The influence of terrain age and altitude on the arthropod communities found on recently deglaciated terrain

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Abstract Climate warming has been more pronounced in the Arctic than elsewhere, resulting in a recent rapid glacial retreat. Over 85% of the Ålmajallojekna glacier has disappeared over the last 115 years and it is one of the fastest retreating glaciers in Sweden. In 2011 and 2012, at 18 sites in the vicinity of the remaining glacier network, we sampled arthropods and related the species richness, abundance and proportion of herbivores to altitude (ranging from 824 to 1,524 m.a.s.l.) and the age of the site (ranging from 0 to >115 years). Temperature was measured at six sites and the average annual air temperature ranged from -3.7°C to 1.1°C. In total, we recorded 3,705 arthropods from 117 species in nine different taxonomic groups. The most abundant and species-rich group was Coleoptera (1,381 individuals, 41 species) followed by Araneae (1,050 individuals, 15 species) and Macrolepidoptera (732 individuals, 17 species). Only at lower altitudes did the abundance and species richness of arthropods increase with increasing age of the site. The results were consistent among the studied taxonomic groups and when controlling for sampling intensity using two different approaches. The proportion of herbivores decreased with increasing age of the site and with increasing altitude. Clearly, altitude appears more important than the age of the site and, at higher altitudes, abundance, species richness and herbivory are low [*Current Zoology* 60 (2): 203–220, 2014].

Keywords Climate change, Glacier foreland, Emerging communities, Insects and arachnids, Subarctic environment, Species richness

Climate warming is more pronounced in the Arctic than elsewhere, resulting in remarkable alterations in cold-adapted ecosystems and rapid glacial retreat over the last few decades (Solomon et al., 2007). Hence, the Arctic ecosystem is predicted to be especially sensitive to threats from climate change (Dormann and Woodin, 2002; Solomon et al., 2007). Arthropods form a major part of the terrestrial species diversity in the Arctic (Chapin and Körner, 1995). Although arthropods can be regarded as indictors of environmental change since they are sensitive and react particularly quickly to changes in the abiotic environment (Thomas, 2005), few studies have explored arthropod diversity in the Arctic so far (Høye and Forchhammer, 2008; Franzén and Öckinger, 2012; Høye and Sikes, 2013; Rich et al., 2013). This is in sharp contrast to the long-term datasets exploring ecological responses to global change in mid and lower latitude ecosystems (Warren et al., 2001; Betzholtz et al., 2013). Results from lower latitudes show that long-term studies are important in understanding recent changes that have occurred (Asher et al., 2001; Conrad et al.,

2006; Nilsson et al., 2008) and can, in turn, influence politicians with their decision-making. The Arctic harbors a species-poor fauna and flora compared to most other ecosystems (Willig et al., 2003) and therefore it is feasible to identify species from many taxonomic groups within a limited time and realize comparative studies across different taxonomic groups. That would not be possible in more species-rich ecosystems.

Glacial retreat implies that potential new habitats become available. Thus, former ice-covered areas provide a unique opportunity to study the establishment of novel cold-adapted communities. In this respect, several studies have focused on the colonization processes of plant species on glacier forelands and the emergence of novel plant communities (Tscherko et al., 2005; Moreau et al., 2008; Mori et al., 2008). In contrast to plants, arthropod communities have been neglected in this context (Janetschek, 1949; Kaufmann et al., 2004; Nagy and Grabherr, 2009). Moreover, it became apparent that arthropod communities on deglaciated terrain are complex (Kaufmann, 2001; Hodkinson et al., 2003, 2004).

Despite a recent increasing interest in Arctic ecology (Høye and Sikes, 2013; Post and Høye, 2013), there remains a lack of studies that focus on the emergence, development and establishment of arthropod communities on former glaciated areas. In particular, studies carried out north of the Arctic Circle are extremely rare (Hodkinson et al., 2004; Vater, 2012).

Different mechanisms have been proposed to explain how cold-adapted ecosystems emerge on formerly glaciated areas. Two key abiotic factors are altitude and age of the deglaciated terrain. While altitude determines the temperature gradient (Hodkinson, 2005), the age of the deglaciated terrain reflects how long it has been since the ice disappeared and thus the time the site has been available for colonization (Mori et al., 2008). Specific dispersal capacity and diet play a key role in colonization patterns and the establishment of arthropod populations (Kaufmann, 2001; Coulson et al., 2003; Hodkinson et al., 2003, 2004). Coulson et al. (2003) suggested that wind dispersal is an important mechanism in arthropod community establishment on recently deglaciated terrain. It has been predicted that emerging habitats are colonized by herbivores earlier than by predators because herbivores are predated by predators that often have larger area requirements compared to their prey (Srivastava et al., 2008; Brose et al., 2012). Counterintuitively, recently deglaciated terrain has been found to have a higher proportion of predators compared to older sites (Kaufmann, 2001; Coulson, 2013).

In this study, we examined the emergence, development and establishment of cold-adapted arthropod communities in the deglaciated terrain surrounding the Ålmajallojekna glacier in northern Sweden. The Ålmajallojekna glacier was the largest glacier in Sweden when it was first explored in 1898 (Westman, 1898). In 2013, its surface was less than 10 % of its size measured in 1898. This rapidly melting glacier is hence suitable for exploring patterns between species richness and abundance of arthropods and the two abiotic key parameters age of deglaciated terrain and altitude. We expected species richness, abundance and the proportion of herbivores to decrease with increasing altitude and to increase with increasing age of the site. To test our hypothesis, we sampled nine arthropod taxa at 18 sites, over two consecutive years, ranging in age from zero to over 115 years and in altitude from 824 m a.s.l. to 1,524 m a.s.l.

1 Material and Methods

1.1 Study area

This study was conducted in the glacier forelands of the Ålmajallojekna glacier (N67°16'25.25, E16°22'45.41). It is located in the northern part of the Scandes (Scandinavian mountain range), north of the Arctic Circle in the Padjelanta National Park (Fig. 1, Supplementary Material Fig. S2). The climate across the Padjelanta National Park area is strongly influenced by Atlantic winds, giving it a maritime climate (Hamberg, 1915; Tengwall, 1920). From the Ålmajallojekna glacier, the closest fjord in Norway is only 35 km away and, thus, relatively warm and moist winds from Norway reach the study area. The growing season is limited to the period from mid-June to the end of August, often characterized by high precipitation. Occasionally, large areas are still covered by snow in July, as happened in 2012. Due to its unique landscape and its rich flora and fauna, including a few species within Scandinavia restricted to this location (Von Sydow, 1983), the national park forms a part of the UNESCO World Heritage site Laponia, covering > 9 000 km^2. There are three glaciers (each with a size of > 0.5 km^2) in the park, of which the Ålmajallojekna is the largest one. The Ålmajallojekna and its forelands nestle in a typical alpine landscape dominated by rocks and mountain heathlands (Selander, 1950).

1.2 Characterization of the Ålmajallojekna and survey of its retreat

Westman (1898) was the first to describe thoroughly the study area, mapping the glacier extent and estab-
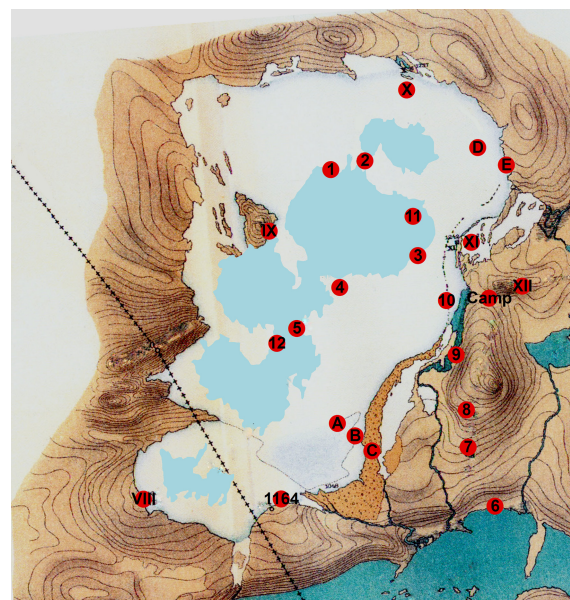

Fig. 1   The map drawn by Westman (1898) with the sites studied in red
Numbers/Letters of sites correspond to those in Table 1. White represents the glacial extent in 1898, while light blue showing the glacial extent in 2009.

lishing reference cairns that are still present (Supplementary Material Fig. S3). In 1898, the glacier covered an area of about 22 km², since then, it has continuously retreated, covering an area of 2.8 km² in 2013 (Fig. 1). As a result of this glacial retreat, rocky habitats completely lacking soil and primary vegetation, rivers and lakes have been created in the former glaciated area. As the Ålmajallojekna is a glacial network, it melts over a large area of varying altitudes and, thus, it does not belong to the more well-studied type of glacier, with a melting ice tongue that leaves a well-defined chronosequence behind (Kaufmann, 2001; Hodkinson et al., 2003; Mori et al., 2008; Albrecht et al., 2010).

The glacial retreat was measured by analyzing maps (1898), aerial photographs (1957/58 and 1980) and SPOT-5 satellite images (2008 to 2013). Based on the glacial cover, we estimated the year when land was revealed under the glacier and classified the glacier foreland into four age classes: i) the area had been deglaciated for 0 – 40 years, ii) the area had been deglaciated for 41 – 90 years, iii) the area had been deglaciated for 91 – 115 years and iv) the area had been deglaciated for more than 115 years. The age class >115 years contained sites that were completely outside the area that was covered by ice in 1898. Drawings and daily notes from an expedition in the area in 1806 indicate that the glacier covered all the sites studied at that time (Wahlenberg, 1808), but more detailed information about the glacial extent at this time is not available.

1.3 Microclimate in the study area

As there is no meteorological station situated close to the study area and temperature (maximum, minimum and variability) is one of the most important factors influencing arthropod distributions (Mellanby, 1939; Høye and Forchhammer, 2008; Coulson, 2013), we decided to measure the local temperature at six representative sites (Fig. 1, Table 1). We used Thermochron iButtons® DS1922L (Dallas Maxim), with an accuracy of 0.1°C, to record the temperature every 68 minutes (due to memory limitations of the iButton), from 25 July 2011 to 8 August 2012. At each of the six sites, we placed iButtons at three different heights: (i) ground level (0 cm), (ii) 10 cm and (iii) 30 cm above ground. We fixed the loggers close to the bottom of tubes from which we had cut away the bottom so that the logger was directly exposed to the air. Three iButtons were damaged; consequently, we were unable to extract any data from them. These were located at site XI (30 cm) and site VIII (0 and 10 cm).

1.4 Arthropod sampling

We sampled arthropods from nine taxonomic groups at the 18 sites. Each site consisted of an area covering 30 m x 30 m (Table 1, Supplementary Material Fig. S4). The sites ranged in altitude from 824 m a.s.l. to 1 524 m a.s.l. (Fig. 1, Table 1). Fourteen sites (1–5, 9, 10, A, B, C, D, E, Camp, XI) were scattered across the four age classes of the glacier foreland, with the remaining four sites (6, 7, 8, IX) situated beyond the 1898 terminus of the glacier, including one nunatak (Fig. 1, Table 1). In each age class, we tried to spread the sites across as many different altitudes as possible (Table 1). At each site, pan traps of two different sizes (50 cm × 20 cm × 15 cm) and yellow traps (30 cm × 20 cm ×6 cm) and flight interception traps with the same size as the yellow traps and pitfall traps, which were not covered over, had a diameter of 7 cm and a depth of 10 cm. At each site, except the Camp site, 12 pan traps (six yellow, three blue and three white), two flight interception traps and 12 pitfall traps, with detergent and 30% propylene glycol added, were put out. At the Camp site, we used additionally 12 pan traps (4 yellow, 4 white and 4 blue, size 30 cm × 20 cm × 6 cm) to be able to evaluate the impact of the number of traps on the number of species and individuals caught. The interception traps were baited with 50 gr. rotten herring to attract more arthropods. This combination of different trap types allowed us to catch a wide variety of species from different taxonomic groups (Westphal et al., 2008; Vater, 2012). The traps were running from 12 July 2011 to 4 August 2011 and from 1 August 2012 to 17 August 2012. Eleven sites were surveyed in 2011 and, in 2012, an additional seven sites were surveyed (Table 1). In both field seasons, the traps were emptied every 10 days. In 2012, the season was delayed because of cold weather (due to a late snowmelt and low temperatures), so the trapping time was adjusted to this and occurred about 2 weeks later compared with 2011. Some of the traps did not work as expected. In particular, traps at the younger sites (with low vegetation cover, no well- developed soils and a coarse substrate), especially close to the recently formed glacier edge were more frequently out of order due to flooding and disturbance from moving ice, snow and rocks.

Thus, only trapping periods with fully functional traps were included in the analyses. Therefore, we calculated the total number of trapping days at each site by multiplying the number of traps used with the number of days they had been in operation. The collected arthropod samples were stored in ethanol (70%) until they were sorted and identified. All spiders (Araneae), beetles (Coleoptera), Diptera (Syrphidae and Tabanidae), stinging wasps (Hymenoptera-Apoidaeae), bugs (Hete-

roptera and Homoptera), scorpion flies (Mecoptera), grasshoppers (Ortoptera), butterflies and moths (Lepidoptera) and caddisflies (Trichoptera) were identified to species level by experts in the respective family. For other taxonomic groups we could not find experts for identification. Each species was classified as either herbivore or predator, based on existing literature and expert opinions (M. Franzén unpublished data). The systematic classification and names followed the dyntaxa database (www.dyntaxa.se). Samples and specimens can be found in the Museum of Zoology at Lund University, Sweden, and in the private collection of Markus Franzén.

1.5 Statistical analyses

In order to test our hypothesis, we carried out three different analyses. First, we related observed species richness and abundance (as response variables) of arthropods to the four predictor variables age of deglaciated terrain, altitude, taxonomic group and the number of trapping days using a generalized linear mixed effects model (GLMM) with a Poisson error distribution and the log link function. Interaction terms were included and, to account for different potential responses of the different taxonomic groups, we allowed random intercepts and slopes for each taxonomic group. In addition, we included the number of trapping days as a covariate to account for trapping efficiency. Due to overdispersion, we controlled individual-level variability in the random structure (Gelman and Hill, 2007). In the statistical analyses, taxonomic group consisted of the six groups: Araneae, Coleoptera, Diptera, Hymenoptera, Lepidoptera and other (including pooled data from bugs, scorpion flies, grasshoppers and caddisflies due to their low numbers). Taxonomic group was not significant in any interactions and was removed from the analysis, because we were only interested in exploring if any of the taxonomic groups showed a contradictory pattern to the age of the site or the altitude. Second, to explore the reliability and robustness of our results, we estimated the total species richness at each of the 18 sites using the non-parametric first-order Jackknife estimation method using EstimateS (Colwell, 2007). The basic idea behind the jackknife estimator lies in systematically re-computing the statistic estimate leaving out one observation at a time from the sample set. We then used the estimated species richness as the response variable in a generalized linear model (GLM) against the predictor variables altitude and age of deglaciated terrain and their interaction. Third, we analyzed the proportion of herbivores against the age of deglaciated terrain, altitude and the number of trapping days as well as their interactions in a GLM. Temperature was correlated to altitude and thus not possible to include in the statistical models (Supplementary Material Fig. S1). Model selection was based on minimizing the second-order Akaike Information Criterion (AIC). The statistical analyses were performed using the R software environment version 3.0.2 (R Development Core Team, 2011).

2 Results

2.1 Temperatures

The yearly average temperature (from 25 July 2011 to 24 July 2012 at 30 cm above ground level) across the six sites ranged from -3.7°C to 1.1°C (Table 1). Daily average temperatures ranged from 10° to -22°C. Daily mean temperatures above 0° were mainly present from June to September, but above-zero daily averages also occurred until January at two sites (Camp site and site 3). The coldest day in the study area was 5 February 2012 with a daily minimum temperature close to -25°C. This was the only day with a temperature below -20°C in the study area. Temperatures below -20°C were only recorded at the wind-exposed sites XI and VIII. Maximum temperatures of 37°C were recorded at Camp site and site XI (clearly a result of sun-exposed loggers), whereas daily maximum temperatures ranged from 16°C to 18°C at the remaining sites. Over one day, an extreme variation in temperatures was common. For instance, on 18 September 2011 at site IX (0 cm height), temperatures increased from below zero to 19°C and then back to temperatures close to zero in the evening. On 8 July 2012 at the Camp site (30 cm height), the temperature increased from subzero temperatures to 36 °C and then back to temperatures around zero in the evening. The highest temperature difference in one hour also happened on 8 July 2012, with a temperature difference of 10°C between 05:00 and 06:00 AM.

2.2 Arthropods

In total, we found 3,704 individuals, representing 117 species (Table 2, Table S1). The most abundant and species-rich group was beetles (1,381 individuals, 41 species) followed by spiders (1,050 individuals, 15 species) and butterflies and moths (732 individuals, 17 species) (Fig. 2). The most abundant species was the harvestman *Mitopus morio* with 620 individuals followed by the burnet moth *Zygaena exulans* with 371 individuals and the beetle *Gonioctena arctica* with 286 individuals. The species occupying most sites were *Zygaena exulans* (16 sites), *M. morio* (15 sites), the butter-

Table 1   Characteristics of the studied sites

Site code[a]	Altitude[b]	Age class[c]	Temperature[d]	Trapping year	Total trapping days[e]	Number of species[f]	Estimated number of species (sd)[g]	Number of arthropod individuals[h]	Proportion of herbivores (%)	Cairn[i]	Latitude	Longitude
1	1 344	1		2011, 2012	700	15	26 (± 5.66)	26	47		N67°16.962'	E16°22.895'
2	1 305	1		2011, 2012	364	10	15 (± 3.99)	17	70		N67°17.027'	E16°23.569'
3	1 208	1	-1.01	2011, 2012	700	17	27 (± 5.29)	28	81	2011	N67°16.301'	E16°24.593'
4	1 254	1		2011, 2012	700	15	25 (± 3.71)	24	60		N67°16.063'	E16°23.052'
5	1 180	1		2011, 2012	532	20	33 (± 8.51)	333	55		N67°15.755'	E16°22.196'
6	824	4		2011, 2012	1 148	57	85 (± 9.90)	380	63		N67°14.387'	E16°26.059'
7	947	4		2011, 2012	1 092	34	46 (± 3.24)	606	57		N67°14.838'	E16°25.542'
8	1 087	4		2011, 2012	1 036	38	59 (± 10.3)	221	47		N67°15.123'	E16°25.517'
9	1 141	3		2011, 2012	952	22	30 (± 6.29)	193	50		N67°15.542'	E16°25.325'
10	1 166	2		2011, 2012	1 232	35	43 (± 7.07)	491	59		N67°15.956'	E16°25.146'
11	1 212		-1.61							2011	N67°16.601'	E16°24.505'
12	1 177									2011	N67°15.643'	E16°21.805'
A	1 102	2		2012	280	16	23 (± 7.50)	58	64		N67°15.028'	E16°22.978'
B	1 041	2		2012	280	20	24 (± 9.01)	113	54		N67°14.932'	E16°23.323'
C	1 008	3		2012	280	23	29 (± 9.75)	207	57		N67°14.817'	E16°23.654'
D	1 082	2		2012	280	15	34 (± 6.75)	47	43		N67°17.120'	E16°25.791'
E	1 023	3		2012	280	18	22 (± 3.75)	158	67		N67°16.984'	E16°26.351'
IX	1 524	4	-3.73	2012	280	8	11 (± 2.50)	18	17	1898	N67°16.498'	E16°21.672'
Camp	1 156	3	1.12	2011, 2012	1 600	40	55 (± 5.88)	580	54		N67°15.971'	E16°25.984'
XI	1 222	3	-1.47	2012	280	18	23 (± 5.25)	205	50	1898	N67°16.399'	E16°25.647'
VIII	1 398		-2.90							1898	N67°14.465'	E16°29.158'
1164	1 156									1898	N67°14.458'	E16°21.861'
XII	1 207									1898	N67°16.061'	E16°26.641'
X	1 221									1898	N67°17.563'	E16°24.402'

[a] IX, XI, VIII, 1164, XII, X refer to site codes used by Westman (1898), numbers to sites studied in 2011 and letters to sites studied in 2012. [b] Altitude in m.a.s.l. [c] The estimated age of the site 1: 0 – 40 years; 2: 41– 90 years; 3: 91– 115 years and 4 >115 years. [d] The average temperature in °C from 25 July 2011 to 24 July 2012 using data from temperature loggers at 30 cm above ground level recording temperature every 68 minutes. [e] The total number trapping days calculated as the number of traps x the number of days in the field. [f] Species richness and abundance of arthropods from 2011 and/or 2012. [g] Estimated first-order Jackknife species richness and standard deviation in brackets. [h] Total number of individuals caught. [i] The year of cairn establishment.

Table 2   The number of individuals of each arthropod species caught, the number of sites occupied, their main feeding strategy (herbivore or predator) and the trap type they were collected in. Species are sorted alphabetically in each taxonomic group. For information about which sites each species occured on see Table S1.

Taxonomic group	Family	Species name	Diet[a]	Individuals[b]	Sites[c]	Trap[d]
ARANEAE	Linyphiidae	*Collinsia holmgreni*	P	12	6	pa,pi
ARANEAE	Linyphiidae	*Erigone arctica*	P	43	10	pa,pi
ARANEAE	Gnaphosidae	*Gnaphosa leporina*	P	81	4	pa,pi,i
ARANEAE	Linyphiidae	*Gonatium rubens*	P	7	3	pa,pi
ARANEAE	Linyphiidae	*Mecynargus paetulus*	P	1	1	pi
ARANEAE	Linyphiidae	*Meioneta nigripes*	P	1	1	pa
ARANEAE	Gnaphosidae	*Micaria alpina*	P	28	6	pa,pi
ARANEAE	Phalangiidae	*Mitopus morio*	P	620	15	pa,pi,i
ARANEAE	Linyphiidae	*Oedothorax retusus*	P	13	5	pi
ARANEAE	Linyphiidae	*Oreoneta sinuosa*	P	11	6	pi
ARANEAE	Linyphiidae	*Oreonetides vaginatus*	P	1	1	pi
ARANEAE	Lycosidae	*Pardosa eiseni*	P	34	4	pa,pi
ARANEAE	Lycosidae	*Pardosa palustris*	P	195	7	pa,pi,i
ARANEAE	Linyphiidae	*Pelecopsis mengei*	P	1	1	pi
ARANEAE	Linyphiidae	*Tiso aestivus*	P	2	2	pa,pi
COLEOPTERA	Byrrhidae	*Byrrhus arietinus*	H	3	2	pi
COLEOPTERA	Byrrhidae	*Byrrhus pilula*	H	5	3	pi,i
COLEOPTERA	Byrrhidae	*Simplocaria metallica*	H	3	2	pi
COLEOPTERA	Cantharidae	*Absidia schoenherri*	P	22	1	pa,pi,i
COLEOPTERA	Carabidae	*Amara alpina*	H	124	9	pa,pi,i
COLEOPTERA	Carabidae	*Amara bifrons*	H	24	4	pa,pi
COLEOPTERA	Carabidae	*Amara praetermissa*	H	6	2	pa,pi
COLEOPTERA	Carabidae	*Amara quenseli*	H	19	2	pa,pi
COLEOPTERA	Carabidae	*Bembidion hastii*	P	7	2	pi
COLEOPTERA	Carabidae	*Carabus violaceus*	P	4	1	pa
COLEOPTERA	Carabidae	*Cymindis vaporariorum*	P	5	3	pa,pi
COLEOPTERA	Carabidae	*Miscodera arctica*	P	8	3	pa,pi
COLEOPTERA	Carabidae	*Nebria nivalis*	P	23	6	pa,pi,i
COLEOPTERA	Carabidae	*Nebria rufescens*	P	27	10	pa,pi
COLEOPTERA	Carabidae	*Notiophilus aquaticus*	P	52	9	pa,pi,i
COLEOPTERA	Carabidae	*Patrobus assimilis*	P	15	2	pi,i
COLEOPTERA	Chrysomelidae	*Gonioctena arctica*	H	286	6	pa,pi,i
COLEOPTERA	Chrysomelidae	*Phratora polaris*	H	96	10	pa,pi,i
COLEOPTERA	Coccinellidae	*Psyllobora vigintiduopunctata*	P	1	1	pa
COLEOPTERA	Dytiscidae	*Agabus thomsoni/lapponicus*	P	2	2	pi
COLEOPTERA	Hydrophilidae	*Helophorus glacialis*	H	3	3	pi
COLEOPTERA	Leiodidae	*Catops alpinus*	P	11	4	pa,pi,i
COLEOPTERA	Nitidulidae	*Meligethes aeneus*	H	1	1	pi
COLEOPTERA	Scarabaeidae	*Aphodius lapponum*	P	38	4	pa,pi,i
COLEOPTERA	Silphidae	*Nicrophorus vespilloides*	P	1	1	pa
COLEOPTERA	Silphidae	*Thanatophilus lapponicus*	P	184	12	pa,pi,i
COLEOPTERA	Silphidae	*Thanatophilus rugosus*	P	1	1	pa
COLEOPTERA	Staphylinidae	*Acidota crenata*	P	1	1	pa
COLEOPTERA	Staphylinidae	*Anthophagus alpinus*	P	100	9	pa,pi,i

Continued Table 2

Taxonomic group	Family	Species name	Diet[a]	Individuals[b]	Sites[c]	Trap[d]
COLEOPTERA	Staphylinidae	*Arpedium quadrum*	P	3	2	pa,pi
COLEOPTERA	Staphylinidae	*Atheta allocera*	P	1	1	pi
COLEOPTERA	Staphylinidae	*Atheta parapicipennis*	P	1	1	pi
COLEOPTERA	Staphylinidae	*Boreaphilus henningianus*	P	2	1	pi
COLEOPTERA	Staphylinidae	*Cephalocousya nivicola*	P	1	1	pi
COLEOPTERA	Staphylinidae	*Coryphiomorphus hyperboreus*	P	1	1	i
COLEOPTERA	Staphylinidae	*Eucnecosum brachypterum*	P	6	1	pi
COLEOPTERA	Staphylinidae	*Geodromicus longipes*	P	261	11	pa,pi
COLEOPTERA	Staphylinidae	*Olophrum boreale*	P	8	5	pa,pi,i
COLEOPTERA	Staphylinidae	*Philhygra sp*	P	1	1	pi
COLEOPTERA	Staphylinidae	*Staphylinus erythropterus*	P	3	2	pa,i
COLEOPTERA	Staphylinidae	*Tachinus elongatus*	P	21	8	pa,pi,i
DIPTERA	Syrphidae	*Dasysyrphus pinastri*	H	3	3	pa
DIPTERA	Syrphidae	*Dasysyrphus tricincta*	H	1	1	pa
DIPTERA	Syrphidae	*Dasysyrphus venustus*	H	2	2	pa,i
DIPTERA	Syrphidae	*Eupeodes corollae*	H	1	1	pa
DIPTERA	Syrphidae	*Eupeodes lapponicus*	H	1	1	pa
DIPTERA	Syrphidae	*Eupeodes latifasciatus*	H	4	2	pa,pi
DIPTERA	Syrphidae	*Helophilus lapponicus*	H	1	1	pa
DIPTERA	Syrphidae	*Leocozona lucorum*	H	1	1	pa
DIPTERA	Syrphidae	*Melanostoma dubium*	H	3	1	pa,i
DIPTERA	Syrphidae	*Melanostoma scalare*	H	2	2	pa
DIPTERA	Syrphidae	*Orthonevra stackelbergi*	H	1	1	pa
DIPTERA	Syrphidae	*Parasyrphus lineolus*	H	4	3	pa,i
DIPTERA	Syrphidae	*Parasyrphus malinellus*	H	1	1	pa
DIPTERA	Syrphidae	*Platycheirus albimanus*	H	1	1	pa
DIPTERA	Syrphidae	*Platycheirus manicatus*	H	8	6	pa,i
DIPTERA	Syrphidae	*Platycheirus nigrofemoratus*	H	1	1	i
DIPTERA	Syrphidae	*Platycheirus subordinatus ?*	H	1	1	i
DIPTERA	Syrphidae	*Platycheirus transfugus*	H	1	1	i
DIPTERA	Syrphidae	*Scellus spinimanus*	H	14	1	pi
DIPTERA	Syrphidae	*Sphaerophoria fatarum*	H	1	1	i
DIPTERA	Syrphidae	*Syrphus ribesii*	H	4	1	i
DIPTERA	Syrphidae	*Syrphus torvus*	H	10	7	pa,pi,i
DIPTERA	Tabanidae	*Hybomitra astuta (syn. polaris).*	H	3	1	pa
DIPTERA	Tabanidae	*Hybomitra nigricornis*	H	3	2	pa,i
HETEROPTERA	Saldidae	*Salda sahlbergi*	H	1	1	pi
HOMOPTERA	Cicadellidae	*Rosenius laciniatus*	H	3	1	pi
HOMOPTERA	Cicadellidae	*Verdanus limbatellus*	H	4	1	pi
HYMENOPTERA	Apidae	*Bombus alpinus*	H	25	12	pa
HYMENOPTERA	Apidae	*Bombus flavidus*	H	1	1	pa,i
HYMENOPTERA	Apidae	*Bombus hyperboreus*	H	3	3	pa
HYMENOPTERA	Apidae	*Bombus jonellus*	H	2	2	pa,i
HYMENOPTERA	Apidae	*Bombus lapponicus*	H	17	7	i
HYMENOPTERA	Apidae	*Bombus monticola*	H	15	11	pa,pi,i
HYMENOPTERA	Apidae	*Bombus polaris*	H	8	6	pa,pi,i

Continued Table 2

Taxonomic group	Family	Species name	Diet[a]	Individuals[b]	Sites[c]	Trap[d]
HYMENOPTERA	Apidae	*Bombus soroeensis*	H	1	1	pa,i
HYMENOPTERA	Apidae	*Bombus sporadicus*	H	2	2	pa
HYMENOPTERA	Formicidae	*Formica sp.*	P	1	1	pa
HYMENOPTERA	Popmpilidae	*Anoplius tenuicornis*	P	1	1	pa
HYMENOPTERA	Vespidae	*Dolichovespula norvegica*	P	2	1	pa
LEPIDOPTERA	Geometridae	*Entephria polata*	H	2	1	pa
LEPIDOPTERA	Geometridae	*Entephria punctipes*	H	2	2	pa
LEPIDOPTERA	Geometridae	*Glacies coracina*	H	36	8	pa,i
LEPIDOPTERA	Geometridae	*Pygmaena fusca*	H	39	7	pa,pi,i
LEPIDOPTERA	Geometridae	*Xanthorhoe decoloraria*	H	9	3	pa,pi
LEPIDOPTERA	Noctuidae	*Discestra melanopa*	H	7	6	pa
LEPIDOPTERA	Noctuidae	*Lasionycta staudingeri*	H	15	7	pa,pi
LEPIDOPTERA	Noctuidae	*Polia richardsoni*	H	1	1	pa
LEPIDOPTERA	Noctuidae	*Sympistis lapponica*	H	3	2	pa
LEPIDOPTERA	Noctuidae	*Sympistis nigrita*	H	6	5	pa,pi
LEPIDOPTERA	Noctuidae	*Xestia alpicola*	H	1	1	pa
LEPIDOPTERA	Nymphalidae	*Boloria napaea*	H	215	14	pa,pi,i
LEPIDOPTERA	Nymphalidae	*Erebia pandrose*	H	10	4	pa,pi,i
LEPIDOPTERA	Pieridae	*Colias tyche*	H	3	1	i
LEPIDOPTERA	Pyralidae	*Catoptria furcatellus*	H	11	5	pa
LEPIDOPTERA	Pyralidae	*Eudonia alpina*	H	1	1	pa
LEPIDOPTERA	Zygaenidae	*Zygaena exulans*	H	371	16	pa,pi,i
MECOPTERA	Boreidae	*Boreus westwoodi*	H	232	6	pa,pi
ORTHOPTERA	Acrididae	*Melanoplus frigidus*	H	20	3	pa,pi,i
TRICHOPTERA	Limnephilidae	*Apatania zonella*	-	74	5	pa,i
TRICHOPTERA	Limnephilidae	*Asynarchus lapponicus*	-	16	3	pa,i
TRICHOPTERA	Limnephilidae	*Limnephilus coenosus*	-	40	3	pa,i
		Total number of inividuals		3703	18	
		Total species richness		117	18	

[a] Diet type, predator (P), herbivore (H). [b] Number of individuals. [c] Number of sites occupied. [d] Collected in trap type, pan trap (pa), pitfall (pi), intersection trap (i).
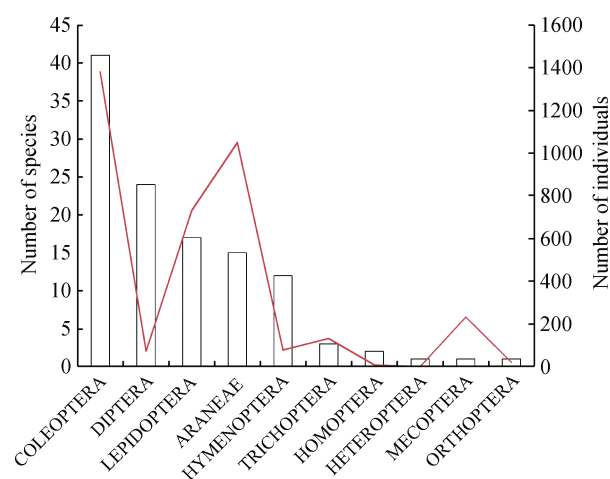

Fig. 2   Abundance and species richness of the different taxonomic groups
Bars represent species richness (left axis) and the line abundance (right axis). In the statistical analyses Trichoptera, Homoptera, Heteroptera, Mecoptera and Orthoptera were pooled together.

fly *Boloria napaea* (14 sites), the beetle *Thanatophilus lapponicus* (12 sites) and the bumblebee *Bombus alpinus* (12 sites). Forty eight species (41%) were only found at one site and 34 species (28%) were only represented by one individual specimen. The number of observed species per site ranged from eight (site IX) to 57 (site 6), the estimated species richness ranged from 11 (site IX) to 85 (site 6), and the number of individuals per site ranged from 17 (site 2) to 606 (site 7) (Fig. 3).

In total, 20 species were recorded at the youngest sites (0–40 years) increasing to 77 species at sites >115 years. The abundance showed a similar pattern with 333 individuals at the lowest aged sites increasing to 1,343 individuals at sites aged 91–115 years.

At higher altitudes, the estimated species richness and abundance were not influenced by the age of the site in contrast to lower altitudes, where abundance increased with increasing age of the site (Fig. 4). This was
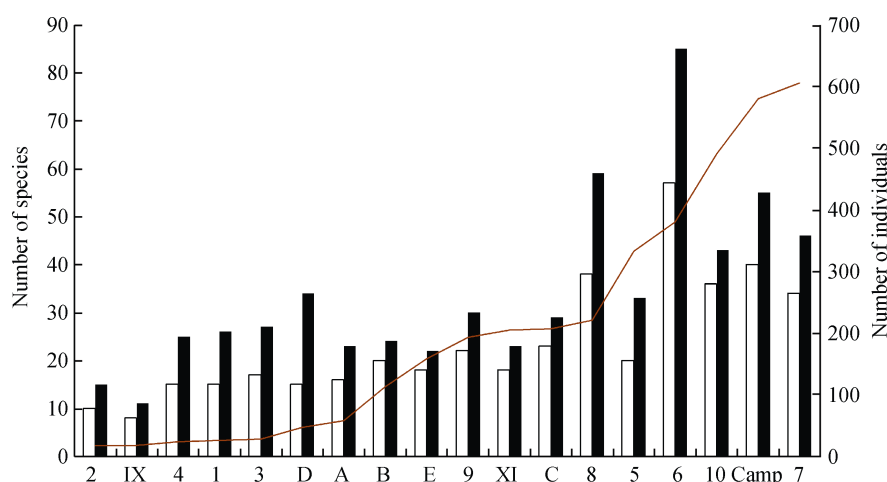
Fig. 3   Abundance (line), observed (open bars) and estimated (filled bars) species richness per site
Bars represent species richness (left axis) and the line abundance (right axis).
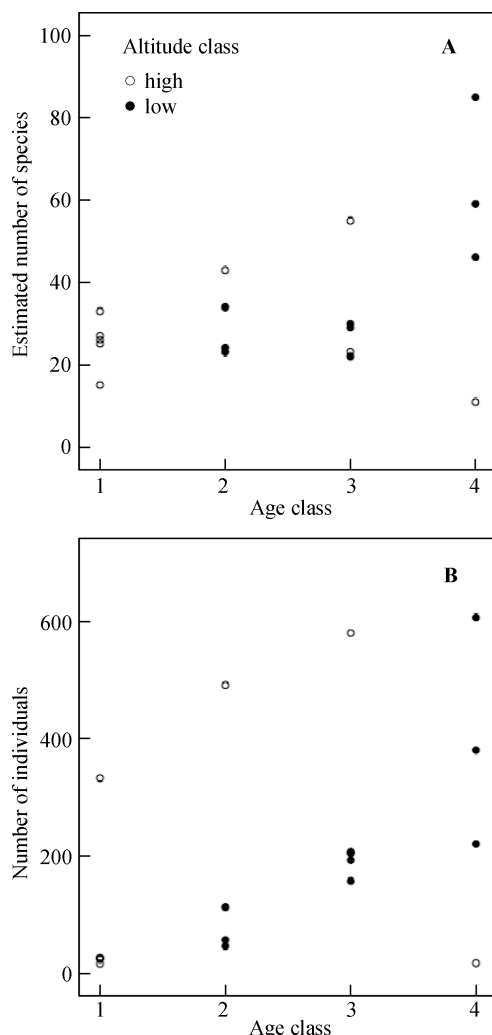

Fig. 4   (A) The interaction between age and altitude. At lower altitudes, abundance increased with increasing age. (B) The same pattern for estimated species richness

Higher altitudes are defined as sites situated >1,175 m a.s.l. and denoted by open circles. Filled dots represent low altitude sites below 1,175 m a.s.l..

evident from the significant interaction term between age and abundance and estimated species richness in the statistical analysis (Table 3). Observed species richness (controlled for sampling intensity) decreased with increasing altitude, but was not related to the age of the sites (Table 3). The six taxonomic groups responded in a similar way to the age of the site and altitude. The proportion of herbivores ranged from 17% to 81% and decreased with increasing age of glaciated terrain and with decreasing altitude (Fig. 5, Table 1). Both species richness and abundance increased with sampling intensity (Table 1).

3   Discussion

It is rare that effects of age of deglaciated terrain and altitude are tested simultaneously on communities of glacier forelands because these parameters are normally correlated since most glaciers studied melt from lower altitudes (old sites) to higher altitudes (young sites), giving rise to the typical chronosequence (Kaufmann, 2001; Hodkinson et al., 2003; Mori et al., 2008; Vater, 2012). Due to the glacier type (glacier network), our study area is unique since the Ålmajallojekna is currently melting at different altitudes and the highest site is, in fact, a nunatak, ice-free for at least 115 years. Arthropods were found at all surveyed sites, even at the youngest sites that have only been free from ice for a few years ago as well as at the highest site – the nunatak. This suggests a high mobility and thus a rapid colonization ability among many arthropod species over the distances examined in this study. Many of these species, such as the harvestman *Mitopus morio*, the beetle *Phratora polaris* and the bumble bee *Bombus alpinus,* are important for the ecosystem and belong to, respec-

tively, the functional groups decomposer, predator and pollinator (Hodkinson et al., 2004; Albrecht et al., 2010; Vater, 2012). The results of recent studies of deglaciated terrain suggest that arthropods are a more important factor in succession than it is apparent from previous vegetation studies. Moreover, it is assumed that invertebrates facilitate plant succession by providing the initial nutrients on recently exposed terrain (Kaufmann, 2002; Kaufmann et al., 2002). The importance of aboveground–belowground interactions in long-term ecosystem development on glacier forelands has also been shown by Bardgett et al. (2005). Albrecht et al. (2010) identified complex interactions between plants and their pollinating insects during succession and discovered that flower visitors are important for the fruit set of many plant species.

Arthropod abundance and estimated species richness increased with increasing age only at lower altitudes. This could be an effect of the higher temperatures at lower altitudes increasing the chances of arthropods surviving and establishing higher local population densities there. At higher altitudes, the temperature might be too low to establish local populations and we found no significant influence of the age of the site at higher altitudes. Clearly, at higher altitudes, lower temperatures, longer periods of snow and ice cover, stronger winds and lack of vegetation make it more difficult to establish reproducing populations (Thomas et al., 1994; Hodkinson et al., 1998; Hoiss et al., 2012). Arthropods

appear to try to colonize areas at higher altitudes, but the harsh environment might limit their population growth (Mellanby, 1939). The results for both abundance and species richness did not change when we removed the nunatak from the statistical analyses; it can be seen as an outlier since it was situated at a high altitude and belongs to the oldest age class (> 115 years). Further, our result for abundance and species richness was robust among the six taxonomic groups. This suggests that the taxonomic groups respond in a similar way to age and altitude even if the species among the groups have very different life histories. We were not able to classify species-specific characteristics such as mobility or diet specialization for single species because of a lack of knowledge.

In this study, we used the observed number of species and controlled for sampling intensity as well as the applied non-parametric first-order Jackknife method to estimate species richness. The first-order Jackknife method has been consistently ranked among the most precise techniques to estimate species richness (Hellmann and Fowler, 1999). Due to the small sample size of many of the taxonomic groups, we could only use the richness estimation on all taxa pooled on each site. The results remained qualitatively similar, both when analyzing observed richness and controlling for sampling intensity and taxonomic group as well as when we analyzed estimated richness. This suggests that our results are robust. Another sampling issue

Table 3 The best-fitting (lowest AIC) generalized linear mixed effects models (GLMM) (a, b) and generalized linear model (GLM) (c, d), for the relationship between abundance (a), species richness (b), estimated first-order Jackknife species richness (c), and herbivory (d) to age, altitude and the number of trapping days. NA - not included in the model, ns - non-significant

	a			b		
	Abundance			Species richness		
Source	Parameter estimate	z	P	Parameter estimate	z	P
Intercept	7.29	3.40	< 0.001	< 0.001	2.24	0.025
Age	-1.39	-2.33	0.020	ns	ns	ns
Altitude	-0.01	-3.27	0.001	< 0.001	-2.10	0.04
The number of trapping days	0.001	5.38	< 0.001	< 0.001	2.43	0.015
Age*Altitude	0.001	2.52	0.012	ns	ns	ns

	c			d		
	Estimated species richness			Proportion herbivory		
Source	Parameter estimate	z	P	Parameter estimate	z	P
Intercept	-74.6	-0.88	0.39	1.34	6.60	XXX
Age	53.7	2.27	0.04	-0.071	3.42	0.004
Altitude	0.08	1.11	0.28	-0.001	3.41	0.004
The number of trapping days	NA	NA	NA	NA	NA	NA
Age*Altitude	-0.040	-2.11	0.053	ns	ns	ns

might be the traps used: we used interception traps, pitfall traps and pan traps in order to catch a variety of arthropods. Pan traps were used to catch bees and flies, flying insects were caught by interception traps (butterflies, moths and beetles) and ground-living arthropods by pit fall traps (spiders and beetles) (Table 2). Regardless of trap type all specimens were used in the statistical analyses.

The proportion of herbivores decreased with increasing site age and decreased with increasing altitude. This was in agreement with our hypothesis; it takes longer for predators to enter the community because they require herbivores as their prey (Siemann et al., 1999). This pattern is not consistent with other studies that have suggested that predators quickly colonize recently deglaciated terrain. Some predators can be very opportunistic and survive on small amounts of prey as well as on other predators (Kaufmann, 2001; Hodkinson et al., 2004). Moreover, many predators are also good

Fig. 5 **The relationship between (A) the proportion of herbivores and the altitude and B) the proportion of herbivory to the age of the site**

dispersers, either due to ballooning, drifting with the wind or through following the glacier front (Kaufmann, 2001; Ingimarsdóttir et al., 2012; Vater and Matthews, 2013; Ingimarsdóttir et al., 2014). This might potentially explain the high proportion of predators at the nunatak (site XI) and the general pattern of increasing numbers of predators with increasing altitude. Further, the high proportion of predators has been explained by aquatic organisms living on fossil carbon sources (Hågvar and Ohlson, 2013). The nunatak had the highest proportion of predators (six out of eight species) of all studied sites. We observed vagrant insects (e.g. the butterfly *Vanessa atalanta* and some hoverflies) gathered on the nunatak. Presumably, exhausted airborne individuals take a rest here when dispersing or when they are searching for the highest peaks in the landscape to find a mate (hilltopping) (Coulson et al., 2003; Pe'er et al., 2004; Ingimarsdóttir et al., 2013). Predators could take advantage of such temporary food resources at higher altitudes. Our results suggest that predators in general enter sites after herbivores, but also that predators can survive better at higher altitudes probably because they can escape the harsh environment by hiding under stones or in the soil and can also utilize fossil carbon sources. We observed larvae of some species at all the sites, but we were not able to separate reproducing species from occasional ones. This problem should remain constant among the sites and is not expected to vary with age or altitude or between predators or herbivores.

Studies in remote areas are increasingly important in order to understand the impacts of climate change. The major reasons why there are so few studies of arthropods in the Arctic are: *i*) the huge challenges for scientific studies, mainly logistical and weather-related issues; *ii*) unpredictable weather and great climatic variability; *iii*) studies are more costly and more risky than those in more densely populated areas, and *iv*) difficulties concerning sampling of arthropods. Clearly, to collect arthropods in the Arctic, a combination of sampling techniques is required (Hodkinson et al., 2001). In our study, we used for all sites the same set of traps, with exception of the Camp site, so the catch should not differ among the sites due to bias in the sampling, especially since we controlled for sampling intensity in the statistical analyses and thus, reduced potential sampling bias.

Climate can vary greatly between areas in the Swedish mountains. This is best demonstrated in the Abisko area (160 km northeast of the study area), famous for a number of ecological studies, where both one of the
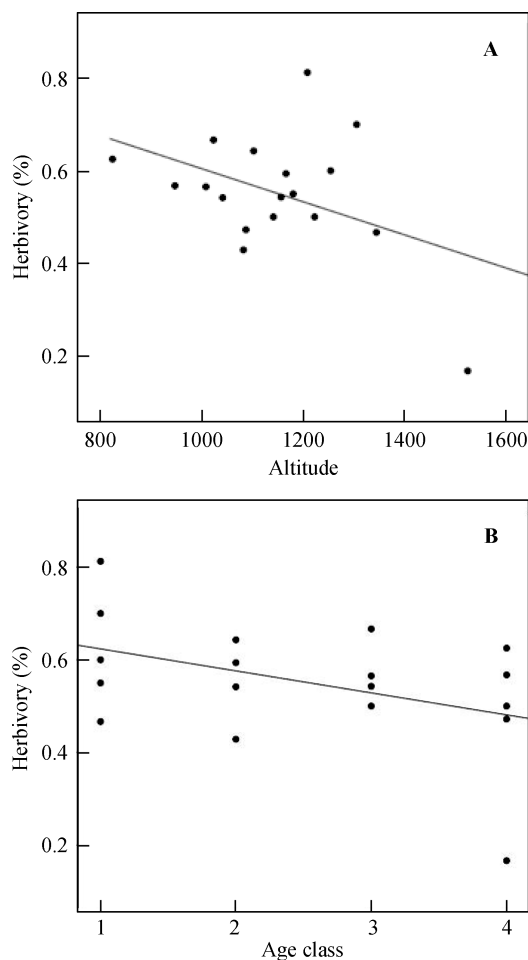
driest and one of the sunniest climates is found in Sweden (Alexandersson, 2002). In contrast, it is only 25 km from Abisko to Riksgränsen, which is one of the sites that receive the most precipitation and the least sun in Sweden. The great variation in climate between closely situated sites might be an explanation for the complexity of the ecological patterns found in mountains, patterns that sometimes contradict each other (Callaghan et al., 2013). This also stresses the importance of carrying out studies in many different mountainous locations to explore if the patterns found are general.

Our temperature data revealed many interesting observations. During the coldest period, extreme temperatures were registered throughout Sweden and, in comparison to the -22°C measured at Ålmajallojekna (Site XI), Kvikkjokk, situated 70 km to the east of the study area, had minimum temperatures between -42°C and -43°C each day from 2 February to 5 February. We were expecting colder days in the study area, but the rather warm temperatures in winter time must have been an effect of the relatively warm and moist winds reaching the area from Norway.

In conclusion, the glacier forelands of the Ålmajallojekna become quickly colonized by arthropods and are a suitable model system to study community composition and colonization processes. The harsh environmental conditions probably limit species' survival and the growth of their populations at higher altitudes, giving no clear relationship between species richness, abundance and the age of the site. Predators are more frequent at young sites as well as at higher altitudes, probably because they can survive on temporarily available food resources such as dispersing insects that do not feed on established vegetation. Our study area is situated in one of the most remote areas in Europe, is protected and experiences very little human influence. This study showed that large changes also occur in landscapes with little or no human influence. The glacier is one of the most rapidly shrinking glaciers in Sweden and is creating new ice-free habitats. In the future, long-term monitoring programs on a wide spectrum of organisms are necessary to improve our understanding of the reaction of the biota to global changes on former glaciated land at different latitudes and in areas experiencing different levels of human impact.

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Supplementary Material

Table S1 **The number of individuals of each arthropod species caught on each site. Sites are sorted by decreasing altitude; species are sorted according to Table 2.**

Species name	1	2	3	4	5	6	7	8	9	10	A	B	C	D	E	Camp	XI	IX
Collinsia holmgreni	1				1			1		2		2	2	4				
Erigone arctica	1	1			4				4	3			4	5	6		16	1
Gnaphosa leporina					39	11	13	18										
Gonatium rubens						1		5								1		
Mecynargus paetulus						1												
Meioneta nigripes					1													
Micaria alpina					5	6		3	3			1				10		
Mitopus morio			1		133	45	39	8	68	83	17	34	30	9	6	82	60	6
Oedothorax retusus					8	2	1	1								1		
Oreoneta sinuosa												1	1	2		2	1	4
Oreonetides vaginatus						1												
Pardosa eiseni									14	13		1				6		
Pardosa palustris					131	7	50	3				1	2			1		
Pelecopsis mengei							1											
Tiso aestivus										1								1
Byrrhus arietinus						2							1					
Byrrhus pilula						3	1			1								
Simplocaria metallica										1				2				
Absidia schoenherri							22											
Amara alpina							24	1	18	17		4	30		11	10	9	
Amara bifrons						11	8	3					2					
Amara praetermissa							5	1										
Amara quenseli						17		2										
Bembidion hastii					2						5							
Carabus violaceus							4											
Cymindis vaporariorum						3	1	1										
Miscodera arctica						5	2	1										
Nebria nivalis	6		6	1	13	1	2			7								
Nebria rufescens	1	4		3	8	1	2	2			3	1	9			1		
Notiophilus aquaticus						4	2	2	5			3	10		3	20	3	
Patrobus assimilis						13	2											
Gonioctena arctica						36	205	15		11			2				17	
Phratora polaris			1		1	4	1		10	2		2	2		37	18	19	
Psyllobora vigintiduopunctata											1							
Agabus thomsoni/lapponicus			1		1					1								
Helophorus glacialis						1	1			1								
Catops alpinus						3			2	3					3			
Meligethes aeneus			1		1													
Aphodius lapponum						24	6	2		6								
Nicrophorus vespilloides							1											
Thanatophilus lapponicus	2		1		3	61	30	12	10	5		6	8	1	45		3	
Thanatophilus rugosus													1					
Acidota crenata									1									

Continued Table S1

Species name	1	2	3	4	5	6	7	8	9	10	A	B	C	D	E	Camp	XI	IX
Anthophagus alpinus		1		1	2	4	2	2	4				1		4	81		
Arpedium quadrum			1	1						2								
Atheta allocera																1		
Atheta parapicipennis									1									
Boreaphilus henningianus																2		
Cephalocousya nivicola																1		
Coryphiomorphus hyper-boreus	1				1													
Eucnecosum brachypterum																6		
Geodromicus longipes						2		2	23	115	14	9	14	5	3	47	27	
Olophrum boreale	1				1					1				2			2	2
Philhygra sp						1												
Staphylinus erythropterus										2							1	
Tachinus elongatus	2				4			1	3					1	7	4	1	
Dasysyrphus pinastri			1		2							1						
Dasysyrphus tricincta					1													
Dasysyrphus venustus						1						1						
Eupeodes corollae			1		1													
Eupeodes lapponicus											1							
Eupeodes latifasciatus			1		1	3												
Helophilus lapponicus	1				1													
Leocozona lucorum											1							
Melanostoma dubium						3												
Melanostoma scalare																	1	1
Orthonevra stackelbergi	1				1													
Parasyrphus lineolus						1					2			1				
Parasyrphus malinellus					1													
Platycheirus albimanus			1		1													
Platycheirus manicatus		1	2		3		1	1		2					1			
Platycheirus nigrofemoratus						1												
Platycheirus subordinatus ?						1												
Platycheirus transfugus	1				1													
Scellus spinimanus							14											
Sphaerophoria fatarum						1												
Syrphus ribesii										4								
Syrphus torvus			3	1	5			1		1	2					1		
Hybomitra astuta (syn. po-laris).			3		3													
Hybomitra nigricornis						2		1										
Salda sahlbergi							1											
Rosenius laciniatus						3												
Verdanus limbatellus							4											
Bombus alpinus	1	4	1	4	11	2		1		1			3	2		4		1
Bombus flavidus																1		
Bombus hyperboreus			1	1	1											1		
Bombus jonellus						1				1								
Bombus lapponicus		2		2	5	1				4	4			3				

Continued Table S1

Species name	1	2	3	4	5	6	7	8	9	10	A	B	C	D	E	Camp	XI	IX
Bombus monticola		1	1	1	4	1		2	1		3		2		1			1
Bombus polaris			1	1	1			1	1						1	3		
Bombus soroeensis			1		1													
Bombus sporadicus		1			1						1							
Formica sp.				1	1													
Anoplius tenuicornis						1												
Dolichovespula norvegica						2												
Entephria polata						2												
Entephria punctipes	1				1					1								
Glacies coracina					1	1				5		2	7		2	14	4	
Pygmaena fusca						4	10	4	1	2			3			15		
Xanthorhoe decoloraria						4	4			1								
Discestra melanopa						1		1	1				1			1	2	
Lasionycta staudingeri			1		1				4		1	1			1	3	4	
Polia richardsoni																1		
Sympistis lapponica		1			1											2		
Sympistis nigrita					1	1		1		1						2		
Xestia alpicola																1		
Boloria napaea			1	3	5	31	18	18	2	102	1	3		2	7	25	1	
Erebia pandrose						2	2	3								3		
Colias tyche						3												
Catoptria furcatellus	1				1	1	2						1			6		
Eudonia alpina						1												
Zygaena exulans	5	1		2	9	41	99	81	1	33	1	10	8	2	12	72		2
Boreus westwoodi								17		32		29	64			56	34	
Melanoplus frigidus						3	16	1										
Apatania zonella						2				6				6	8	52		
Asynarchus lapponicus			2		2					6						10		
Limnephilus coenosus								2		26						12		
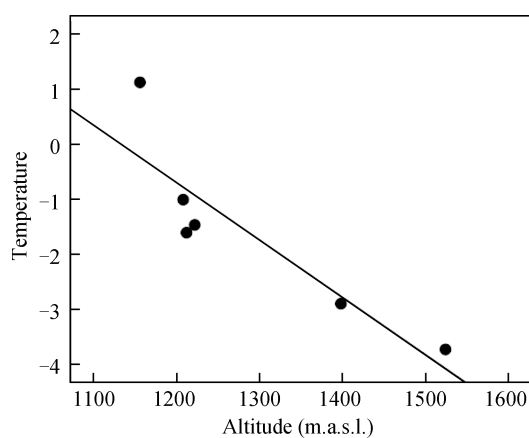
Fig. S1 **Mean annual temperatures (2011-07-25 to 2012-07-24) in relation to altitude at the six measured sites ($r^2 = 0.79$)**
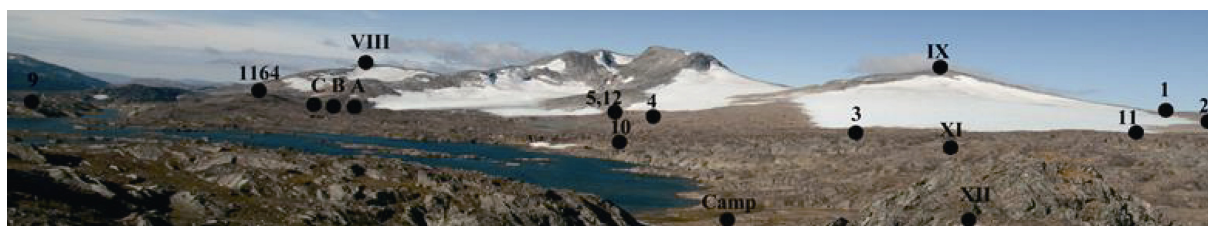
Fig. S2   A photograph of the Ålmajallojekna glacier and the approximate location of the surveyed sites

The sites situated outside the area covered by the photograph are not shown. Photograph taken from site XII on 7 September 2013. Photograph: Markus Franzén.
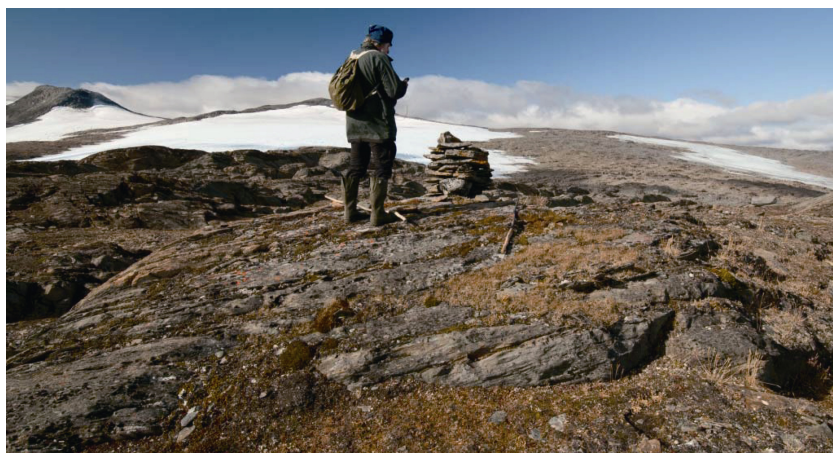

Fig. S3   The cairn at site XI created in 1898 marks the glacier edge in that year
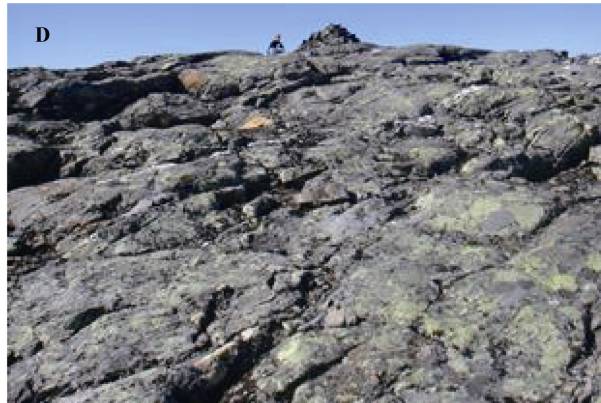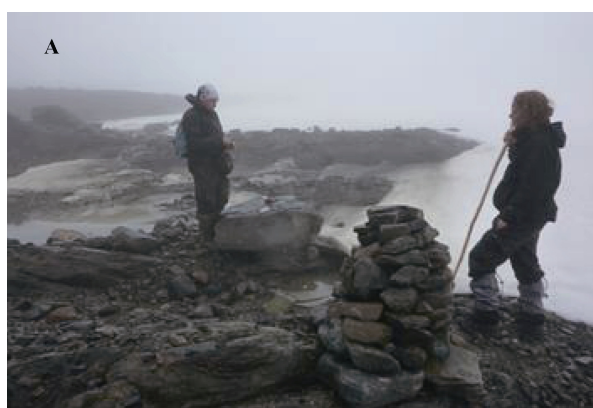
Photograph: Markus Franzén.

Fig. S4   Four different sites surveyed

A) site 3 and the cairn built in 2011 showing the glacier border in 2011; **B**) site D with an age of about 40 years; **C**) site 6 situated outside the glacial border in 1898 (>115 years); **D**) site XI and the former nunatak. Photographs: A - MF, B - JW, C, D -CJ.