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The Araneae of Svalbard: the relationships between specific environmental factors and spider assemblages in the High Arctic

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Abstract

As top predators in the Arctic invertebrate fauna, spiders in Svalbard are key components of the terrestrial ecosystem. However, most descriptions consist of observations of species occurrence and few repeated sampling campaigns investigating these heterogeneous assemblages, or the relationship between microhabitats and seasonality, exist. Spider assemblages were evaluated along four altitudinal transects (c. 10–300 m above mean sea level) on the west coast of Spitsbergen, Svalbard, throughout the summer of 2012. The slopes were selected to include most of the vegetation types typical for this region of Svalbard. Eleven of the known 15 native spider species were collected (10 Linyphiidae and 1 Gnaphosidae). We used Generalised Linear Models (GLM) for each spider species to identify the factors best explaining spider species abundance and distribution. The distribution of the majority of spider species was best described by vegetation or topography and none was accurately predicted by temperature. Only two species (*Erigone arctica palaearctica* and *Hilaira glacialis*) were common at all four sites and these two constituted 54% (1650 and 639 individuals, respectively) of the total spider individuals trapped. That assemblages of linyphiid spiders can differ greatly over small local and temporal scales further demonstrates the complexity of the Arctic terrestrial invertebrate community.

Keywords Linyphiidae · Spitsbergen · Species distribution · Elevation · Diversity

Introduction

It is often believed that Arctic ecosystems have few trophic levels and are "simple" (Summerhayes and Elton 1923; Hodkinson and Coulson 2004), but this view is challenged by the diversity of invertebrates often occurring in these regions

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(Hodkinson 2013; Coulson et al. 2014; Wirta et al. 2014; Hansen et al. 2016a). Probably, the most complete inventory of the invertebrate fauna for any High Arctic region is for the archipelago of Svalbard (Hodkinson 2013) with some 1100 known terrestrial and freshwater species names presented (Coulson 2007). The community composition, and local distribution, of invertebrate species is expected to depend on microhabitat conditions and consists of both generalist and specialist species (Hodkinson 2013). Although few studies have compared regions in Svalbard, there is clear evidence of contrasts in the invertebrate community compositions (Hodkinson et al. 2004; Seniczak et al. 2014, 2015). Coulson et al. (2003) detected a weak relationship between the soil microarthropod community and plant species at a local scale. A key taxon in this community is the Araneae. As top predators in the arthropod world, spiders are potentially important in structuring this community (Pace et al. 1999; Hodkinson et al. 2001, 2002; Hawes 2007). They are often amongst the first colonisers during the initial stages of primary succession (Lindroth et al. 1973; Fridriksson 1975; Hodkinson et al. 2001; Hawes 2008) and have been suggested to play a key role in trapping allochthonous nutrients and accelerating the establishment of

higher plants—the autotrophic successional process (Hodkinson et al. 2002). But the local distribution and patterns of spider assemblages in Svalbard, with its relatively poor species richness, are largely unknown.

Eighteen species of spider have been recorded in Svalbard, three of which are introductions and have not established in the natural environment (Aakra and Hauge 2003; Coulson et al. 2014, 2015). Among the naturally occurring spiders, the Linyphiidae dominate with 14 species, while one gnaphosid is present (Holm 1958, 1960, 1967; Hinz 1976; Koponen 1980; Aakra and Hauge 2003; Coulson et al. 2014). The Linyphiidae are known for their dispersal ability (Glick 1939; Freeman 1946; Duffey 1956, 1998; Johnson 2010) and represent a family distributed widely throughout the Arctic.

Previous reports of the spider fauna of Svalbard consist of mainly descriptive studies of species occurrence (Holm 1958, 1960, 1967; Hinz 1976; Koponen 1980; Coulson and Refseth 2004 and references therein; Coulson et al. 2014). However, several studies from Greenland, the Yukon, and Alaska suggest that spider assemblages diverge over small scales depending on environmental characteristics such as vegetation types and altitudinal gradients (Cotton 1979; Bowden and Buddle 2010a, b; Sikes et al. 2013; Hansen et al. 2016a, b). Tolbert (1975) observed a strong correlation between the aspect of a slope and arthropod distributions, including in the Araneae. Temperature can also vary depending on vegetation structure and local physical characteristics (Rypstra 1986; Rushton and Eyre 1992; Coulson et al. 1993; Bonte et al. 2002; Scherrer and Körner 2010, 2011) and it is an important limiting resource for Arctic arthropods (Sømme and Block 1991). Interspecific competition, both as exploitation and interference competition, has been shown to affect spider species with overlapping habitat preferences and can be considered a further microhabitat segregation process between species (Marshall and Rypstra 1999). We therefore predicted that distinct linyphiid species assemblages could be detected over small local and temporal scales despite their apparent generalist habit and dispersal abilities. Such structure in spider assemblages would be expected to have a potential effect on the structure of the soil invertebrate communities comprising prey items for the Araneae. We here examine the distribution of a key element of the invertebrate fauna of an Arctic region and determine if variations in local-scale environmental factors, such as topography, vegetation, and temperature, can explain this distribution.

Materials and methods

Svalbard

Spitsbergen is the largest island in the High Arctic archipelago of Svalbard (Fig. 1). Although some 60% out of its roughly 60,000 km^2 is covered by glaciers, the influence of the West Spitsbergen current, an arm of the North Atlantic Current, helps maintain relatively mild temperatures on the west coast of Spitsbergen (Hisdal 1985). The annual mean air temperature recorded at the meteorological station at the airport in Longyearbyen, situated in the inner arm of a large fjord on the west coast, is − 4.6 °C (mean summer temperature + 5.2 °C) and with 191 mm annual precipitation for the period 1981–2010 (Førland et al. 2011).

Sampling

Fieldwork took place between 12 June and 8 August 2012 which comprises the main summer period. Pitfall trap transects were established in the vicinity of Longyearbyen. Four slopes (Fig. 1) were selected so as to sample the vegetation types typical for western Svalbard, from slopes with thermophilic plant species such as dwarf birch (*Betula nana*) to polar desert characterised by the poppy species, *Papaver cornwallisense* and *Papaver dahlianum* (Elvebakk 1994; Solstad et al. 2014) (Table 1). The four slopes were selected to present either northerly aspects (Hanaskogdalen and Breinosa), or southerly facing aspects (Colesdalen and Hiorthfjellet). The meteorological station at Svalbard airport lies in the same Adventdalen valley system as the Hiorthfjellet, Hanaskogdalen, and Breinosa sampling sites and is some 16 km from Breinosa, the most distant of these. Colesdalen lies approximately 18 km southeast from the meteorological station.

Three parallel transects were established up the slope at each of the four sampling sites along which the pitfall traps were located. Trapping sites were placed into a vegetation category based on Elvebakk (1994, 2005) (Table 1, 2). The three broadly parallel transect lines at each site were located 40–50 m apart, except for the first two sampling locations at Hiorthfjellet which were located only 20 m apart due to spatial constraints. Each sampling location had the same vegetation type across all three transects. At the Hanaskogdalen and Hiorthfjellet sites, there were four sampling locations along each transect, while five sampling locations were established at Breinosa and Colesdalen due to the extra length of the transects at these sites (Table S1). Five pitfall traps were located perpendicular to the hill at each sampling location and were spaced at between 1 and 5 m. The pitfall traps consisted of white plastic cups with a diameter of 65 mm. See Fig. 2 for an illustration of the experimental design. Approximately 50 mL of saturated saline water with a drop of detergent was added to each trap. Using non-toxic saturated NaCl solution ensured that the traps did not dry out due to evaporation between sampling and prevented harm to, or disturbance by, inquisitive animals such as the Arctic fox (*Vulpes lagopus*), Svalbard reindeer (*Rangifer tarandus platyrhynchus*), and Arctic skua (*Stercorarius parasiticus*) known to cause problems with earlier pitfall trap campaigns

Fig. 1 Location of Svalbard and the study sites. *Ha* Hanaskogdalen, *Hi* Hiorthfjellet, *B* Breinosa, and *C* Colesdalen
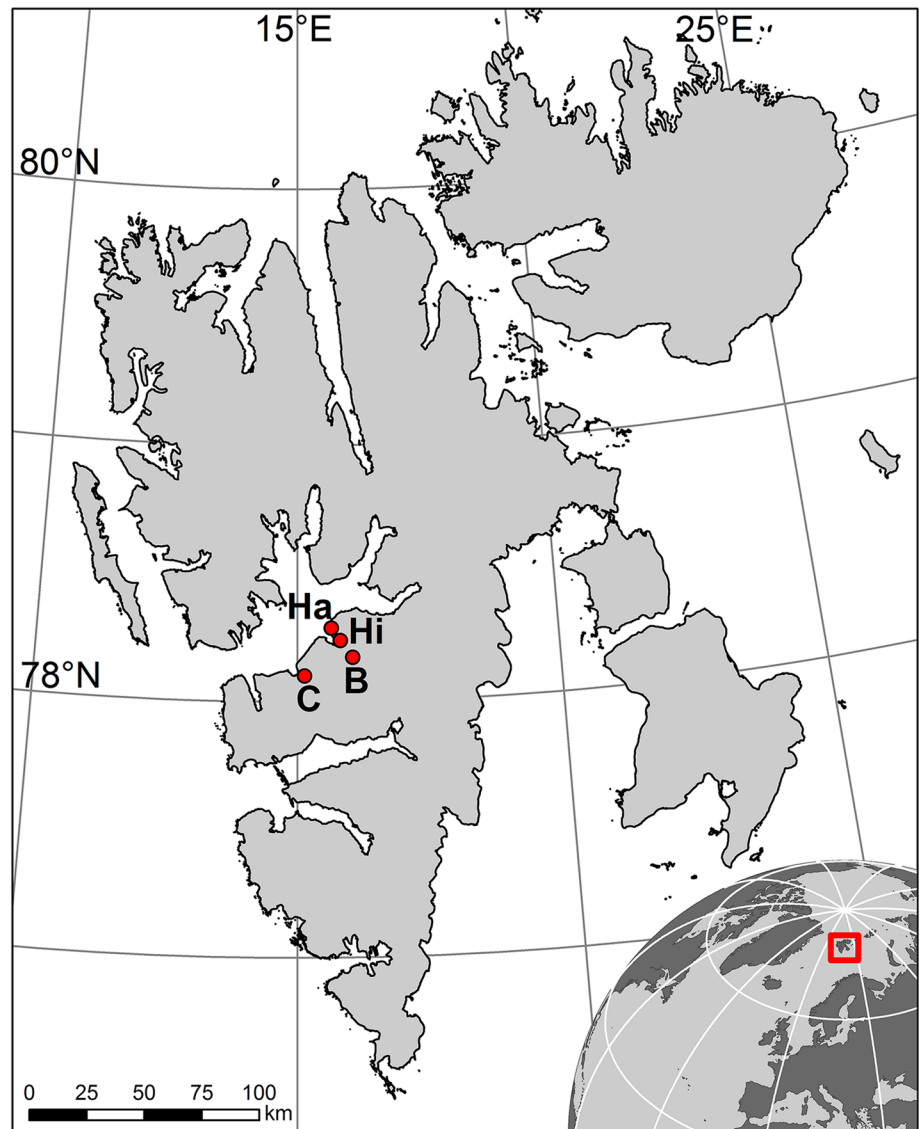
Table 1 Vegetation types at the trapping sites

Vegetation type	Abbreviation
Moss/Grass tundra	MGT
Cassiope tetragona tundra	COT
Permafrost veins, moss/herbs	PMH
Betula nana/Dryas octopetala dominated	BND
Papaver dahlianum/cornwallisense intermittent unstable slopes	PIS
Dryas octopetala tundra	DOT
Dry moss tundra	DMT
Pioneer vegetation on unstable rocky substrate	PVI
Papaver dahlianum/cornwallisense polar desert	PPD
Grass/herbs dominated	GRH

Categories were based broadly on Elvebakk (1994, 2005)

in Svalbard. Traps were usually emptied once every second week.

Temperature loggers, iButtons (DS1922) inside waterproof casings (Maxim Integrated, San Jose, CA, USA), were placed in the soil surface (depth 5–10 mm) at each sampling location along the middle transect in each site. To compare soil and local air temperature, air temperature loggers (Tinytag TGP-4020 Gemini, Chichester, West Sussex, U.K.) within solar shields were positioned one metre above the ground at the bottom and top sampling location of the middle transects (except for Hiorthfjellet, which only had soil temperature measured). Logging interval was 1 h.

The collected invertebrates were transferred to 96% ethanol within 24 h of trap emptying and the catch sorted into Diptera (Culicidae/Chironomidae and Brachycera), Hymenoptera (Apocrita and Symphyta), Hemiptera (Aphidinae), Coleoptera (Staphylinidae and Curculionidae), and Araneae.

Table 2 Spiders collected from the four slopes. The data are totals from two sampling periods and three transects

	Level 1	Level 2	Level 3	Level 4	Level 5	Sum
Breinosa (North facing)						
Erigone arctica palaearctica Braendegaard, 1934	318	303	155	10	3	789
Hilaira glacialis (Thorell, 1871)	79	76	26	3	–	184
Collinsia spetsbergensis (Thorell, 1871)	39	22	63	37	2	163
Mughiphantes sobrius (Thorell, 1871)	1	–	1	46	7	55
Agyneta nigripes (Simon, 1884)	–	–	–	–	36	36
Collinsia holmgreni (Thorell, 1871)	–	4	–	–	–	4
Erigone psychrophila (Thorell, 1871)	3	–	–	–	–	3
Improphantes complicatus (Emerton, 1882)	–	–	–	1	–	1
Hanaskogdalen (North facing)						
Erigone arctica palaearctica Braendegaard, 1934	2	30	14	2		48
Hilaira glacialis (Thorell, 1871)	84	9	–	–		93
Collinsia spetsbergensis (Thorell, 1871)	2	47	20	7		76
Mughiphantes sobrius (Thorell, 1871)	–	–	1	2		3
Colesdalen (South facing)						
Erigone arctica palaearctica Braendegaard, 1934	88	27	112	–	7	234
Hilaira glacialis (Thorell, 1871)	41	40	32	1	1	115
Walckenaeria clavicornis (Emerton, 1882)	3	4	34	14	1	56
Mughiphantes sobrius (Thorell, 1871)	4	27	35	37	–	103
Mecynargus borealis (Jackson, 1930)	–	–	53	10	–	63
Micaria constricta Emerton, 1894	1	–	5	54	–	60
Agyneta nigripes (Simon, 1884)	1	–	1	10	14	26
Improphantes complicatus (Emerton, 1882)	–	1	59	82	–	142
Collinsia spetsbergensis (Thorell, 1871)	–	2	–	–	–	2
Collinsia holmgreni (Thorell, 1871)	–	–	8	–	–	8
Hiorthfjellet (South facing)						
Erigone arctica palaearctica Braendegaard, 1934	374	10	35	1		420
Hilaira glacialis (Thorell, 1871)	26	22	34	–		82
Walckenaeria clavicornis (Emerton, 1882)	15	8	11	8		42
Mughiphantes sobrius (Thorell, 1871)	2	10	18	2		32
Mecynargus borealis (Jackson, 1930)	3	3	10	5		21
Micaria constricta Emerton, 1894	–	–	5	9		14
Agyneta nigripes (Simon, 1884)	1	–	–	2		3
Improphantes complicatus (Emerton, 1882)	–	–	–	1		1
Collinsia spetsbergensis (Thorell, 1871)	–	–	1	–		1

Level 1 of Hanaskogdalen contains data from only one sampling period (Period 2)

Araneae species identification

Only adults among the linyphiid spiders were identified to species level since it was not possible to reliably determine juvenile linyphiids on the basis of morphology. Only one species belonging to the family Gnaphosidae is recorded from Svalbard so all juvenile gnaphosid spiders were presumed to belong to this species. Identification to species level (including gender) was achieved using the reference collection prepared by Kjetil Aakra (Midt-Troms museum, Norway) and relevant literature (Holm 1937, 1956, 1958, 1967; Brændegaard 1946; Parker 1969; Agnarsson 1996; Saaristo and Koponen 1998). Nomenclature of spiders follows the World Spider Catalog (2017). The identification was accomplished using a stereo microscope at ×40 magnification to examine the pedipalps of males and the epigyne on females (their secondary sexual characters). Identified material is deposited at the Midt-Troms Museum (9050 Storsteinnes, Norway).

Statistics

All analyses were performed in R (version 2.15.3, R Core Team 2013). We used Generalised Linear Models (GLM) for each spider species to identify the factors best explaining spider species abundance and distribution. Juvenile and
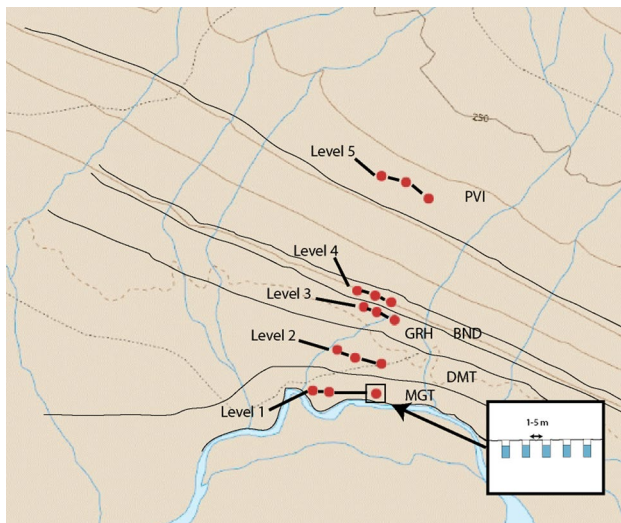
Fig. 2 Sampling design using Colesdalen as an example site. The sampling was performed over 5 separate levels using three transects. Each transect station consisted of 5 traps spaced between 1 and 5 m apart. The black lines indicate how the sampled habitats changed along the transects and were divided into quite clear horizontal bands. *MGT* moss/grass tundra, *DMT* dry moss tundra, *GRH* grass/herbs dominated, *BND* Betula nana/Dryas octopetala dominated, *PVI* pioneer vegetation on unstable rocky substrate

subadult linyphiid spiders were not considered for a distribution model as these could not be identified to the species level.

Negative binomial distribution was used for the response variables (counts) as we had evidence of overdispersion (Venables and Ripley 2002) which was a consequence of aggregative behaviour of spiders and of the repeated counts at the same location. We did try generalised linear mixed models with a Poisson distribution (with site as a random factor, fitted with glmer in the library lme4), but because we had only two counts at each site and because of the sparseness of data, the models did not always converge. For those models that converged, models with a negative binomial distribution had wider confidence intervals than the mixed models (i.e. were conservative), so we decided to use a negative binomial distribution for all cases. We used the pscl package (Jackman 2012). Model selection took place via AICc, which was calculated using the MuMIn package (Bartoń 2013). The models with the lowest AICc values can be considered as the best predictive models, and when models differ by less than 2 units of AICc, the simplest models were retained to avoid overfitting (e.g. Burnham and Anderson 2002). Model fit was assessed by investigating residual plots. The covariates were divided into four groups: vegetation (vegetation type and vegetation cover), topography (elevation, steepness, and aspect), temperature (average, maximum, and minimum ground temperature), and topography + vegetation (vegetation, vegetation cover, aspect, and steepness). Confounding was assessed by inspecting the correlation between predictor variables, and because of strong confounding some of the covariates were not tested in the same model. These include vegetation type and vegetation cover, vegetation type/cover and elevation, vegetation type and aspect, and all temperature data with either the topography group or the vegetation group. The values of the temperature data (maximum, minimum, and average temperature) are based on temperatures logged in the period from 9 to 31 July 2012, as this is when data from all sites were available.

Results

Araneae

Eleven species of spiders from two families were identified. Ten of the species belonged to the Linyphiidae. The most numerous was *Erigone arctica palaearctica* Braendegaard, 1934 comprising 39% (779 males and 871 females) of individuals identified. *Hilaira glacialis* (Thorell, 1871) was also abundant forming a further 15% (372 males and 267 females) of the catch. Together, these two species totalled 54% of the spiders identified. Of the remaining linyphiid spiders, *Collinsia spetsbergensis* (Thorell, 1872) (73 males and 186 females), *Mughiphantes sobrius* (Thorell, 1871) (110 males and 86 females), and *Improphantes complicatus* (Emerton, 1882) (84 males and 60 females) comprised 6, 5, and 3% of the total trap catch respectively. Three linyphiid species each contributed 2% of the total catch: *Walckenaeria clavicornis* (Emerton, 1882) (49 males and 49 females), *Mecynargus borealis* (Jackson, 1930) (30 males and 56 females), and *Agyneta nigripes* (Simon, 1884) (38 males and 34 females). The only non-linyphiid spider collected, *Micaria constricta* Emerton, 1894 (Gnaphosidae), made up 2% (34 males, 21 females, and 19 juveniles) of the total spider catch. The remaining two species all comprised < 1% of the individuals caught: *Collinsia holmgreni* (Thorell, 1871) (8 males and 4 females) and *Erigone psychrophila* Thorell, 1871 (2 males and 1 female). 23% of the total catch were juvenile or subadult linyphiid spiders and were not identified to the species level.

Spider assemblages at the four sampling locations

The south-facing slopes had the greatest spider species diversity with 10 species recorded from Colesdalen and nine species recorded from Hiorthfjellet. *Micaria constricta*, *W. clavicornis*, and *M. borealis* were only found on these two slopes and *I. complicatus* was almost absent outside of Colesdalen where it was quite common. Along the north-facing slopes, eight species were recorded from Breinosa and only four species from Hanaskogdalen. Few *C.*

spetsbergensis were found outside of the north-facing slopes. The greatest totals of spiders were collected on the slopes at Breinosa with Colesdalen second, Hiorthfjellet third, while Hanaskogdalen had the fewest spiders collected (Table 2). The differences between the sites in the total number of spiders were largely due to the variation in the two most common spider species found, *E. arctica palaearctica* and *H. glacialis*. The greatest trap catch tended to be found towards the lower regions of the hills, but again this trend is largely created by the distribution of *E. arctica palaearctica* and *H. glacialis*.

Change in numbers of spiders collected within the season

Erigone arctica palaearctica, C. spetsbergensis, I. complicatus, M. borealis, M. sobrius, A. nigripes, and *W. clavicornis* showed a general decline in trap catch as the sampling season progressed (Figs. 3, 4 and 5), while *H. glacialis* and *M. constricta* showed an increase in numbers trapped during this period (Figs. 3, 4). For *M. constricta*, the observed increase was due to a sharp increase in males and juveniles, while the numbers of females collected was stable over the period. There was no clear trend between the numbers of males and females trapped for the other identified spider species. The proportion of juveniles among the linyphiid spiders increased toward the end of July and decreased again in early August (Fig. 5).

Modelling spider distribution

Since *M. constricta, W. clavicornis,* and *M. borealis* were only found on the south-facing slopes, their distribution was only modelled for Hiorthfjellet and Colesdalen. Similarly, *C. spetsbergensis* was only modelled for the north-facing slopes and *I. complicatus* only modelled for Colesdalen since these species occurred almost exclusively at these sites. *Erigone psychrophila* and *C. holmgreni* were not modelled due to their sparse numbers.

Three species were best explained by models based on topography. See Online Resource for AICc (Table S2). The best model for *M. constricta* had steepness, elevation, and an interaction between catch date (Period, as a factor), steepness, and elevation. Numbers of spiders increased with steepness, but this effect was diminished by later catch date (Table 3). *Collinsia spetsbergensis* also had steepness, elevation, and catch date as the covariates in the best model. Numbers of spiders increased with steepness and decreased with increasing elevation (Table 3). The best model for *M. sobrius* had elevation and catch date as the covariates. The number of spiders decreased with later catch dates (Table 4).

Vegetation best explained the distribution of three of the identified species. Among these species, the best model for both *I. complicatus* and *M. borealis* contained the factors vegetation group and period as the covariates, while *A. nigripes* was best explained by vegetation group alone (Table 3, 4).


Fig. 3 Total catches of females (circles) and males (triangles) of *Erigone arctica palaearctica* (**a**), *Improphantes complicatus* (**b**), *Collinsia spetsbergensis* (**c**), and *Hilaira glacialis* (**d**). Breinosa is shown in red, Hiorthfjellet in blue, Hanaskogdalen in black, and Colesdalen in yellow
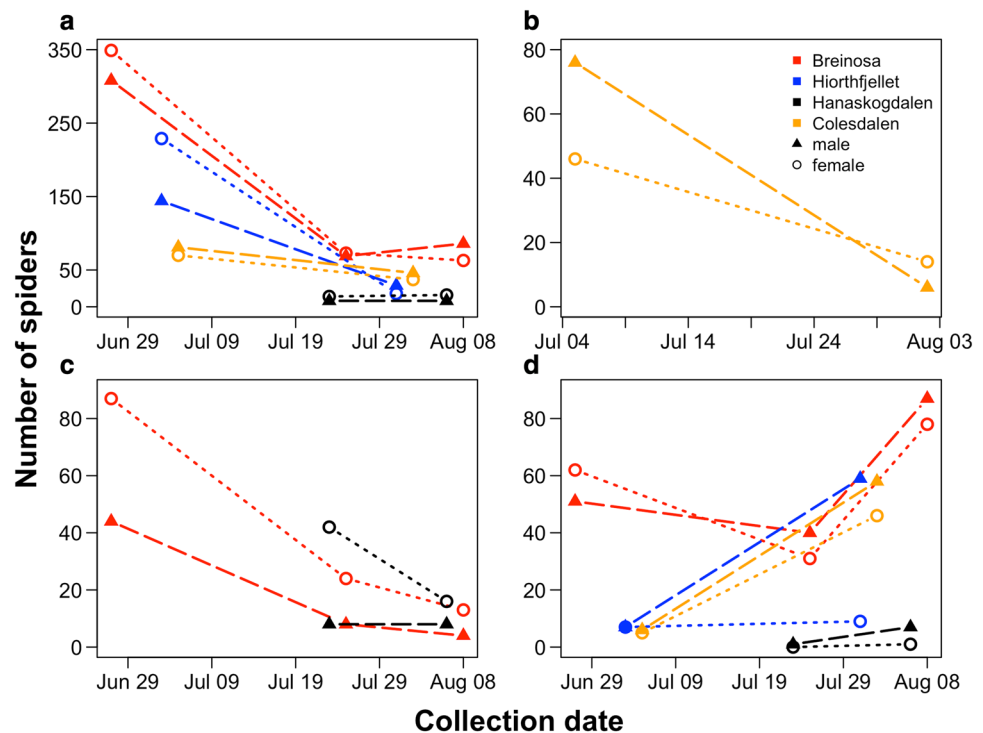
Fig. 4 Total catches of females (circles), males (triangles), and juveniles (stars) of *Micaria constricta* (**a**), *Agyneta nigripes* (**b**), *Mecynargus borealis* (**c**), and *Mughiphantes sobrius* (**d**). Breinosa is shown in red, Hiorthfjellet in blue, Hanaskogdalen in black, and Colesdalen in yellow
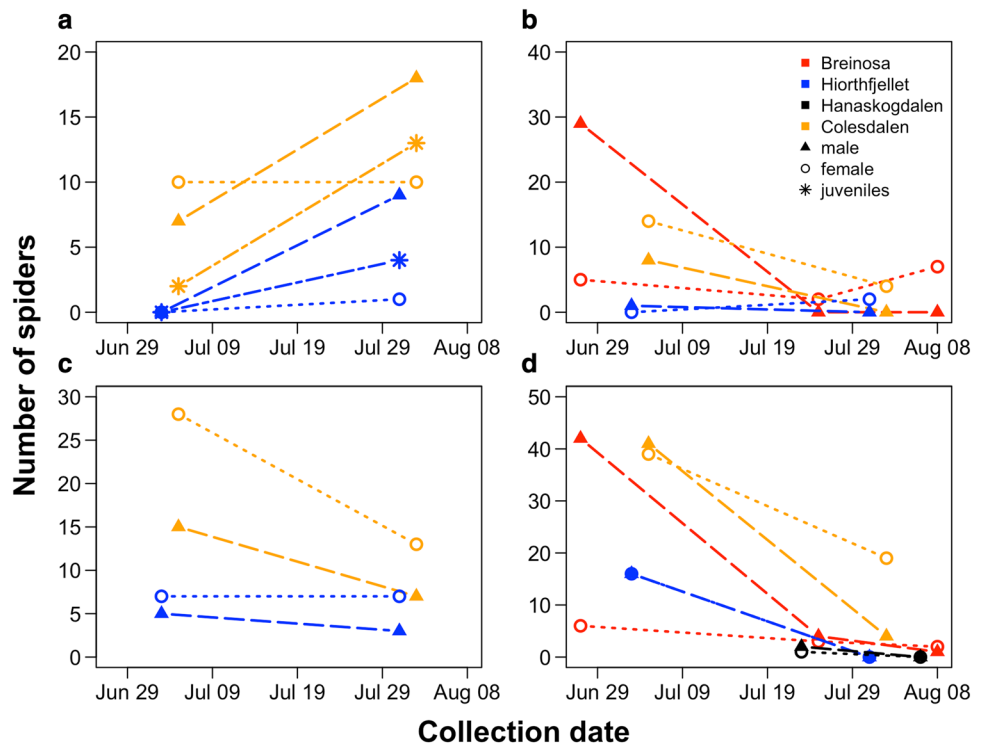
Fig. 5 Total catches of females (circles) and males (triangles) of *Walckenaeria clavicornis* (**a**) and the proportion of juveniles (stars) among the linyphiid spiders in the traps (**b**). Breinosa is shown in red, Hiorthfjellet in blue, Hanaskogdalen in black, and Colesdalen in yellow
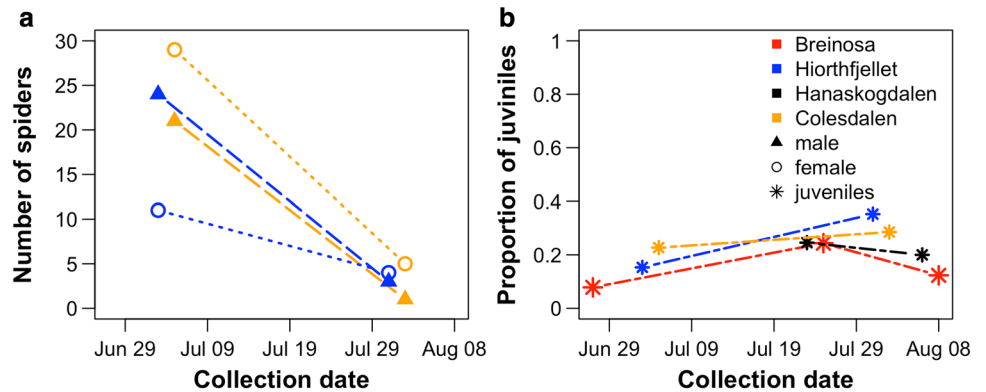
The distribution of the three remaining species was best explained by both vegetation and topography (Table S2). For *W. clavicornis,* the best model contained vegetation cover, steepness, and an interaction between period and the two other variables. An increase in vegetation cover was associated with an increase in spider numbers, but this effect was diminished by later catch date (Table 3). *Erigone arctica palaearctica* was best modelled with vegetation cover, steepness, aspect, catch date (period), and a third-order interaction between vegetation cover, aspect, and steepness. Spider numbers increased with increasing vegetation cover and decreased with increasing steepness, but the positive effect of vegetation cover was larger with increasing steepness values. This effect was slightly larger for the north-facing slopes than for the south-facing slopes (Table 4). *Hilaira glacialis* was also best modelled using vegetation cover, steepness,

aspect, and period with a third-order interaction between vegetation cover, aspect, and steepness. Spider numbers increased with increasing vegetation cover, decreased with increasing steepness, and were higher in south- than north-facing slopes. The effect of vegetation cover was larger with increasing steepness values and was also larger in north- than south-facing slopes (Table 4).

Insecta

Insect groups found in the traps included Diptera (4701 Culicidae/Chironomidae and 2593 Brachycera), Hymenoptera (1918 Apocrita, 92 adult Symphyta and 14 larvae), Coleoptera (213 Curculionidae, 1,109 Staphylinidae), and Hemiptera (931 Aphidinae). Coleoptera only occurred on

Table 3 The upper and lower confidence intervals (UCI and LCI) and estimates of the parameters of models best describing the distribution of five out of nine spider species modelled

	Estimate	UCI	LCI	Z value	P value
Micaria constricta Emerton, 1894					
(Intercept)	0.003	0.555	0	− 2.183	0.029
Steepness	1.296	1.549	1.085	2.858	0.004
Elevation	0.951	1.098	0.824	− 0.686	0.493
Period (3)	14.189	3108.154	0.065	0.965	0.335
Steepness: period (3)	0.894	1.074	0.743	− 1.198	0.231
Elevation: period (3)	1.05	1.212	0.909	0.663	0.507
Collinsia spetsbergensis (Thorell, 1871)					
(Intercept)	12.945	24.72	6.779	7.759	< 0.001
Elevation	0.991	0.995	0.987	− 4.63	< 0.001
Steepness	1.033	1.057	1.01	2.849	0.004
Period (2)	0.279	0.595	0.131	− 3.303	0.001
Period (3)	0.239	0.48	0.119	− 4.022	< 0.001
Period (4)	0.15	0.318	0.071	− 4.941	< 0.001
Walckenaeria clavicornis (Emerton, 1882)					
(Intercept)	0.181	0.797	0.041	− 2.261	0.024
Vegetation cover	1.029	1.045	1.014	3.74	< 0.001
Steepness	1.03	1.061	0.999	1.892	0.058
Period (3)	0.536	12.841	0.022	− 0.385	0.7
Vegetation cover: period (3)	0.964	0.996	0.933	− 2.184	0.029
Steepness: period (3)	1.063	1.135	0.996	1.836	0.066
Improphantes complicatus (Emerton, 1882)					
(Intercept)	0.283	2.197	0.037	− 1.207	0.228
Vegetation (BND)	75.868	632.525	9.1	3.99	< 0.001
Vegetation (GRH)	66.42	554.84	7.951	3.874	< 0.001
Vegetation (PVI)	Not est.	Not est.	Not est.	Not est.	Not est.
Vegetation (MGT)	Not est.	Not est.	Not est.	Not est.	Not est.
Period (3)	0.165	0.361	0.075	− 4.512	< 0.001
Mecynargus borealis (Jackson, 1930)					
(Intercept)	2.092	4.35	1.006	1.977	0.048
Vegetation (COT)	1.132	2.543	0.504	0.252	0.801
Vegetation (DMT)	0	0	0	0	1
Vegetation (GRH)	5.458	Not est.	Not est.	− 1.52	< 0.001
Vegetation (DOT)	0.468	1.246	0.176	4.111	0.129
Vegetation (PVI)	Not est.	Not est.	Not est.	Not est.	Not est.
Vegetation (MGT)	0.103	0.493	0.022	− 2.843	0.004
Period (3)	0.549	0.968	0.312	− 2.073	0.038

All values are back transformed since the model used a log link. Estimates > 1 indicate increasing numbers of spiders with increasing covariate numbers, while estimates < 1 indicate reduced numbers of spiders with increasing covariate values compared to the intercept. Some parameters could not be estimated because no individuals were caught (not est.)

BND Betula nana/Dryas octopetala dominated, *GRH* grass/herbs dominated, *PVI* pioneer vegetation on unstable rocky substrate, *MGT* moss/grass tundra, *COT Cassiope tetragona* tundra, *DMT* dry moss tundra, *DOT Dryas octopetala* tundra

Table 4 Upper and lower confidence intervals (UCI and LCI) and estimates of the parameters of models best describing the distribution of four out of nine spider species modelled

	Estimate	UCI	LCI	Z value	P value
Erigone arctica palaearctica Braendegaard, 1934					
(Intercept)	2.249	13.188	0.384	0.898	0.302
Vegetation cover	1.033	1.054	1.012	3.180	0.001
Steepness	0.892	0.967	0.823	− 2.771	0.006
Aspect (S)	0.16	2.994	0.009	− 1.226	0.220
Period (2)	0.278	0.63	0.123	− 3.069	0.002
Period (3)	0.286	0.455	0.18	− 5.282	< 0.001
Period (4)	0.245	0.484	0.124	− 4.053	< 0.001
Vegetation cover: steepness	1.002	1.004	1.001	4.008	< 0.001
Vegetation cover: aspect (S)	1.029	1.067	0.993	1.567	0.117
Steepness: aspect (S)	0.993	1.203	0.82	− 0.071	0.944
Vegetation cover: steepness: aspect (S)	0.998	1	0.995	− 1.716	0.086
Hilaira glacialis (Thorell, 1871)					
(Intercept)	0.254	3.424	0.019	− 1.033	0.302
Vegetation cover	1.036	1.065	1.008	2.532	0.011
Steepness	0.762	0.862	0.673	− 4.309	< 0.001
Aspect (S)	58.961	2187.503	1.589	2.211	0.027
Period (2)	4.262	10.508	1.729	3.149	0.002
Period (3)	2.799	4.428	1.769	4.396	< 0.001
Period (4)	2.685	5.291	1.363	2.855	0.004
Vegetation cover: steepness	1.005	1.007	1.003	5.044	< 0.001
Vegetation cover: aspect (S)	0.948	0.988	0.908	− 2.496	0.013
Steepness: aspect (S)	0.912	1.173	0.709	− 0.719	0.472
Vegetation cover: steepness: aspect (S)	0.999	1.002	0.996	− 0.563	0.573
Agyneta nigripes (Simon, 1884)					
(Intercept)	1.667	7.308	0.38	0.677	0.498
Vegetation (COT)	Not est.	Not est.	Not est.	Not est.	Not est.
Vegetation (DMT)	Not est.	Not est.	Not est.	Not est.	Not est.
Vegetation (DOT)	0.1	0.937	0.011	− 2.017	0.044
Vegetation (GRH)	0.1	1.641	0.006	− 1.613	0.107
Vegetation (PVI)	1.4	11.03	0.178	0.32	0.749
Vegetation (MGT)	0.05	0.423	0.006	− 2.751	0.006
Vegetation (PIS)	0.04	0.331	0.005	− 2.985	0.003
Vegetation (PMH)	Not est.	Not est.	Not est.	Not est.	Not est.
Vegetation (PPD)	2.733	17.652	0.423	1.057	0.291
Mughiphantes sobrius (Thorell, 1871)					
(Intercept)	4.559	9.821	2.116	3.874	< 0.001
Elevation	0.997	1.002	0.992	− 1.334	0.182
Period (2)	Not est.	Not est.	Not est.	Not est.	Not est.
Period (3)	0.204	0.477	0.088	− 3.672	< 0.001
Period (4)	0.075	0.341	0.017	− 3.359	0.001

All values are back transformed since the model used a log link. Estimates > 1 indicate increasing numbers of spiders with increasing covariate numbers, while estimates < 1 indicate reduced numbers of spiders with increasing covariate values compared to the intercept. Some parameters could not be estimated because no individuals were caught (not est.)

COT Cassiope tetragona tundra, *DMT* dry moss tundra, *DOT* Dryas octopetala tundra, *GRH* grass/herbs dominated, *PVI* pioneer vegetation on unstable rocky substrate, *MGT* moss/grass tundra, *PIS* Papaver dahlianum/cornwallisense intermittent unstable slopes, *PMH* permafrost veins, moss/herbs, *PPD* Papaver dahlianum/cornwallisense polar desert

the south-facing slopes. See Online Resource for distribution (Table S3).

Discussion

General distribution of Araneae in Svalbard

Eleven of the 15 previously recorded native spider species were present (73%) along the transects at Breinosa and Colesdalen. The high proportion of total available species sampled from one small region in Isfjord suggests that either the spider assemblages in Svalbard are species poor and homogeneous or that only incomplete records from other regions in Svalbard exist. The majority of the records of the Araneae of Svalbard originate from the Isfjord region, but collections from other regions have not identified distinctly different spider assemblages (Tambs-Lyche 1967; Hågvar and Hegstad 1969; Hodkinson et al. 2001, 2002; Aakra and Hauge 2003; Coulson et al. 2011). At a geographic scale, the spider assemblages in Svalbard appear therefore to be quite homogeneous and are composed mainly of linyphiid species, a family considered to be a habitat generalist and tolerant of the polar environment (Hodkinson et al. 2001, 2002; Hawes 2007). Therefore, that such extremely clear differences in spider assemblages between sampling sites and along the transects were observed was somewhat unexpected although a similar assemblage structure and dependence on small habitat variations in Arctic regions have recently been observed in the Yukon (Bowden and Buddle 2010a, b), Alaska (Sikes et al. 2013) and Greenland (Hansen et al. 2016a, b).

Microclimate and habitat choice

The microclimate of a site is arguably the most dominant factor influencing small soil- and surface-dwelling invertebrates. Moring and Stewart (1994), DeVito et al. (2004) and Frick et al. (2007) showed that for wolf spiders (Lycosidae) the preferred habitat for each species represented a rather narrow range of habitat conditions. Thompson et al. (2015) also found niche partitioning in *Pahoroides* (Synotaxidae) in New Zealand, while Portela et al. (2013) found niche partitioning in two wandering spiders (Ctenidae) in Brazil. This kind of partitioning is likely to be valid for other spider families as well. For the nine species for which the distribution could be modelled, none was best explained by ground temperature. Although temperature is probably one of the most important factors determining the distribution of a species, it is notoriously difficult to reliably measure the temperature that the

animal actually experiences. Ground surface microhabitat temperatures are appreciated to be often significantly greater than air temperature (Convey et al. under review; Migała et al. 2014). Scherrer and Körner (2010, 2011) used infrared thermometry to document and highlight the surprisingly large variation in surface temperature of alpine landscapes over even short horizontal distances and hence surface temperature variation may be as great within a site as between sites. Moreover, dark spider bodies will react rapidly to temperature variations, while the instrument temperature sensors employed have a greater thermal mass, react slower, record point temperature measurements, and are located at a fixed position in the three-dimensional microhabitat structure. Since spiders are mobile, they can also use behavioural thermoregulation strategies, something they have in common with many Arctic arthropods (Carrel 1978; Humphreys 1987; Sømme and Block 1991). Temperature can affect the distribution of species directly (Entling et al. 2007), but it can also modify the activity of arthropods and this will affect their capture rate in pitfall traps (Saska et al. 2013). All of this complicates the use of temperature for describing habitat choice despite its ecological importance. One species, *M. sobrius,* was best explained by elevation where the predicted numbers of individuals collected slowly declined with increasing elevation. The model, however, would predict that the bottom of the slopes had the highest spider abundance but often the lowest sites on the slopes had the fewest trap catches. Proxy variables, such as elevation, have been employed as descriptors when studying invertebrate assemblages from different habitats, (e.g. Otto and Svensson 1982; McCoy 1990; Buddle and Draney 2004; Bowden and Buddle 2010a; Davies et al. 2011). But elevation per se is not a determining factor, rather elevation integrates various factors of ecological importance (Körner 2007). The vegetation cover of the sites varied significantly from complete cover to largely open ground and rock. Vegetation best explained the distribution of two species: *Improphantes complicatus* was predicted to have higher capture rates in the *B. nana/D. octopetala* vegetation and the grass/herb-dominated areas, while *M. borealis* was estimated to be most abundant in the grass/herb-dominated areas. Nevertheless, the statistical precision was low and too few individuals were collected to create a satisfactory model. Hansen et al. (2016a, b) found *E. arctica* to be significantly linked to wet fen habitats in a way that suggests habitat specialisation. This was not found to be the case in our study where *E. arctica palaearctica* had a very general dispersion. *Erigone arctica palaearctica* and *H. glacialis* had a modelled greater capture rate with increasing vegetation cover. The decreasing capture rate of these two species with increased steepness might be due to avoidance of habitats with strong irradiance from

the sun, the preferred habitat of their prey, or simply that the vegetation cover of steep slopes tends to be somewhat poorer compared to flat ground. Except for a different timing of the peak of activity, *E. arctica palaearctica* and *H. glacialis* were remarkably similar in their distribution. It has been argued that temporal segregation might lead to similar species being able to co-exist (Williams 1962; Breymeyer 1966; Uetz 1977; Buddle and Draney 2004), which may explain the observed trapping patterns with the number of *E. arctica palaearctica* peaking in June, while the number of *Hilaira glacialis* peaking in August. *Hilaira glacialis* and *W. clavicornis* showed higher capture rates with increasing vegetation cover but also had higher capture rates with increasing steepness in contrast to *E. a. palaearctica*. Harwood et al. (2001) found that linyphiid spiders in the UK located their webs in areas with a high abundance of prey. It is possible that the prey of these spiders are more abundant in vegetation, while they also prefer the increase in local temperature that results as the slope gets steeper and angle of incidence with the sun increases, particularly considering that *W. clavicornis* was found on the south-facing slopes only. *Collinsia spetsbergensis* had a higher capture rate with increasing steepness, but a decreasing rate with increasing elevation. This could indicate that it prefers a warm habitat, but, paradoxically, it is almost exclusively found on the north-facing slopes. It is also, together with *E. psychrophila*, the species with the most northerly distribution of the spiders discussed here, occurring throughout the majority of the Palaearctic (Marusik et al. 2006). The uneven rocky substrate that often is associated with steep slopes may confer certain advantages, for example associated with particular hunting strategies and distribution of its prey. *Agyneta nigripes* occurs mostly in the *Papaver* polar desert and pioneer vegetation/unstable rocky substrate. While this species was almost exclusively found in these areas, the model fails to produce satisfactory 95% confidence intervals likely due to the low number of individuals collected. Since this species occurred at the top of the transects in both Breinosa and Colesdalen where few other spiders were collected, it is perhaps favoured by low vegetation cover.

Both *E. psychrophila* and *C. holmgreni* occurred in low numbers and it is not possible to draw clear conclusions as to their distribution. *Erigone psychrophila* has been found in large numbers in other locations in the High Arctic, for example Zackenberg, Greenland (Høye and Forchhammer 2008), where it was the most numerous spider collected. It is also reported as widespread on the west coast of Spitsbergen (Holm 1958). It is therefore likely that its preferred habitat is not within the areas sampled during this study. *Collinsia holmgreni* is reported as rare in Spitsbergen but common in Greenland and is considered to be a species that prefers

humid environments, such as snow beds (Holm 1958; Cotton 1979).

Micaria constricta is the only gnaphopsid species collected, and it is also larger than the other species collected. It is an active diurnal hunter (Roberts 1995) instead of web-spinning as for the linyphiids (Heydemann 1961). The clear trend of increasing catches with increasing steepness on the south-facing slopes is likely linked to its active mode of hunting and its probable dependence on the greater surface temperatures associated with open and bare ground compared to tundra heaths (Coulson et al. 1993; Scherrer and Körner 2010, 2011).

In addition to the environmental variables and factors assessed in this study, there are other potentially important ones that were not assessed. Approximately 1300 reindeer are present in the Adventdalen valley system and another 210–510 in Colesdalen and Semmeldalen (Stein et al. 2012; Peeters et al. 2017). Grazing by herbivores may impact spiders (Bell et al. 2001; Suominen et al. 2003; Prieto-Benítez and Méndez 2011). Additional factors known to affect the distribution of spiders include litter depth (Uetz 1979), vegetation height (Pétillon et al. 2008), soil humidity (ter Braak 1986), other climatic and landscape metrics (Jiménez-Valverde et al. 2010; Lafage et al. 2015), and even soil type (Řezáč et al. 2007). Some of these will already be at least indirectly, if not completely, captured by variables that were included in the models (vegetation type and height, for example, are obviously linked and would result in strong cofounding if treated as separate), but there are always factors that are not captured in a model. Nonetheless, the rather clear results for many of the spiders modelled in this study indicate that important aspects of their habitat choice have been captured directly, or indirectly, in this study.

Variation in capture rates over time

Spider trap catch varied seasonally. There was a rather dramatic decrease in the number of trapped *E. arctica palaearctica, C. spetsbergensis, I. complicatus, M. sobrius, W. clavicornis, A. nigripes*, and, to some extent, *M. borealis* (reduced catch in Colesdalen, stable catch in Hiorthfjellet) while the number of *H. glacialis* and *M. constricta* increased during the short summer period. Pitfall trap data must be interpreted with care (Adis 1979) since such traps are passive and catch is a combination of individual densities and activity. For example, there may be great variance in the relationship between numbers captured in pitfall traps and the actual density of spiders, and this relationship can vary with season (Topping and Sunderland 1992). Moreover, trap design is appreciated to influence catching efficiency (Luff 1975). For a more detailed review of the complications and limitations of pitfall trapping see also Brown and Matthews (2016). Hence, due to the sampling methodology, the change

in trap catches of adult spiders may be explained by a change in spider activity rather than a change in relative numbers. Nonetheless, a tendency for a bimodal distribution of linyphiid spiders in Zackenberg, west Greenland, was observed by Høye and Forchhammer (2008) who suggested that males die early in the season shortly after mating. Other authors argued that the male peak is often correlated with mate searching activity (Schmoller 1970; Muma 1973; Doane and Dondale, 1979). A similar peak in males was observed for two species, *M. sobrius* and *A. nigripes,* but only at Breinosa. For the other sites, and the other spider species, the decline in trap catch is similar for both sexes. Buddle and Draney (2004) used pitfall traps to investigate the phenology of linyphiid spiders in a deciduous forest in Canada. They observed that for many species the female and male peak is more or less simultaneous. Male and females were, respectively, actively searching for mates and ideal locations to deposit their eggs. The two-week sampling period used for the current study is perhaps the reason for the apparent simultaneous peak for females and males for most sites among the spider species collected, aggregating into one trap catch short time variations in activity or density. The presence of both adults and juvenile spiders both early and late in the season indicates that the Linyphiidae in Svalbard overwinter in a range of different life stages.

Taxonomic confusion of *Walckenaeria* in Svalbard

Although the invertebrate fauna of Svalbard is one of the better known in the Arctic (Hodkinson 2013), there is still the potential for taxonomic confusion due to synonyms and misidentification (Coulson et al. 2014). Most of the recent checklists and literature do not list *W. clavicornis* as present in Svalbard, but a very similar species, *Walckenaeria karpinskii* (O.P.-Cambridge, 1873), is recorded as being present (Aakra and Hauge 2003; Coulson and Refseth 2004 and references therein; Coulson et al. 2014; Coulson 2015). Previously, Hinz (1976) reported *W. clavicornis* as present in his material from Svalbard, while Koponen (1980) collected a single female in Adventfjorden. In Greenland, both *W. karpinskii* and *W. clavicornis* are present and Holm (1967) described the confusion that can arise when attempting to differentiate between these two species. Interestingly, Holm also listed Spitsbergen as a part of the distribution for *W. clavicornis* but not for *W. karpinskii*, but without providing a reference. In his previous work on the spiders of Spitsbergen (Holm 1958, 1960), he listed *W. karpinskii* but not *W. clavicornis*. As we found a sizable amount of *W. clavicornis* but no *W. karpinskii*, we suggest that past observations of *W. karpinskii* might be due to taxonomic confusion and misidentification.

Araneae absent in our material

In addition to *W. karpinskii*, only three species previously recorded from Svalbard did not appear in the collected material (*Collinsia thulensis* (Jackson, 1934), *Erigone tirolensis* L. Koch, 1872, and *Oreonetides vaginatus* (Thorell, 1872)). Their absence could have several explanations, such as their general low abundance in Svalbard, but may also be a product of the collection method and habitats sampled. Bristowe (1933) reported that the most common spiders found in Svalbard were *E. psychrophila*, while in our material it was the rarest with only 3 individuals found. Rather than suggesting that the spider assemblage has radically changed since the 1930s, this probably illustrates the effect of different sampling strategies and the importance of sampling habitat selection. In Québec, Canada, a survey of ground-living spider assemblages in six different mountain habitats only found *O. vaginatus* in one of them (Koponen 1987). In another survey undertaken in six different adjacent habitats (10 to 100 m apart) on a dune system in North Greenland, *C. thulensis* and *E. psychrophila* were found only sparsely outside of one habitat (Cotton 1979). *Erigone tirolensis* is listed by Duffey (2005) as a typical mountainous species with stenotopic characteristics, defined as a species that only tolerates a narrow range of environmental conditions/habitats (Lincoln et al. 1998; Calow 1999; Ramade 2002). This suggests that these species have specific habitat preferences that might not have been covered by the present study.

The tundra habitat is characterised by a mosaic of plant species with large variation in community structure over short spatial distances (Jónsdóttir 2005). Studies such as those described here demonstrate that this high spatial variability is reflected in some invertebrate assemblages. Sikes et al. (2013) suggested that the Linyphiidae, spiders with high dispersive abilities in all age classes, might be suited to habitat specialisation since their dispersal ability compensates for the risks of being too specialised and not finding appropriate habitats. However, the detailed dynamics of the complex Arctic invertebrate assemblages are still largely unknown.

Conclusions

The spider fauna of Svalbard is diverse and consists of species with generally wide Arctic, or Palaearctic, distributions. Yet, the local assemblages are distinctly heterogeneous. These, and individual species distribution patterns, can be related to various environmental factors, with vegetation and/or topography being the best predictors depending on the species examined. This study demonstrates the complex composition of spider assemblages in the Arctic and hints

at niche specialisation within the Linyphiidae, a typically generalist *Araneae* family.

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