) found surface-active collembola on grounds not older than two years.

Here we clearly have two potential nourishment sources for beetles and spiders. It is uncertain how attractive mites are as nourishment for beetles and spiders due to their small size or hard outer shell. We caught several species of relatively large Isotomidae and Sminthuridae species of collembola in our sites age 3, 39-40 years. These could be attractive nourishment sources for several of the predator groups. According to Hopkin (1997) generalist spiders will eat collembola if they come across them and among beetles (Notiophilus sp.) there are collembola specialists. Agusti et al. (2003) found that *linyphiid* spiders (Erigone spp.) include Collembola as alternative prey in arable fields.

This raises the question; what supports the mite and collembola populations? Collembola are typical saprophages, detritivores or frugivores. A look at the gut content of some of the collembola caught in our traps revealed plant cells possibly from mosses. Bardgett et al. (2007) found that functioning microbial communities are sustained by ancient carbon from recently exposed glacier substrates. Some collembola feed on or include cyanobacteria in their diet (Hodkinson et al. 2004). If cyanobacteria are the underlying nourishment source Hodkinson et al. (2002) proposal that “community assembly by autotrophs is preceded by a heterotrophic phase that may be instrumental in facilitating the establishment of green plants" is wrong.

4.3.3 Comparisons with other glacier forelands

Vaters (2006) research on glacier forelands in southern Norway is comparable to ours on the basis of species of beetles and spiders. Our sites one and two aged 3 and 39-40 years respectively are comparable to the first two sites at all locations aged 0-20 and 21-40 years respectively. Vater (2006) investigated all taxa collected and has a low taxonomical resolution but a few species reoccur within the 40 year succession. *Amara alpina, Nebria nivalis* and *Pardosa traili* were identified. Bembidion spp., nebria spp. and staphylinidae spp. were also found. A comparison with Kaufmann (2001) study from the Austrian central alps, shows that we have several species in common within the first 40 years of succession, among the beetles; *Nebria rufescens, Amara quenseli Chrysomela collaris, Notiophilus aquaticus* and *Cymindis Vaporarium* and staphylinidae spp species are also caught but are omnipresent through the chronosequence. *Erigone tirolensis* is the only shared spider within 40 years. *Gonatium rubens* is also present but appears later than 138 years. According to Kaufmann (2001) "Carabids of the genus *Nebria* and staphylinid beetles and lycosid and linyphiid (*Erigone tirolensis*) spiders are the first to establish on the barren moraine". Herbivorous beetles do not occur after 30 years. Further investigation by Kaufmann et al. (2002) of the soil fauna revealed that the pioneer sites were dominated by "epigeal predators (carabidae and aranei)". A study done by Gobbi et al. (2006) in the Forni valley in the Italian Alps, also found that barren pioneer ground, 24 years and less, was dominated by predators carabidae and araneae. *Amara* quenseli was the only mutually shared species within the vegetation free zone and was present at 24 years. *Cymindis Vaporarium and Notiophilus aquaticus* was also present but appeared on vegetated grounds at 54 years. In comparison with Hodkinson et al. (2004) chronosequence in the high Arctic at Midtre Lovenbre spanning from two to 1900 years we have one species in common. *Erigone arctica* appeared at all sites from 16 years and beyond. According to Hodkinson et al. (2004) "Initial colonization was almost exclusively by detritivores and omnivores". No beetles were located in this study. A check at The Norwegian biodiversity Information Centre (2009) showed that *Amara alpina* and *Amara* quenseli are present at Svalbard (Bengtson et al. 1975) and as stated earlier

Simplocaria metallica has been registered. *Collensia holmgreni* and *Erigone tirolensis* has also been registered on Svalbard.

Our study and others shows that there is a clear pioneer community. Other similarities are also obvious. Our species establishes relatively quickly, 63% of the beetles and 39% of the spiders are present already at 63 years. In total 52% of the species are present at 31% of the age gradient. Species tend to persist after their first appearance. Only *Bembidion hastii* and *Simplocaria metallica* are numerous early in the succession and then disappear completely towards the end (appendix 6 and 7). Hågvar et al. (2009) study on acari in the same location found the same pattern, half of the species was present after 60 years in the 250 year foreland and they seem to persist after first appearance. According to Vater (2006) the same pattern emerges “community change during succession is dominated by the addition of taxa rather than taxa replacement”. Kaufmann (2001) also found that there is only a minor increase after 50 years. Kaufmann et al. (2002) also states that the soil fauna changed little beyond 50 years. And Gobbi et al. (2006) Showed that the highest species richness increase was within the first 61 years. Community assembly in the high arctic is slower then on the European mainland, but there seem to be a similar high increase within the first years of succession. Hodkinson et al. (2004) found that the different taxa had the highest increase within the first 36-100 years and seem to persist after their first appearance. In all studies the arthropod diversity is greatest towards the end of the chronosequence.

4.4 The ophilione - Mitopus morio

The ophilione *Mitopus morio* was caught in large numbers through the whole gradient. *Mitopus morio* is a generalist predator mainly eating living wingless arthropods, and frequently eating collembola, coleopteran larva and acarina (Phillipson 1960). We argue that *Mitopus morio* would, if included in the analysis, and should be regarded as a pioneer species. According to Vater (2006) *Mitopus morio* was "commonly found on every foreland". And Kaufmann et al. (2002) state that "pioneer sites are dominated by ophilione". Kaufmann (2001) also had the ophilione *Mitopus glacialis* as a pioneer species.

Acknowledgments

We would like to thank our supervisor Prof. Sigmund Hågvar for good discussions, support and professional guidance. Everyone at Finse Alpine Research Center and especially ErikaLeslie for her hospitality and for transportation. Sindre Thon Bråten for field and laboratory assistance. Oddvar Hansen and Sigmund Hågvar for beetle taxonomy and Kjetil Åkra for the spider taxonomy. Thanks to Preben Ottesen for lending us specially modified pitfall traps, saving us a lot of work. Also a huge thanks to Christian E. Mong, for proof reading and for introducing us to the wonderful world of R and Detrended Correspondence Analysis. Dr. Amber E. Vater for sending us her PhD thesis and Alvar J. Wattne , Nils H. Boisen for proof reading and suggestions on improvement and Silje Vang for help with layout. We are very grateful for the support and kind encouragement from our families, friends and fellow students. And great thank to all the people we might have forgotten.

Literature cited

Aakra, K. (2009). (Mail 25.05.2009).

Aakra, K. & Hauge, E. (2003). Checklist of Norwegian spiders (Arachnida: Araneae), including Svalbard and Jan Mayen. *Norwegian Journal of Entomology*, 50: 109-129.

Agusti, N., Shayler, S. P., Harwood, J. D., Vaughan, I. P., Sunderland, K. D. & Symondson, W. O. C. (2003). Collembola as alternative prey sustaining spiders in arable ecosystems: prey detection within predators using molecular markers. *Molecular Ecology*, 12: 3467-3475.

Bardgett, R. D., Richter, A., Bol, R., Garnett, M. H., Baumler, R., Xu, X. L., Lopez-Capel, E., Manning, D. A. C., Hobbs, P. J., Hartley, I. R., et al. (2007). Heterotrophic microbial communities use ancient carbon following glacial retreat. *Biology Letters*, 3: 487-490.

Bengtson, S. A., Fjellberg, A. & Solhøy, T. (1975). *Amara quenselii* new record (*Coleoptera: Carabidae*) new to Svalbard, Norway. *Norwegian Journal of Entomology*, 22: 81-82.

Chapman, J. W., Reynolds, D. R. & Smith, A. D. (2003). Vertical-Looking Radar: A New Tool for Monitoring High-Altitude Insect Migration. *BioScience*, 53: 503-511.

Coulson, S. I., Hodkinson, I. D. & Webb, N. R. (2003). Microscale distribution patterns in high Arctic soil microarthropod communities: the influence of plant species within the vegetation mosaic. *Ecography*, 26: 801-809.

Frouz, J., Keplin, B., Pizl, V., Tajovsky, K., Stary, J., Lukesova, A., Novakova, A., Balik, V., Hanel, L., Materna, J., et al. (2001). Soil biota and upper soil layer development in two contrasting post-mining chronosequences. *Ecological Engineering*, 17: 275-284.

Gjelstrup, P. (2000). Soil mites and collembolans on Surtsey, Iceland, 32 years after the eruption. *Surtsey Research Progress Report*: Surtsey Research Society. 43-50 p.

Gobbi, M., De Bernardi, F., Pelfini, M., Rossaro, B. & Brandmayr, P. (2006). Epigean arthropod succession along a 154-year glacier foreland cronosequence in the Forni Valley (Central Italian Alps). *Arctic Antarctic and Alpine Research*, 38: 357-362.

Greenslade, P. J. M. (1964). Pittfall trapping as a method for studying populations of carabidae (*Coleoptera*). *Journal of Animal Ecology*, 33: 301-310.

Hansen, V. & Larsson, S. G. (1965). Biller, 21, Snudebiller. 524 p.

Hansen, V. & Larsson, S. G. (1973). Biller, 9, Blødvinger, klannere m.m. (Malacodermata, Fossipedes, Macrodactylia og Brachymera). 344 p.

Hauge, E., Hågvar, S. & Østbye, E. (1978). Pit-fall catches of surface-active arthropods in some high mountain habitats at Finse, south Norway. Ill. The species of Araneida *Norwegian Journal of Entomology* 25: 207 - 220.

Hauge, E. & Ottesen, P. (2002). Spiders (*Araneae*) in low alpine areas at Finse, Southern Norway. 49: 117-138.

Hawes, T. (2008). Aeolian fallout on recently deglaciated terrain in the high Arctic. *Polar Biology*, 31: 295-301.

Hill, M. O. & Gauch, H. G. (1980). Detrenden correspondence-analysis - an improved ordination technique. *Vegetatio*, 42: 47-58.

Hodkinson, I. D., Webb, N. R., Bale, J. S., Block, W., Coulson, S. J. & Strathdee, A. T. (1998). Global change and Arctic ecosystems: Conclusions and predictions from experiments with terrestrial invertebrates on spitsbergen. *Arctic and Alpine Research*, 30: 306-313.

Hodkinson, I. D., Coulson, S. J., Harrison, J. & Webb, N. R. (2001). What a wonderful web they weave: spiders, nutrient capture and early ecosystem development in the high Arctic - some counter-intuitive ideas on community assembly. *Oikos*, 95: 349-352.

Hodkinson, I. D., Webb, N. R. & Coulson, S. J. (2002). Primary community assembly on land - the missing stages: why are the heterotrophic organisms always there first? *Journal of Ecology*, 90: 569-577.

Hodkinson, I. D. & Coulson, S. J. (2004). Are high Arctic terrestrial food chains really that simple? - The Bear Island food web revisited. *Oikos*, 106: 427-431.

Hodkinson, I. D., Coulson, S. J. & Webb, N. R. (2004). Invertebrate community assembly along proglacial chronosequences in the high Arctic. *Journal of Animal Ecology*, 73: 556-568.

Hopkin, S. P. (1997). *Biology of the springtails (Insecta: Collembola)*. Oxford: Oxford University Press. 330 p.

Hågvar, S. (1969). *Some observations on Coleoptera, Hymenoptera and Siphonaptera in Svalbard 1968*. Norsk Polarinstitutt Årbok 1969. Oslo: Norsk Polarinstitutt

Hågvar, S. (1975). Studies on the ecology of Melasoma collaris L. (Col., Chrysomelidae) in alpine habitats at Finse, south Norway. Norwegian journal of entomology, 22: 31-47.

Hågvar, S., Østbye, E. & Melåen, J. (1978). Pit-fall catches of surface-active arthrpods in some high mountain habitats at Finse,south norway II. General results at group level, with emphasis on *ophiliones*, *araneida* and *coloptera*. *Norwegian Journal of entomology*, 25: 195-205.

Hågvar, S., Solhøy, T. & Mong, C. E. (2009). Primary Succession of Soil Mites (*Acari*) in a Norwegian Glacier Foreland, with Emphasis on *Oribatid* Species. *Arctic, Antarctic, and Alpine Research*, 41: 219-227.

IPCC. (2007). Climate Change 2007: The Physical Science Basis: Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. In Solomon, S. (ed.): Cambridge University Press.

Litteratur cited

Johnson, E. A. & Miyanishi, K. (2008). Testing the assumptions of chronosequences in succession. *Ecology Letters*, 11: 419-431.

Jongman, R. H., Braak, C. J. F. t. & Van Tongeren, O. F. R. (1995). *Data analysis in community and landscape ecology*. New ed. Cambridge: Cambridge University Press. 299 p.

Kaufmann, R. (2001). Invertebrate succession on an alpine glacier foreland. *Ecology*, 82: 2261-2278.

Kaufmann, R. (2002). Glacier foreland colonisation: distinguishing between short-term and long-term effects of climate change. *Oecologia*, 130: 470-475.

Kaufmann, R., Fuchs, M. & Gosterxeier, N. (2002). The soil fauna of an Alpine glacier foreland: Colonization and succession. *Arctic Antarctic and Alpine Research*, 34 (3): 242-250.

Kaufmann, R. & Raffl, C. (2002). Diversity in primary succession: The chronosequence of a glacier forland. *Global Mountain Biodiversity* 179-192.

Krebs, C. J. (2001). *Ecology : the experimental analysis of distribution and abundance*. 5th ed. San Francisco, Cal.: Benjamin Cummings. 695 p.

Kronestedt, T. (2004). Studies on species of Holarctic Pardosa groups (*Araneae, Lycosidae*). VI. On the identity of *Pardosa luciae Tongiorgi* with notes on *P. trailli* (O. P.-Cambridge) and some other species in the P. nigra-group. In Thaler, K. (ed.), Diversität und Biologie von Webspinnen, Skorpionen under anderen Spinnentieren. *Denisia*, 12: 281-290.

Leather, S. R. (2005). *Insect sampling in forest ecosystems*. Malden, Mass.: Blackwell Publ. 303 p.

Lindroth, C. H. (1961). *Svensk insektfauna. 9, Skalbaggar. Coleoptera : sandjägare och jordlöpare : Fam. Carabidae* Stockholm.

Lindroth, C. H. (1985). *Fauna entomologica Scandinavica; The Carabidae (Coleoptera) of Fennoscandia and Denmark*, vol. 15, part 1. Copenhagen: E.J. Brill / Scandinavian Science Press. 225 p.

Lindroth, C. H. (1986). *Fauna entomologica Scandinavica; The Carabidae (Coleoptera) of Fennoscandia and Denmark*, vol. 15, part 2. Copenhagen: E.J. Brill / Scandinavian Science Press. 497 p.

Matthews, J. A. (1992). *The ecology of recently-deglaciated terrain : a geoecological approach to glacier forelands and primary succession*. Cambridge studies in ecology. Cambridge: Cambridge University Press. 386 p.

Molles, M. C. (2005). *Ecology: concepts and applications*. Boston: McGraw-Hill. 622 p.

Nesje, A. (2004). Breene i Europa minker. *Cicerone*, 13: 24-26.

Norwegian biodiversity Information Centre (2009). Available at: www.biodiversity.no/.

Oksanen, J., Kindt, R., Legendre, P., O'Hara, B., Simpson, G. L., Solymos, P., Stevens, M. H. H. & Wagner, H. (2008). *vegan: Community Ecology Package*. R package version 1.15-1 ed.

Ottesen, P. S. (1996). Niche segregation of terrestrial Alpine beetles (*Coleoptera*) in relation to environmental gradients and phenology. *Journal of Biogeography*, 23: 353-369.

Palm, T. (1948). *Svensk insektfauna. 9, Skalbaggar (Coleoptera) Kortvingar: Fam. Staphylinidae, underfam. Micropeplinae, Pholeocharine, Olisthaerinae, Proteininae, Omaliinae*. Stockholm.

Palmer, M. (2009). *The ordination web page*. [Web Page]. Stillwater. Available at: http://ordination.okstate.edu/index.html (accessed: 17.02.2009).

Palmgren, P. (1975). Die Spinnenfauna Finnlands und Ostfennoskandiens VI: *Linyphiidae* 1. *Fauna fenn* (20): 1-102.

Palmgren, P. (1976). Die Spinnenfauna Finnlands und Ostfennoskandiens VII. *Linyphiidae* 2. *Fauna fenn*, 29: 1-126.

Phillips, I. D. & Cobb, T. P. (2005). Effects of Habitat Structure and Lid Transparency on Pitfall Catches. *Environmental Entomology*, 34: 875-882.

Phillipson, J. (1960). A Contribution to the Feeding Biology of *Mitopus morio* (F) (*Phalangida*). *Journal of Animal Ecology*, 29: 35-43.

Pickett, S. T. A. (1987). Space-for-time substitution as an alternative to long-term studies. In Likens, G. E. (ed.) *Long-term studies in ecology: Approaches and alternatives*, pp. 110-135. New York: Springer.

Polis, G. A., Anderson, W. B. & Holt, R. D. (1997). Toward an integration of landscape and food web ecology: The dynamics of spatially subsidized food webs. *Annual Review of Ecology and Systematics*, 28: 289-316.

R Development Core Team. (2008). *R: A language and environment for statistical computing*. Computing, R. F. f. S. (ed.). Vienna, Austria.

Raffl, C., Mallaun, M., Mayer, R. & Erschbamer, B. (2006). Vegetation succession pattern and diversity changes in a glacier valley, Central Alps, Austria. *Arctic Antarctic and Alpine Research*, 38: 421-428.

Schowalter, T. D. (2000). *Insect ecology: an ecosystem approach*. San Diego, Calif.: Academic Press. 483 p.

Sigurðardóttir, H. (2002). Status of collembolans (*Collembola*) on Surtsey, Iceland, in 1995 and first encounter of earthworms (*lumbricidae*) in 1993. In report, S. R. (ed.). *Surtsey Research 11*: Surtsey Research Society. 51-55 p.

Silfverberg, H. (1992). Enumeratio Coleopterorum Fennoscandiae, Daniae et Baltiae. Helsingfors: Helsingfors Entomologiska Bytesförening. 94 p.

Skubala, P. & Gulvik, M. (2005). Pioneer oribatid mite communities (*Acari, Oribatida*) in newly exposed natural (glacier foreland) and anthropogenic (post-industrial dump) habitats. *Polish Journal of Ecology*, 53: 395-407.

Spence, J. R. & Niemela, J. K. (1994). Sampling carabid assemblages with pitfall traps - the madness and the method. *Canadian Entomologist*, 126: 881-894.

Strand, A. (1969). *Simplocaria metallica* Sturm New to Svalbard. *Norwegian Journal of Entomology*, 16: 25-26.

Sørlie, R. (2001). *Ectomycorrhiza on Salix herbacea L. in the glacier foreland of Midtdalsbreen, Finse, Norway*. Oslo: R. Sørlie. 75 p.

Topping, C. J. & Sunderland, K. D. (1992). Limitations to the use of pitfall traps in ecological - studies exemplified by a study of spiders in a field of winter-wheat. *Journal of Applied Ecology*, 29: 485-491.

Vater, A. E. (2006). *Invertebrate and arachnid succession on selected glacier forelands in southern Norway*. Doctor of Philosophy University of Wales Swansea, Department of Geography.

Vetaas, O. R. (1997). Relationships between Floristic Gradients in a Primary Succession. *Journal of Vegetation Science*, 8: 665-676.

Walker, L. R. & Del Moral, R. (2003). *Primary succession and ecosystem rehabilitation.* Cambridge: Cambridge University Press. 442 p.

Wessa, P. (2009). *Free Statistics Software, Office for Research Development and Education, version 1.1.23-r3*. Available at: http://www.wessa.net/.

Østbye, E. & Hågvar, S. (1996). Pit-fall catches of surface-active arthropods in high mountain habitats at finse, south Norway. IV. *coleoptera. Fauna Norvegica. Serie B, Norwegian journal of entomology*, 43: 1-18.

Appendices

Appendix 1: Site characteristics of the six sampling sites, including start and stop dates of sampling at the Midtdalsbreen glacier foreland, Finse, Norway. The initiating dates in 2008 correspond to the date when all traps where snow-free. Start 07= Sampling start 2007, Stop 07= Sampling stop 2007, start 08= Sampling start 2008, stop 08= Sampling stop 2008 and M.V.C= Mean vegetation cover.

Site No.	Trap No.	Age (Years)	Distance (Meters)	M.V.C (Percentage)	Start 07 (Date)	Stop 07 (Date)	Start 08 (Date)	Stop 08 (Date)
1	101 -120	3	15	0	-	-	28.6.08	23.8.08
2	1-20	39- 40	70	6	7.7.07	15.9.07	28.6.08	23.8.08
3	21-40	62-63	472	91	7.7.07	1.9.07	28.6.08	23.8.08
4	41-60	78-79	807	80	7.7.07	15.9.07	28.6.08	23.8.08
5	61-80	159-160	1012	80	7.7.07	1.9.07	28.6.08	23.8.08
6	81-100	204-205	1100	96	7.7.07	15.9.07	26.7.08	23.8.08

Appendix 2: List of DCA axes one scores for the DCA-1-3 analysis.

DCA-1	DCA1	DCA-2	DCA1	DCA-3	DCA1
Bem.has	3.35	Bem.has	3.75	Bem.has	3.09
Sim.met	2.77	Sim.met	3.04	Sim.met	2.86
Col.hol	2.42	Col.hol	2.57	Neb.niv	2.73
Eri.tir	2.39	Eri.tir	2.44	Eri.arc	2.61
Neb.niv	2.32	Neb.niv	1.98	Col.hol	2.37
Par.tra	1.90	Hil.fri	1.89	Hil.fri	2.16
Hil.fri	1.73	Par.tra	1.81	Eri.tir	1.86
Eri.arc	1.58	Hel.gla	1.34	Par.tra	1.83
Ama.alp	1.09	Eri.arc	1.26	Geo.lon	1.06
Hel.gla	1.04	Ama.alp	1.13	Ama.alp	0.99
Geo.lon	0.89	Geo.lon	0.84	Neb.ruf	0.62
Arp.qua	0.37	Neb.ruf	0.46	Arp.qua	0.48
Neb.ruf	0.27	Pat.sep	0.42	Ama.que	0.12
Pat.sep	0.16	Cur.cyc	0.14	Cur.cyc	-0.18
Ama.que	0.03	Gny.cae	0.13	Pat.sep	-0.21
Gny.cae	0.01	Ama.que	-0.10	Byr.fas	-0.48
Cur.cyc	-0.03	Not.aqu	-0.13	Oti.nod	-0.58
Not.aqu	-0.28	Pel.bor	-0.16	Arc.alp	-0.68
Pel.bor	-0.31	Arc.alp	-0.18	Ath.hyp	-0.79
Bor.hen	-0.36	Bat.gra	-0.25	Pel.bor	-0.87
Oti.nod	-0.38	Bor.hen	-0.28	Cym.vap	-0.92
Arc.alp	-0.38	Oti.nod	-0.28	Tis.aes	-0.96
Cep.niv	-0.46	Byr.fas	-0.30	Lio.alp	-1.20
Byr.fas	-0.48	Cep.niv	-0.32	Gna.lep	-1.55
Bat.gra	-0.48	Cym.vap	-0.43	Sco.eva	-1.60
Cym.vap	-0.62	Pel.men	-0.56	Ant.alp	-1.74
Pel.men	-0.84	Ath.hyp	-0.76	Oma.cae	-1.78
Ath.hyp	-0.87	Agy.nig	-0.87	Par.pal	-1.81
Euc.bra	-0.95	Euc.bra	-0.93	Gon.rub	-1.87
Tis.aes	-1.04	Ore.vag	-0.96	Euc.bra	-1.94
Agy.nig	-1.10	Tis.aes	-0.96	Oed.ret	-2.03
Aci.cre	-1.14	Aci.cre	-1.01	Par.sep	-2.04
Ore.vag	-1.17	Par.sep	-1.10	Pel.men	-2.16
Lio.alp	-1.25	Arp.qua	-1.13	Ozy.arc	-2.31
Bry.rug	-1.29	Sco.eva	-1.18		
Sco.eva	-1.34	Bry.rug	-1.23		
Mec.mor	-1.40	Ozy.arc	-1.24		
Chr.col	-1.41	Lio.alp	-1.26		
Par.sep	-1.42	Chr.col	-1.28		
Ozy.arc	-1.50	Mec.mor	-1.29		
Ant.alp	-1.55	Ant.alp	-1.51		
Par.pal	-1.72	Par.pal	-1.71		
Wal.kar	-1.78	Wal.kar	-1.75		
Gna.lep	-1.81	Gna.lep	-1.80		
Tac.elo	-1.89	Tac.elo	-1.90		
Myc.eri	-1.90	Myc.eri	-1.91		
Myc.nig	-1.92	Myc.nig	-1.92		
Oed.sp.	-1.96	Oed.sp.	-1.95		
Oma.cae	-2.01	Oma.cae	-2.03		
Gon.rub	-2.03	Gon.rub	-2.08		
Oed.ret	-2.09	Oed.ret	-2.19		

Appendix 3: List of DCA axes one scores for beetles in the DCA-4-6 analysis.

DCA-4	DCA1	DCA-5	DCA1	DCA-6	DCA1
Bem.has	2,98	Bem.has	3,01	Bem.has	2,71
Sim.met	2,45	Sim.met	2,79	Sim.met	2,49
Neb.niv	2,20	Neb.niv	2,23	Neb.niv	2,43
Ama.alp	1,48	Hel.gla	1,57	Ama.alp	1,25
Hel.gla	1,42	Ama.alp	1,41	Geo.lon	1,17
Geo.lon	1,28	Geo.lon	1,12	Arp.qua	0,89
Arp.qua	1,14	Pat.sep	0,65	Neb.ruf	0,50
Pat.sep	0,29	Neb.ruf	0,35	Ama.que	0,02
Neb.ruf	0,11	Bor.hen	-0,01	Pat.sep	-0,22
Ama.que	-0,06	Oti.nod	-0,09	Cur.cyc	-0,54
Bor.hen	-0,22	Cur.cyc	-0,18	Byr.fas	-0,73
Oti.nod	-0,32	Pel.bor	-0,34	Pel.bor	-0,79
Cur.cyc	-0,38	Not.aqu	-0,35	Oti.nod	-0,80
Pel.bor	-0,54	Byr.fas	-0,37	Ath.hyp	-0,91
Not.aqu	-0,56	Cep.niv	-0,40	Cym.vap	-1,24
Cep.niv	-0,64	Ama.que	-0,41	Lio.alp	-1,51
Byr.fas	-0,65	Chr.col	-0,58	Ant.alp	-1,72
Euc.bra	-0,79	Bry.rug	-0,60	Euc.bra	-1,80
Bry.rug	-0,82	Cym.vap	-0,62	Oma.cae	-2,02
Cym.vap	-0,85	Euc.bra	-0,69		
Chr.col	-0,92	Ath.hyp	-0,89		
Ath.hyp	-1,04	Aci.cre	-1,07		
Gny.cae	-1,10	Gny.cae	-1,10		
Aci.cre	-1,19	Tac.elo	-1,27		
Lio.alp	-1,39	Ant.alp	-1,33		
Tac.elo	-1,39	Lio.alp	-1,40		
Ant.alp	-1,42	Arp.qua	-1,42		
Myc.nig	-1,57	Myc.nig	-1,45		
Myc.eri	-1,70	Myc.eri	-1,66		
Oma.cae	-1,88	Oma.cae	-1,91		

Appendix 5: List of DCA axis one scores for spiders in the DCA-7-9 analysis.

DCA-7	DCA 1	DCA-8	DCA 1	DCA-9	DCA 1
Oed.ret	2.30	Oed.ret	2.27	Eri.arc	2.66
Wal.kar	2.10	Wal.kar	2.08	Hil.fri	2.63
Gon.rub	2.09	Gon.rub	2.06	Col.hol	2.45
Par.pal	2.07	Par.pal	2.04	Par.tra	1.17
Gna.lep	2.04	Gna.lep	2.02	Eri.tir	1.07
Mec.mor	1.67	Mec.mor	1.65	Arc.alp	0.62
Oed.sp.	1.54	Oed.sp.	1.49	Par.sep	0.07
Ore.vag	1.13	Ore.vag	1.11	Ozy.arc	-0.35
Sco.eva	0.89	Tis.aes	0.84	Tis.aes	-0.61
Tis.aes	0.86	Sco.eva	0.83	Pel.men	-0.95
Ozy.arc	0.69	Ozy.arc	0.54	Sco.eva	-1.04
Par.sep	0.19	Bat.gra	0.11	Gna.lep	-1.98
Agy.nig	0.19	Agy.nig	0.07	Par.pal	-2.11
Bat.gra	0.18	Par.sep	0.00	Gon.rub	-2.13
Pel.men	0.01	Pel.men	-0.11	Oed.ret	-2.20
Arc.alp	-0.38	Arc.alp	-0.51		
Hil.fri	-0.47	Hil.fri	-0.57		
Eri.arc	-1.11	Eri.arc	-1.06		
Par.tra	-1.42	Par.tra	-1.47		
Eri.tir	-1.95	Eri.tir	-1.85		
Col.hol	-2.72	Col.hol	-2.71		

Appendix 6: An overview of the different species of beetles found at the Midtdalsbreen glacier foreland, Finse, Norway in the 2007 and 2008 season. Showing the age and distance of the different sites along with the species and their abundance at that given site. *Byrrhidae* = Byr, *Carabidae* = Car, *Chrysomelidae* = Chrys, *Cryptophagidae* = Cryp, *Curculionidae* = Curc, *Hydrophilidae* = Hydr, *Leiodidae* = Leiod and *Staphylinidae* = Staph

	Distance (m)	15	70	70		472	472		807	807		1012	1012		1100	1100	
	Age (year)	3	39	40		62	63		78	79		159	160		204	205	
	Sampling year	2008	2007	2008	**Both**	2007	2008	**Both**	2007	2008	**Both**	2007	2008	**Both**	2007	2008	**Both**
Byr	*S. metallica*	**2,1**	20,8	7,7	**28,5**	0	1,3	**1,3**	2	0	**2**	0	0	**0**	0	0	**0**
Car	*A. alpina*	**7,7**	37,5	36,6	**74,1**	8,8	45,8	**54,6**	17	53,7	**70,7**	12,4	10,3	**22,7**	91,5	77	**168,5**
Car	*A. quenseli*	**5**	0	0	**0**	160,6	230,1	**390,7**	208,6	205,3	**413,9**	0	2,1	**2,1**	10,3	12	**22,3**
Car	*B. hastii*	**171,1**	36,81	32,3	**69,11**	0	0	**0**	0	0	**0**	0	0	**0**	0	0	**0**
Car	*N. nivalis*	**22**	16,85	14,2	**31,05**	5,3	5,7	**11**	21	14,9	**35,9**	1,1	0	**1,1**	2	1	**3**
Staph	*A. quadrum*	**1,1**	0	0	**0**	0	0	**0**	0	5,8	**5,8**	0	0	**0**	1	5	**6**
Staph	*G. longipes*	**3,5**	17,8	15	**32,8**	8,9	67,9	**76,8**	56,9	29,2	**86,1**	6,1	3,1	**9,2**	19,6	8	**27,6**
Car	*N. rufescens*	**0**	1	3,4	**4,4**	6,5	12,7	**19,2**	93,6	82,2	**175,8**	0	1	**1**	5,1	2	**7,1**
Car	*P. septentrionis*	**0**	62,3	9,6	**71,9**	158,8	218,5	**377,3**	357,3	276,6	**633,9**	223,3	97,5	**320,8**	152,6	76	**228,6**
Curc	*O. nodosus*	**0**	1	0	**1**	1,1	9,7	**10,8**	9,2	15,7	**24,9**	1,3	1,1	**2,4**	14	5	**19**
Hydr	*H. glacialis*	**0**	0	1,4	**1,4**	0	0	**0**	1	1,2	**2,2**	0	1,1	**1,1**	0	1	**1**
Staph	*B. henningamus*	**0**	3	0	**3**	0	6,7	**6,7**	2	14,5	**16,5**	0	3,2	**3,2**	5,3	19	**24,3**
Staph	*O. annularis*	**0**	1,05	0	**1,05**	0	0	**0**	0	0	**0**	0	0	**0**	0	0	**0**
Byr	*B. fasciatus*	**0**	0	0	**0**	3,3	7,1	**10,4**	23,4	28,1	**51,5**	21,7	5,1	**26,8**	22	4	**26**
Byr	*C. cyclolepidia*	**0**	0	0	**0**	42,2	79,6	**121,8**	35,3	26,6	**61,9**	0	0	**0**	0	0	**0**
Car	*C. vaporariorum*	**0**	0	0	**0**	25,9	32	**57,9**	10,2	17,8	**28**	44,7	32,7	**77,4**	14,1	5	**19,1**
Car	*N. aquaticus*	**0**	0	0	**0**	17,7	16,8	**34,5**	6	20	**26**	4,8	1,1	**5,9**	15,1	1	**16,1**
Staph	*A. crenata*	**0**	0	0	**0**	1	3,8	**4,8**	0	0	**0**	1	4,2	**5,2**	3,5	0	**3,5**
Staph	*A. hypnorum*	**0**	0	0	**0**	0	17,3	**17,3**	1	9	**10**	3,5	3,1	**6,6**	9,3	15	**24,3**
Staph	*C. nivicola*	**0**	0	0	**0**	1,1	4,9	**6**	6	15,7	**21,7**	2,86	4,2	**7,06**	7,1	3	**10,1**
Staph	*D. tectum*	**0**	0	0	**0**	1,1	0	**1,1**	0	0	**0**	0	0	**0**	0	0	**0**
Staph	*L. alpestris*	**0**	0	0	**0**	17,1	70,1	**87,2**	168,2	49,7	**217,9**	1	32,6	**33,6**	268,2	340	**608,2**
Staph	*O. laqueatus*	**0**	0	0	**0**	1,1	0	**1,1**	0	0	**0**	0	0	**0**	0	0	**0**
Car	*P. borealis*	**0**	0	0	**0**	0	0	**0**	25,1	10	**35,1**	4,4	1	**5,4**	3,1	1	**4,1**
Chrys	*C. collaris*	**0**	0	0	**0**	0	0	**0**	0	2,2	**2,2**	8	2,1	**10,1**	140	5	**145**
Cryp	*Atomaria sp.*	**0**	0	0	**0**	0	0	**0**	1	0	**1**	0	0	**0**	0	0	**0**
Curc	*A. cruentatum*	**0**	0	0	**0**	0	0	**0**	0	2,2	**2,2**	0	0	**0**	0	0	**0**
Staph	*A. alpinus*	**0**	0	0	**0**	0	0	**0**	11,4	6,7	**18,1**	18,7	15,1	**33,8**	141,8	97	**238,8**
Staph	*B. rugipennis*	**0**	0	0	**0**	0	0	**0**	1	0	**1**	0	0	**0**	3	4	**7**
Staph	*E. brachypterum*	**0**	0	0	**0**	0	0	**0**	5,1	8,7	**13,8**	0	0	**0**	8,1	5	**13,1**
Staph	*G. caerulea*	**0**	0	0	**0**	0	0	**0**	0	7,9	**7,9**	0	0	**0**	0	0	**0**
Staph	*O. caesuin*	**0**	0	0	**0**	0	0	**0**	0	2,4	**2,4**	4,3	13,5	**17,8**	34,5	51	**85,5**
Staph	*A. laeuicauda*	**0**	0	0	**0**	0	0	**0**	0	0	**0**	1,4	0	**1,4**	2	0	**2**
Staph	*M. inaris*	**0**	0	0	**0**	0	0	**0**	0	0	**0**	0	1,1	**1,1**	0	0	**0**
Chrys	*G. arcica*	**0**	0	0	**0**	0	0	**0**	0	0	**0**	0	0	**0**	4	0	**4**
Leiod	*H. spinipes*	**0**	0	0	**0**	0	0	**0**	0	0	**0**	0	0	**0**	0	1	**1**
Staph	*B. niger*	**0**	0	0	**0**	0	0	**0**	0	0	**0**	0	0	**0**	0	2	**2**
Staph	*M. erichsonanus*	**0**	0	0	**0**	0	0	**0**	0	0	**0**	0	0	**0**	3,5	28	**31,5**
Staph	*M. nigraus*	**0**	0	0	**0**	0	0	**0**	0	0	**0**	0	0	**0**	1	5	**6**
Staph	*T. elongatus*	**0**	0	0	**0**	0	0	**0**	0	0	**0**	0	0	**0**	7,1	17	**24,1**
	Number of species	**7**	**10**	**8**	**11**	**16**	**17**	**19**	**22**	**24**	**27**	**17**	**20**	**22**	**27**	**27**	**30**

.

Appendix 7: An overview of the different species of spiders found at the Midtdalsbreen glacier foreland, Finse, Norway in the 2007 and 2008 season. Showing the age and distance of the different sites along with the species and their abundance at that given site. *Gnaphosidae* = Gna, *Linyphiidae* = Lin, *Lycosidae* = Lyc and *Thomisidae* = Tho

	Distance (m)	**15**	70	70		472	472		807	807		1012	1012		1100	1100	
	Age (year)	**3**	39	40		62	63		78	79		159	160		204	205	
	Sampling year	**2008**	2007	2008	**Both**	2007	2008	**Both**	2007	2008	**Both**	2007	2008	**Both**	2007	2008	**Both**
Lin	*C. holmgreni*	**3,3**	74,5	40,5	**115**	0	1,1	**1,1**	3	2,3	**5,3**	4,5	6	**10,5**	3	1	**4**
Lin	*E. arctica*	**7,1**	2,1	5,6	**7,7**	4,3	30,4	**34,7**	8,1	39,1	**47,2**	0	0	**0**	0	2,4	**2,4**
Lin	*E. tirolensis*	**7,7**	27,3	36,2	**63,5**	0	2,7	**2,7**	0	2,2	**2,2**	3,1	4,1	**7,2**	0	3,5	**3,5**
Lyc	*P. trailli*	**10,3**	22,1	26,8	**48,9**	5,5	6,7	**12,2**	21,3	46,8	**68,1**	1,4	2	**3,4**	4	0	**4**
Lin	*H. frigida*	**0**	29,7	70,6	**100,3**	0	10,2	**10,2**	2	24,6	**26,6**	7,7	18,8	**26,5**	21,4	26	**47,4**
Lyc	*A. aculeate*	**0**	0	1	**1**	0	0	**0**	0	0	**0**	0	1,1	**1,1**	0	0	**0**
Lin	*B. gracilis*	**0**	0	2,5	**2,5**	0	1,3	**1,3**	1	0	**1**	5,7	5,2	**10,9**	3,1	2,4	**5,5**
Lyc	*A. alpigena*	**0**	0	0	**0**	21,6	33,8	**55,4**	10,1	34,5	**44,6**	8,7	33,8	**42,5**	0	0	**0**
Lin	*T. aestivus*	**0**	0	0	**0**	19,5	52,1	**71,6**	14,2	46	**60,2**	13,1	19,8	**32,9**	79,6	76,6	**156,2**
Lin	*A. nigripes*	**0**	0	0	**0**	0	2,7	**2,7**	0	1,1	**1,1**	2,9	9,5	**12,4**	0	1,2	**1,2**
Lin	*P. mengei*	**0**	0	0	**0**	0	6,4	**6,4**	0	0	**0**	26,6	19,4	**46**	0	2,2	**2,2**
Lin	*S. evansi*	**0**	0	0	**0**	0	13,5	**13,5**	0	4,4	**4,4**	8,7	89,1	**97,8**	5,6	32,1	**37,7**
Lin	*T. tenebricola*	**0**	0	0	**0**	0	0	**0**	1	0	**1**	0	0	**0**	0	0	**0**
Lin	*O. vaginatus*	**0**	0	0	**0**	0	0	**0**	0	1,1	**1,1**	5,7	8,4	**14,1**	10	10,6	**20,6**
Tho	*O. arctica*	**0**	0	0	**0**	0	0	**0**	0	0	**0**	9,9	19,9	**29,8**	2	0	**2**
Lyc	*P. septentrionalis*	**0**	0	0	**0**	0	0	**0**	0	0	**0**	8,6	22,7	**31,3**	0	0	**0**
Lin	*G. rubens*	**0**	0	0	**0**	0	0	**0**	0	0	**0**	0	2,1	**2,1**	35,6	31	**66,6**
Lin	*M. morulus*	**0**	0	0	**0**	0	0	**0**	0	0	**0**	0	1	**1**	2	9,1	**11,1**
Lyc	*P. paludicola*	**0**	0	0	**0**	0	0	**0**	0	0	**0**	0	1	**1**	226,3	87,9	**314,2**
Lin	*T. flavipes*	**0**	0	0	**0**	0	0	**0**	0	0	**0**	0	1,1	**1,1**	0	0	**0**
Lin	*C. brevipes*	**0**	0	0	**0**	0	0	**0**	0	0	**0**	0	0	**0**	3	0	**3**
Gna	*G. leporina*	**0**	0	0	**0**	0	0	**0**	0	0	**0**	0	0	**0**	14,2	14,3	**28,5**
Lin	*I. kochiellus*	**0**	0	0	**0**	0	0	**0**	0	0	**0**	0	0	**0**	1	0	**1**
Lin	*L. antroniensis*	**0**	0	0	**0**	0	0	**0**	0	0	**0**	0	0	**0**	1	0	**1**
Lin	*M. paetulus*	**0**	0	0	**0**	0	0	**0**	0	0	**0**	0	0	**0**	1	0	**1**
Gna	*M. alpina*	**0**	0	0	**0**	0	0	**0**	0	0	**0**	0	0	**0**	2	0	**2**
Lin	*O. retusus*	**0**	0	0	**0**	0	0	**0**	0	0	**0**	0	0	**0**	56,4	23,6	**80**
Lin	*Oedothorax sp.*	**0**	0	0	**0**	0	0	**0**	0	0	**0**	0	0	**0**	6,7	0	**6,7**
Lyc	*P. hyperborea*	**0**	0	0	**0**	0	0	**0**	0	0	**0**	0	0	**0**	2	0	**2**
Lin	*P. variegata*	**0**	0	0	**0**	0	0	**0**	0	0	**0**	0	0	**0**	1	0	**1**
Lin	*W. karpinskii*	**0**	0	0	**0**	0	0	**0**	0	0	**0**	0	0	**0**	5	3,4	**8,4**
Lin	*I. complicatus*	**0**	0	0	**0**	0	0	**0**	0	0	**0**	0	0	**0**	0	1,2	**1,2**
Lin	*Lepthyphantes sp.*	**0**	0	0	**0**	0	0	**0**	0	0	**0**	0	0	**0**	0	1,2	**1,2**
	Number of species	**4**	**5**	**7**	**7**	**4**	**11**	**11**	**8**	**10**	**12**	**13**	**18**	**18**	**22**	**18**	**28**

Appendix 8: List of beetles used in ordination plot. Nomenclature according to (Silfverberg 1992). Abbr=Abbreviation used in ordination plot, NI= Nourishment imago, NJ= Nourishment juvenile, L= literature (1=Hågvar (1975), 2=Hansen & Larsson (1965), 3= Hansen & Larsson (1973)). Trophic guilds: F=fungivores, including slime-mould feeding; H=herbivours, including feeding on pollen and algae, but excluding woody tissue; Pr=predacious; S=saprophagous.

Abbr	**Staphylinidae**	**Author**	**NJ**	**NI**	**Biotope/comments**	**L**
Oxy ann	*Oxypoda annularis*	Mannerheim, 1830		Pr?	Aleocharinae	
Del tec	*Deliphrum tectum*	Paykull, 1789		S?	Omalinae, habitual in dung and rotting fungus	
Oxy laq	*Oxytelus laqueatus*	Marsham, 1802		S	Oxytelinae	
Tac elon	*Tachinus elongatus*	Yllenhal, 1810		Pr/S	Tachyporinae	
Aci cre	*Acidota crenata*	Fabricius, 1792		S?	Omalinae	
Cep niv	*Cephalocousya nivicola*	Thomson, 1871		Pr?	Aleocharinae	
Arp qua	*Arpedium quadrum*	Gravenhorst, 1806		S?	Omalinae	
Euc brac	*Eucnecosum brachypterum*	Gravenhorst, 1802		S?	Omalinae	
Ath hyp	*Atheta hypnorum*	Kiesenwetter, 1850		Pr?	Aleocharinae	
Ath lae	*Atheta laevicauda*	J. Sahlberg, 1876		Pr?	Aleocharinae	
Lio alp	*Liogluta alpestris*	Heer, 1839		Pr?	Aleocharinae	
Gny cae	*Gnypeta caerulea*	Sahlberg, 1831		Pr?	Aleocharinae	
Bry rug	*Bryoporus rugipennis*	Pandelle, 1869		Pr?	Tachyporinae	
Bry nig	*Bryoporus* niger	Campbell 1993		Pr?	Tachyporinae	
Myc nig	*Mycetoporus nigrans*	Mäklin, 1853		Pr?	Tachyporinae	
Myc eri	*Mycetoporus erichsonanus*	Fagel, 1965		Pr?	Tachyporinae	
Myc ina	*Mycetoporus inaris*	Luze, 1901		Pr?	Tachyporinae	
Ant alp	*Anthophagus*	Paykull, 1790		Pr	Omalinae, Powerful mandibles	

	alpines				indicates predation	
Oma cae	*Omalium caesum*	Gravenhorst, 1806		S?	Omalinae	
Bor hen	*Boreaphilus henningianus*	Sahlberg, 1832		Pr	Omalinae, Powerful mandibles indicates predation	
Geo lon	*Psephidonus longipes*	Mannerheim, 1830 (Formerly *Geodromicus longipes*)		Pr	Omalinae	
	Chrysomelidae					
Gon arc	*Gonioctena arctica*	Mannerheim, 1853	H	H	Salix?	
Chr coll	*Chrysomela collaris*	Linnaeus, 1758	H	H	Typical in outer part of snow beds with *Salix herbacea.*	1
	Curculionidae					
Api cru	*Apion cruentatum*	Walton, 1844			Rumex?	
Oti nod	*Otiorhynchus nodosus*	Müller, 1764	H?	H?	Island: Rumex, Saxifraga, Trifolium. Adult?	2
	Carabidae					
Ama alp	*Amara alpina*	Paykull, 1790	Pr	H/Pr	Lindroth 1962 - Sv. Larva predominantly predatory	
Ama que	*Amara quenseli*	Schönherr, 1806	Pr	H/Pr		
Cym Vap	*Cymindis vaporariorum*	Linnaeus, 1758	Pr	Pr		
Pat sep	*Patrobus septentrionis*	Dejean, 1828	Pr	Pr		
Bem has	*Bembidion hastii*	Sahlberg, 1827	Pr	Pr		
Not aqu	*Notiophilus aquaticus*	Linnaeus, 1758				
Pel bor	*Pelophila borealis*	Paykull, 1790	Pr	Pr		
Neb ruf	*Nebria rufescens*	Ström, 1768	Pr	Pr		
Neb niv	*Nebria nivalis*	Paykull, 1790	Pr	Pr		
	Byrrhidae				Larva of Byrrhidae reportedly feeds of mosses.	3

Sim met	*Simplocaria metallica*	Sturm, 1807	H?		mosses
Cur cyc	*Curimopsis cyclolepidia*	Münster, 1902	H?		mosses
Byr fas	*Byrrhus fasciatus*	Forster, 1771	H?		mosses
	Hydrophilidae				
Hel gla	*Helophorus glacialis*	Villa, 1833	H	H	Algae in water and moist places
	Leiodidae				
Hyd spi	*Hydnobius spinipes*	Gyllenhal, 1813	S	S	Hypha
	Cryptophagidae				
Atomara sp	*Atomaria* sp.		S	S	Fungi spores

Appendix 9: List of spiders used in ordination plot. Nomenclature according to Aakra & Hauge (2003), Abbr=Abbreviation used in ordination plot.

Abbr	Linyphiidae	Author
Agy nig	*Agyneta nigripes*	Simon, 1884 - Formerly Meioneta n. (see Saaristo & Tanasevitch 1996).
Bat gra	*Bathyphantes gracilis*	Blackwall, 184
Cer bre	*Ceratinella brevipes*	Westring, 1851
Col hol	*Collinsia holmgreni*	Thorell, 1871
Eri arc	*Erigone arctica*	White, 1852
Eri tir	*Erigone tirolensis*	L.Koch, 1872
Gon rub	*Gonatium rubens*	Blackwall, 1841
Hil fri	*Hilaira frigida*	Thorell, 1872
Imp com	Improphantes complicatus	Emerton, 1882 - Formerly Lepthyphantes c. (see Saaristo & Tanasevitch 1996).
Inc koc	*Incestophantes kochiellus*	Strand, 1900 - Formerly Lepthyphantes k. (see Saaristo & Tanasevitch 1996).
Lep sp.	*Lepthyphantes* sp.	
Lep ant	*Lepthyphantes antroniensis*	Schenkel, 1933
Mec mor	*Mecynargus morulus*	O.P.-Cambridge, 1873
Mec pae	*Mecynargus paetulus*	O.P.-Cambridge, 1875
Oed ret	*Oedothorax retusus*	Westring, 1851
Oed sp.	*Oedothorax* sp.	
Ore vag	*Oreonetides vaginatus*	Thorell, 1872
Pel men	*Pelecopsis mengei*	Simon, 1884
Poe var	*Poeciloneta variegata*	Blackwall, 1841 - Formerly P. globosa (Wider, 1834).
Sco eva	*Scotinotylus evansi*	O.P.-Cambridge, 1894
Ten ten	*Tenuiphantes tenebricola*	Wider, 1834- Formerly Lepthyphantes t. (see Saaristo & Tanasevitch 1996).
Tis aes	*Tiso aestivus*	L.Koch, 1872
Wal kap	*Walckenaeria karpinskii*	(O.P.-Cambridge, 1873)
	Lycosidae	
Alo acu	Alopecosa aculeate	Clerck, 1757
Arc alp	Arctosa alpigena	Doleschall, 1852 - Formerly Tricca a. (see Dondale & Redner 1983).
Par hyp	*Pardosa hyperborea*	Thorell, 1872
Par pal	*Pardosa paludicola*	Clerck, 1757
Par sep	*Pardosa septentrionalis*	Westring, 1861
Par tra	*Pardosa trailli*	O. P.-Cambridge, 1873
Ten fla	Tenuiphantes flavipes	Blackwall, 1854 - Formerly Lepthyphantes f. (see Sdaaristo & Tanasevitch 1996).
	Gnaphosidae	
Gna lep	*Gnaphosa leporina*	

Mic alp	*Micaria alpina*	L. Koch, 1872
	Thomisidae	
Ozy arc	*Ozyptila arctica*	Kulczynski, 1908