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Cushion plants act as facilitators for soil microarthropods in high alpine Sweden

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Abstract

Cushion plants can have positive impacts on plant richness in severe environments and possibly across trophic levels on arthropods, an under-studied topic. This study examined whether soil communities under cushions have higher richness and abundance of soil microarthropods than adjacent non-cushion vegetation, and whether differences in collembolan and mite abundance and species richness between cushions and adjacent vegetation increase with elevation. Paired soil samples were taken under cushions of *Silene acaulis* along the elevation gradient (1000, 1100, 1200, 1300, 1400 m a.s.l.), under cushions of *Diapensia lapponica* on the exposed ridge above the treeline (1000 m a.s.l.), and under adjacent non-cushion plant vegetation. In total, 5853 individuals of collembolans (n = 1705) and mites (n = 4148) were obtained from soil samples and identified to order/ species level. *S. acaulis* cushions had a positive effect on species richness and abundance of collembolans, with richness effects from 1100 m a.s.l. upwards. Oribatid mite richness and abundance were also higher under cushions compared with adjacent vegetation. Species richness of collembolans and oribatids declined with increasing elevation from 1200 m a.s.l. Collembolan abundance peaked at mid-elevation (1200 m a.s.l.) under cushions and adjacent vegetation, while oribatid mite abundance peaked at 1300 m a.s.l. under both vegetation types. *D. lapponica* cushions on the exposed ridge had significant positive effects on species richness, abundance and diversity index of collembolans, and abundance of oribatids. Cushion plants play an important role in supporting the biodiversity of soil fauna in severe alpine environments, with the positive effects of cushion plants increasing with environmental severity.

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Introduction

Facilitation is defined as an interaction in which the presence of one species alters the environment in a way that enhances growth, survival, or reproduction of a second, neighboring species (Bronstein 2009). Facilitation effects tend to occur in high-stress environments such as Arctic and alpine ecosystems (Antonsson et al. 2009), and the impact of facilitation tends to increase with environmental stress (Choler et al. 2001; Brooker et al. 2008). However, studies of positive interactions have primarily focused on plant-plant interactions (Callaway and Walker 1997; Choler et al. 2001; Brooker et al. 2008).

The intimate association of various organisms with certain plant species within terrestrial habitats is relatively well-known, in particular for pollinators and phytophagous larvae of insects or phytoparasites. Plant-arthropod interactions in natural alpine habitats have been studied, but mainly for pollinators and benthic or soil surface species (Cardinale et al. 2002; Molina-Montenegro et al. 2006; Sieber et al. 2011; Molenda et al. 2012; Reid and Lortie 2012), with fewer studies on cushion plant-soil arthropod interactions (Coulson et al. 2003; Minor et al. 2016).

Cushion-forming plant species are a common component of communities in alpine environments around the world. Globally, 338 cushion plant species have been recorded in 34 families and 78 genera, mainly in harsh alpine and other cold regions (Hauri and Schröter 1914; Arredondo-Núñez et al. 2009). Cushion plants offer a broad scope of research topics and the ecological evidence to date strongly suggests that cushion plants can be keystone species in their ecosystems (Reid et al. 2010). Predicted changes associated with a changing climate in regions with a high cushion plant abundance make such plants very appropriate for ecological observations and experiments.

Cushion plants act as foundation and nurse species in alpine ecosystems, providing structurally unique microhabitats with more stable environmental conditions, and positively influencing the richness and abundance of other organisms (Badano and Cavieres 2006; Cavieres et al. 2007; Molenda et al. 2012; Bonanomi et al. 2015). Soils under *Silene acaulis* cushions have been shown to have higher organic carbon (C) content, salinity, total nitrogen (N) and C/N ratio, and lower pH compared with soil under adjacent vegetation (Bonanomi et al. 2015).

In a study in a rocky alpine meadow in British Columbia, Canada, *S. acaulis* had a higher visitation rate and diversity index of both surface arthropods and pollinators relative to 11 species of non-cushion plants (Reid and Lortie 2012). Higher richness, abundance, and diversity index of ground arthropods and higher richness and abundance, but not diversity, of plants have been observed in cushions of *S. acaulis* in comparison with non-cushion adjacent vegetation in the same area (Molenda et al. 2012). Coulson et al. (2003) found higher soil microarthropod densities under *S. acaulis* cushions than under five other vascular plants in a high-Arctic vegetation mosaic.

The aims of the present study were to: i) compare soil microarthropod communities inhabiting soil under two cushion plant species, *S. acaulis* along an elevation gradient and *Diapensia lapponica* on an exposed ridge, with those inhabiting soil under adjacent non-cushion vegetation; and ii) evaluate the effect of elevation gradient and facilitation by cushion plants on microarthropod communities under these two types of vegetation. The hypotheses tested were that: 1) soil communities under cushions of *S. acaulis* and *D. lapponica* have higher richness and abundance of soil microarthropods (mites, collembolans) than soil communities under adjacent non-cushion vegetation; and 2) a

facilitation effect, measured as the difference in collembolan and mite abundance and species richness between *S. acaulis* cushions and adjacent vegetation, increases with increasing elevation.

Methods and study area

Characteristics of the study area

The study was carried out in northernmost Sweden, at Latnjajaure Field Station (LFS) in the Latnjavagge valley (68°21'N, 18°30'E). The valley is covered with snow for most of the year, and the climate is classified as sub-Arctic (Polunin 1951; Alatalo and Molau 1995). It has cool summers and relatively mild, snow-rich winters, with mean annual air temperature ranging from -0.76 to -2.92°C between 1993 and 2013 (Alatalo et al. 2017a). Mean annual precipitation since 1993 is 846 mm, but in individual years it has ranged from 607 mm (1996) to 1091 mm (2003). July is the warmest month, with mean temperature ranging from 5.9°C in 1995 to 13.1°C in 2013 (Alatalo et al. 2017a). The vegetation in the valley comprises a wide range of communities that reflect of local soil type and environmental properties, varying from dry to wet and poor and acidic to base-rich (Molau and Alatalo 1998).

Cushion plants

Silene acaulis (Caryophyllaceae) is a herbaceous cushion plant characteristic of alpine and Arctic tundra habitats in Asia, Europe, Greenland, and North America. It has a disjunct circumpolar distribution in sub-Arctic, Arctic, and alpine locations and a gap in the Siberia region (Junttila and Robberecht 1993; Gussarova et al. 2015). In Europe, the southernmost populations of *S. acaulis* are found in the Alps, Balkans, British Isles, Carpathian Mountains, Cantabrian Mountains, and Pyrenees (Ferrarini et al. 2019b). *S. acaulis* is widespread in the Latnjavagge valley (1000 m a.s.l.) to the peak of Latnjačorru mountain (1446 m a.s.l.). As at other sites, the cushion morphology of *S. acaulis* changes with elevation, with the cushions becoming smaller and more compact at higher elevation (Alatalo and Molau 1995; Bonanomi et al. 2015). *S. acaulis* is a long-lived perennial that forms light-green, moss-like dense dwarf cushions with pink flowers (Morris and Doak 1998). It has high germination rates, and the cushion growth form enables its seedlings to tolerate frost and drought (Milbau et al. 2009). Its small seeds can be dispersed by wind (Gehring and Delph 1999). *S. acaulis* is polymorphic, with reproductive systems and gender frequencies varying between populations (Alatalo and Molau 1995; Philipp 1997).

Diapensia lapponica (Diapensiaceae) is another cushion-forming and long-lived (up to 400 years) circumpolar Arctic-alpine evergreen perennial species, adapted to the harshest of environments with exposed cold, windswept conditions (Day and Scott 1984; Molau 1997). It forms cushion domes or mats, radiating from a single, stout, woody tap-root, which act as solar heat traps and warm up the soil beneath the cushions (Day and Scott 1984; Molau 1997). The leaves are glabrous, and frost-resistance of the cushion is imparted by extremely dense leaf aggregation (Molau 1997). *D. lapponica* is common at exposed sites, such as windswept ridge crests, and is indifferent to substrate acidity. In locations with active soil processes, e.g., solifluction, *D. lapponica* can be found in microhabitats with longer duration of annual snow cover (Molau 1996). It is a slow-growing species, e.g.,

at Latnjajaure the average age at which the plant becomes reproductive is 18 years (Molau 1997). Seedling recruitment of *D. lapponica* typically takes place during colder years, e.g., in the Latnjavagge valley there is a negative correlation between seedling recruitment and mean annual temperature (Molau 1997). Although *D. lapponica* is a weak competitor, it can grow in adverse habitats, often on acid soils or low-nutrient soils (Day and Scott 1984; Molau 1997). Where the climate and soil permit, *D. lapponica* clumps can be invaded and overgrown by competing species (Day and Scott 1984). Research to date on this plant species has focused on recruitment and persistence of *D. lapponica* seedlings (Sutton et al. 2006), age-related growth and reproduction (Molau 1997), survival and genetic divergence (Ikeda et al. 2008), and pollen limitation of reproduction (Elberling 2001). However, there is a lack of data on the influence of *D. lapponica* cushions on soil fauna.

Sampling and identification of soil fauna

In peak summer (25 July) 2013, soil cores (part of a plant cushion with underlying soil) were taken from individual cushions of *S. acaulis* and from adjacent non-cushion vegetation (50–100 cm distance from *S. acaulis* cushions), in a pairwise design along an elevation gradient from the bottom of the Latnjavagge valley (above treeline) along the south-west facing slope to the peak of Latnjačorru mountain (1446 m a.sl.). Sampling was carried out at (m a.s.l.): 1000 (68°21′30.24″N, 18°29′49.5″E), 1100 (68°21′30.06″N, 18°30′7.08″E), 1200 (68°21′30.84″N, 18°30′27.36″E), 1300 (68°21′33.78"N, 18°30′46.57"E), and 1400 (68°21′45.80"N, 18°31′13.27"E), along the same elevation transect as in a previous study on the facilitation effect of *S. acaulis* on plants (Antonsson et al. 2009). In total, 50 samples were taken (10 at each elevation, 5 samples under each vegetation type).

In addition to the altitudinal gradient study of *S. acaulis* cushions, on 27 July 2013, 14 soil cores were taken from cushions of *D. lapponica* and 14 from adjacent non-cushion vegetation in a pairwise design along a ridge at 1000 m a.s.l. (68°21′23,7"N, 18°29′ 41.16"E) in the Latnjavagge valley (Molau 1996). Photo documentation of the vegetation along the elevation gradient and the exposed ridge is provided in supplementary electronic materials to this paper (Figs. S1-S6).

All the samples were sampled by metal corer 3.6 cm in diameter (10 cm² in area) and to a maximum depth of 6–12 cm (depending on soil depth) (Figs. S7-S8). The samples were stored in plastic bags in coolboxes until extraction of soil fauna, which was performed within five days of field sampling using a modified high-gradient extraction apparatus of Tullgren type (self-constructed after Crossley and Blair 1991) applied over seven days.

Collembolans and mites were sorted under a binocular stereomicroscope (Olympus SZ61) and identified under a phase-contrast microscope (Leica DM2500). Collembolans were identified to species level using basic taxonomic keys (Zimdars and Dunger 1994; Fjellberg 1998, 2007; Bretfeld 1999; Potapov 2001; Thibaud et al. 2004; Janssens and Christiansen 2011). Within mites, oribatids were identified to species level using taxonomic keys (Olszanowski 1996; Walter and Proctor 1999, Chapter 3; Weigmann 2006).

Statistical analyses

To characterize collembolans and oribatids communities at the sites, abundance (A), dominance (D), and species richness (S) were analyzed as community parameters. The dominance of an individual species was expressed as $D = N_i/N \times 100$ (%), where $N_i =$ total

number of individuals of species *i* and N = total number of individuals at each site. Diversity and evenness indices were calculated, namely Shannon diversity index (H´) and Pielou evenness index (J´), to document the character of the microarthropod communities. Species dominance rank curves with a comparison of trend lines between *S. acaulis* cushions and adjacent vegetation along the elevation gradient were constructed, to assess the differences in structure of soil microarthropod communities (MS Excel 2016). The significance of differences between the trends of the rank dominance curves for the cushions and adjacent vegetation was analyzed. Probability (p) values for differences in the intercepts and in slopes between the regression lines were calculated with ANCOVA (Lowry 2021).

Repeated-measure ANOVA was used to test the significance of abundance variance of soil microarthropods between vegetation types along the elevation gradient. When the data were not normally distributed, Box-Cox transformation was applied. Species of collembolans with more than 100 specimens and species of oribatids with more than 50 specimens in the total material were tested to check for significant differences in ecological parameters between *S. acaulis* cushions and adjacent vegetation along the elevation gradient. The Wilcoxon Matched Pairs Test was used to confirm significant differences between *S. acaulis* cushions and adjacent vegetation for mean abundance, species richness and diversity indices of collembolans and oribatids, and mean abundance of dominant collembolans and oribatids species, for every elevation separately.

Significance of variance in mean abundance of all Acari groups and collembolans, species richness of collembolans and oribatids, and mean abundance of dominant collembolan and oribatid mite species (species with more than 15 specimens in total material) between *D. lapponica* and adjacent vegetation was tested with the Mann–Whitney Test. All tests were performed using Statistica for Windows, version 12 (2013).

Non-metric multidimensional scaling (NMDS) ordination was used to display patterns of soil microarthropod distribution under *S. acaulis* cushions and adjacent vegetation. A two-dimensional solution was generated without data transformation in the autopilot mode, with the slow and thorough option and Sørensen (Bray–Curtis) distance (appropriate for community data). NMDS was performed using PC-ORD version 7.2 (McCune and Mefford 2016), using a data matrix of the abundance of the selected collembolan and oribatid species (collembolans with more than 100 specimens and oribatids with more than 50 specimens in the total material), calculated for all three vegetation types and elevation.

Results

Comparison of *Silene acaulis* and adjacent vegetation along an elevation gradient

In total, 3807 soil mites and 1392 collembolans were recorded along the elevation gradient, in association with *S. acaulis* cushions and adjacent vegetation. Within the mites, oribatids (2835 individuals), Prostigmata (745 individuals), and Gamasina (193 individuals) were the most numerous groups. Astigmatina represented only a negligible proportion of the total Acari numbers and were therefore excluded from statistical analyses. The recorded collembolan individuals belonged to 10 families, 30 genera and 41 species. The oribatids, the dominant group of soil mites, were identified to species level, with 107 species belonging to 28 families and 52 genera recorded.

Abundances of all Acari and dominant Acari groups were higher under *S. acaulis* cushions than under adjacent vegetation at all elevations, but only the total for all Acari

Table 1 Mean abundance [ind.m⁻²], species richness, diversity, and evenness indices of microarthropod groups under *S. acaulis* cushions and adjacent vegetation along an elevation gradient

	1000 m a.s.l		1100 m a.s.l		1200 m a.s.l		1300 m a.s.l		1400 m a.s.l	
	Silene	adj.veg	Silene	adj.veg	Silene	adj.veg	Silene	adj.veg	Silene	adj.veg
A—total Acari	80,208	46,788	**97,311**	**70,771**	109,892	48,360	123,064	66,446	75,883	29,685
S.D	48,982	16,070	42,363	12,549	115,491	22,126	83,805	50,646	14,668	35,823
A—Prostigmata	28,898	8060	30,668	10,812	25,163	6881	8060	8453	10,812	8650
S.D	30,213	9985	51,091	7156	38,746	5247	6035	5672	9951	17,739
A—Gamasina	2949	3932	3342	6487	5701	1966	5701	1769	**5701**	**393**
S.D	3475	3743	1645	3585	5126	1554	3215	2899	2815	879
A—Uropodina	1966	197	393	786	0	197	393	0	0	0
S.D	3333	440	538	1758	0	440	879	0	0	0
A—Astigmatina	393	393	197	393	1180	0	0	0	0	197
S.D	583	538	440	538	822	0	0	0	0	440
A—Oribatida	46,001	34,206	62,711	52,292	77,849	39,317	108,909	56,224	59,369	20,445
S.D	22,771	8352	12,748	11,926	75,050	22,089	76,550	48,101	18,397	17,548
A—Collembola	27,719	26,539	35,386	26,736	40,694	32,437	26,343	23,394	15,924	18,479
S.D	20,914	11,463	19,174	9257	21,497	20,299	11,151	16,917	9790	14,268
St—Collembola	19	23	20	16	21	18	17	14	16	11
Sm—Collembola	9.0	9.4	10.2	7.8	9.6	7.4	8.0	5.0	5.4	3.6
S.D	3.5	3.8	1.6	1.6	2.5	1.9	1.2	1.2	2.4	2.5
H´—Collembola	1.8	1.7	2.0	1.7	1.9	1.6	1.7	1.0	1.3	0.8
S.D	0.5	0.6	0.2	0.5	0.2	0.3	0.1	0.4	0.5	0.7
J´—Collembola	0.9	0.8	0.9	0.8	0.9	0.8	0.8	0.7	0.8	0.5
S.D	0.1	0.1	0.1	0.2	0.1	0.2	0.1	0.3	0.1	0.4
St—Oribatida	29	25	34	35	38	30	23	10	44	14
Sm—Oribatida	9.4	7.0	13.4	11.0	11.6	9.4	9.0	3.4	13.6	4.0
S.D	4.4	2.5	2.3	1.7	6.9	5.5	2.1	2.1	7.6	1.9
H´—Oribatida	1.9	1.7	2.2	2.0	2.0	1.9	1.9	0.8	2.2	1.1

Table 1 (continued)

	1000 m a.s.l		1100 m a.s.l		1200 m a.s.l		1300 m a.s.l		1400 m a.s.l	
	Silene	adj.veg	Silene	adj.veg	Silene	adj.veg	Silene	adj.veg	Silene	adj.veg
S.D	0.7	0.4	0.3	0.3	0.5	0.7	0.3	0.7	0.6	0.7
J′—Oribatida	0.9	0.9	0.9	0.8	0.9	0.9	0.9	0.6	0.9	0.8
S.D	0.1	0.1	0.1	0.1	0.1	0.0	0.1	0.4	0.1	0.3

Significance of variance was tested using Wilcoxon Matched Pairs Test. Significant differences shown in bold

A: abundance, *Sr*: total species richness, *Sm*: mean species richness per sample, *H′*: Shannon diversity index, *J′*: Pielou evenness index, *Silene*: *S. acaulis*, *adj.veg*: adjacent vegetation

* p<0.05

combined at 1100 m a.s.l. showed a significant difference (Table 1). Oribatids had the highest abundance of all soil mites across the elevation transect, representing more than 70% of all collected mites. Oribatid abundance under *S. acaulis* cushions increased with elevation to 1300 m a.s.l. and at 1400 m a.s.l. there was a decrease. The abundance of the mites under adjacent vegetation plots showed no distinct trend. The predatory groups Prostigmata and Gamasina had different abundance distributions between the two vegetation types at different elevation levels. Gamasina were more abundant under adjacent vegetation at 1000 and 1100 m a.s.l., but appeared in distinctly higher abundance under *S. acaulis* cushions at higher elevations, with a significant difference ($p < 0.05$) only at the highest elevation 1400 m a.s.l. (Table 1). Prostigmata showed the opposite abundance distribution trend. These mites were distinctly more abundant under *S. acaulis* cushions up to 1200 m a.s.l., while their abundances at higher elevations were similar within both vegetation types. Similarly to oribatids, collembolans were more abundant under *S. acaulis* cushions, except at 1400 m a.s.l., where the abundance was higher under adjacent vegetation. A statistically significant effect ($p < 0.01$) of vegetation type on totals of mites and collembolans, and on the oribatids and Gamasina groups, was obtained (Table 2). However, a significant effect of elevation or a combined effect of elevation and vegetation type on these microarthropod groups was not observed.

Total species richness of collembolans under *S. acaulis* cushions along the whole elevation transect was slightly higher ($S = 34$) than under adjacent vegetation ($S = 31$). Species richness within all *S. acaulis* cushions at the different elevations studied was also higher than under adjacent vegetation, except at 1000 m a.s.l. (Table 1). Total species richness of collembolans at each elevation and mean species richness per sample under both vegetation types decreased continuously to the highest elevation, with a significant difference at 1300 m a.s.l. ($p < 0.05$). For oribatids, differences in total species richness (ie. all elevations together) between Silene cushions ($S = 87$) and adjacent vegetation ($S = 67$) were more distinct compared with collembolans. Species richness at each elevation, except 1100 m a.s.l., was higher under *S. acaulis* cushions than under adjacent vegetation (Table 1). Mean species richness of oribatids was significantly higher under *S. acaulis* cushions at 1300 and 1400 m a.s.l. ($p < 0.05$).

Diversity and evenness indices of oribatids and collembolans under *S. acaulis* cushions compared with adjacent vegetation showed higher mean values at all elevation levels. For collembolans, the Shannon diversity index was significantly different for elevation at level 1300 m a.s.l. ($p < 0.05$), while for oribatids the index was significantly different at elevation 1400 m a.s.l. ($p < 0.05$) (Table 1). Significant effects of elevation and vegetation type on collembolan diversity, and of vegetation type on evenness index, were detected (Table 2). Oribatid diversity was significantly affected by the elevation and vegetation type.

In NMDS ordination, the best three-dimensional solution, for which the first two dimensions are shown in (Fig. 1), had final stress of 17.12 ($p < 0.001$) after 500 iterations. This was confirmed by a Monte Carlo Permutation Test with $p < 0.005$, and mean stress of 17.45 for real data and 250 runs for both real and randomized data. The first three axes explained 38.1%, 20.3%, and 16.5% of the variance, respectively. The NMDS results confirmed the impact of elevation on community composition. The diagram revealed the similarity of communities at lower elevations (1000 to 1200 m), and more diverse communities at the two highest elevations. Using species dominance rank curves also revealed greater differences in collembolan and oribatid community structure between *S. acaulis* cushions and adjacent vegetation at the two highest elevations (Fig. 2 and Fig. 3).

Species of collembolans and oribatids were divided into three groups depending on their preference for vegetation types along the elevation gradient. The first group,

Table 2 Statistical parameter estimates from repeated measure ANOVA analyses testing the effect of vegetation type, elevation, and their interaction on microarthropod groups abundance, species richness, diversity, and evenness indices

Predictor	F	p	df
A—total Acari			
elevation	1.748	0.179	4
vegetation type	**186.011**	**< 0.001**	**1**
altitude*vegetation type	2.095	0.119	4
A—Gamasina			
elevation	0.674	0.618	4
vegetation type	**131.665**	**< 0.001**	**1**
altitude*vegetation type	2.095	0.119	4
A—Oribatida			
elevation	1.642	0.203	4
vegetation type	**201.033**	**< 0.001**	**1**
altitude*vegetation type	1.461	0.251	4
A—Collembola			
elevation	2.089	0.120	4
vegetation type	**12.252**	**< 0.01**	**1**
altitude*vegetation type	0.075	0.989	4
S—Collembola			
elevation	**10.831**	**< 0.001**	**4**
vegetation type	**5.446**	**0.030**	**1**
altitude*vegetation type	0.706	0.597	4
H´—Collembola			
elevation	**10.223**	**< 0.001**	**4**
vegetation type	**12.750**	**< 0.01**	**1**
altitude*vegetation type	0.477	0.752	4
J´—Collembola			
elevation	1.138	0.367	4
vegetation type	**77.253**	**< 0.001**	**1**
altitude*vegetation type	1.001	0.430	4
S—Oribatida			
elevation	2.624	0.065	4
vegetation type	**13.305**	**< 0.01**	**1**
altitude*vegetation type	1.507	0.238	4
H´—Oribatida			
elevation	**3.049**	**0.041**	**4**
vegetation type	**14.706**	**< 0.01**	**1**
altitude*vegetation type	2.407	0.083	4

Significant differences shown in bold. Oribatid evenness could not be tested due to non-normal data distribution even after transformation

P: probability value, *df*: degrees of freedom, *A*: abundance, *S*: species richness, *H´*: Shannon diversity index, *J´*: Pielou evenness index. Data Box Cox-transformed to normalized distribution

with the majority of species, preferred *S. acaulis* cushions (collembolans: *Ceratophysella scotica*, *Desoria violacea*, *Folsomia palearctica*, *F. quadrioculata*, *Friesea mirabilis*, *F. truncata*, *Isotomiella minor*, *Parisotoma notabilis*; oribatids: *Ceratozetes*
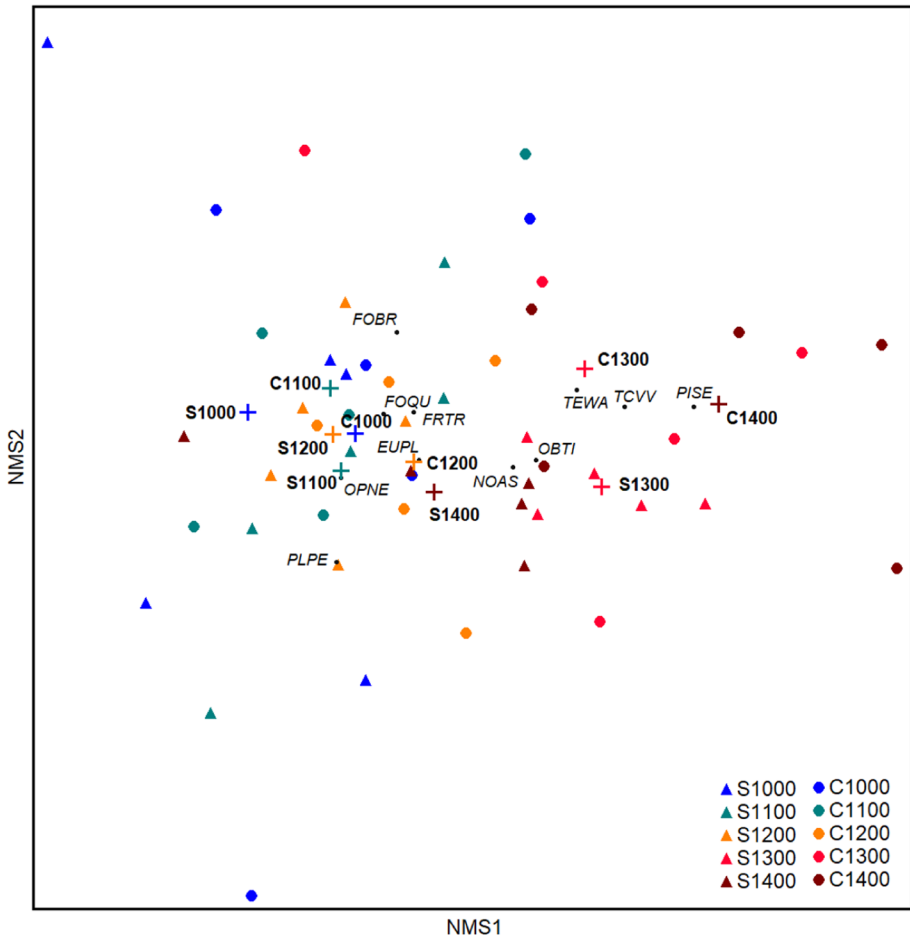
Fig. 1 Non-metric multidimensional scaling (NMDS) ordination plot of collembolan and oribatid communities under *S. acaulis* cushions and adjacent vegetation along an elevation gradient in an alpine region in northern Sweden. S – *S. acaulis* cushions centroids, C – adjacent vegetation centroids, 1000–1400 – elevation levels; for species abbreviations see Table 3

thienemanni, Dissorhina ornata, Eupelops plicatus, Nothrus aff. *silvestris, Oribatula tibialis, Platynothrus peltifer*) (Table S1). The second group, which showed higher abundances under adjacent vegetation, comprised a few collembolan species, namely *Desoria olivacea, Folsomia brevicauda* and *Tetracanthella wahlgreni*, and the oribatid mite *Tectocepheus velatus velatus*. The third group of species showed no distinct preference for vegetation type (collembolans: *Isotoma viridis, Pseudanurophorus binoculatus, Pseudisotoma sensibilis*; oribatids: *Oppiella neerlandica*).

Variance of abundance between *S. acaulis* cushions and adjacent vegetation was tested for the most abundant collembolan and oribatid species (Table 3), but no significant differences were observed.
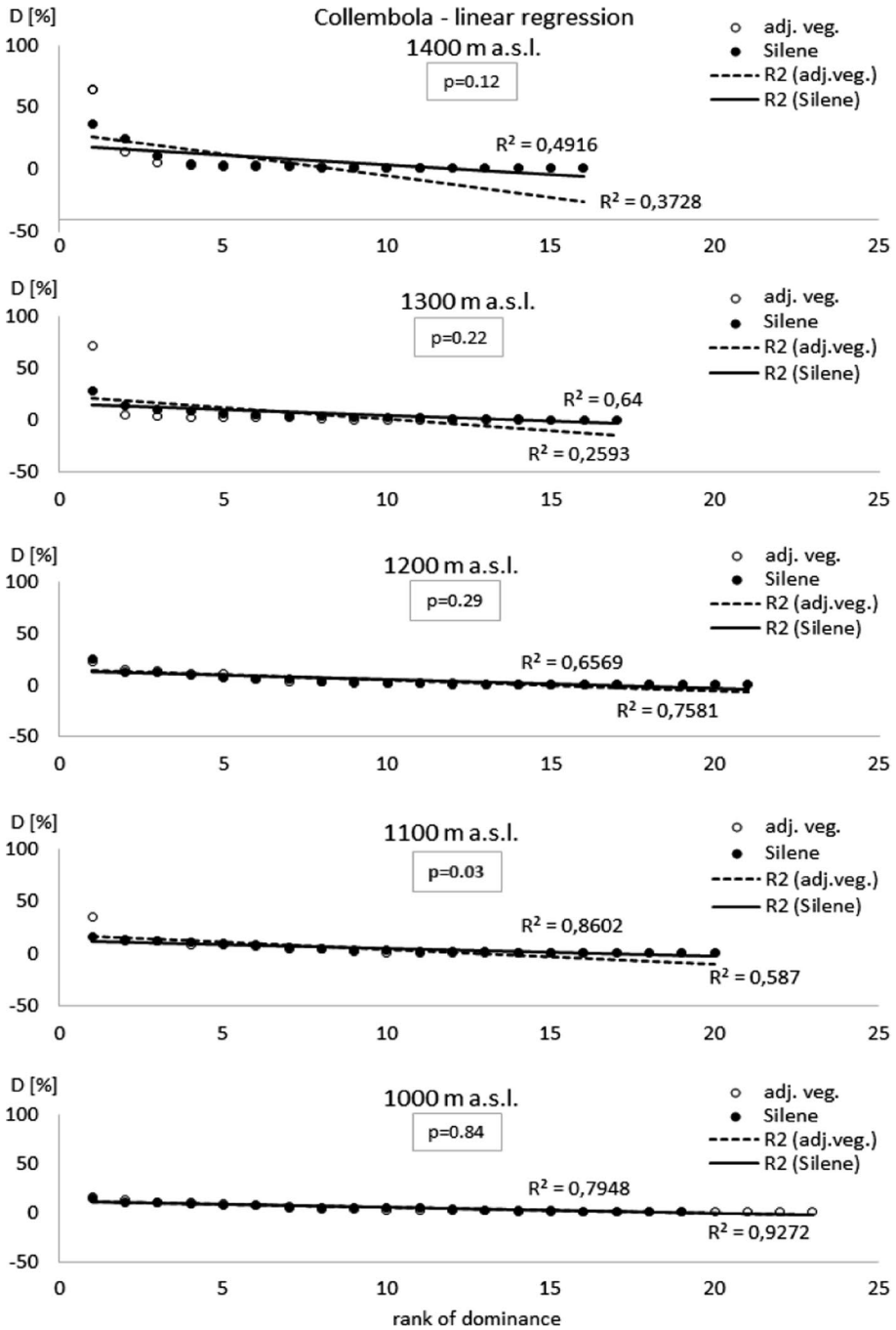
Fig. 2 Ranking of collembolan species dominance under *S. acaulis* cushions and adjacent vegetation along an elevation gradient. Silene—dominance of species observed under *S. acaulis* cushions, adj.veg.—dominance of species observed under adjacent vegetation
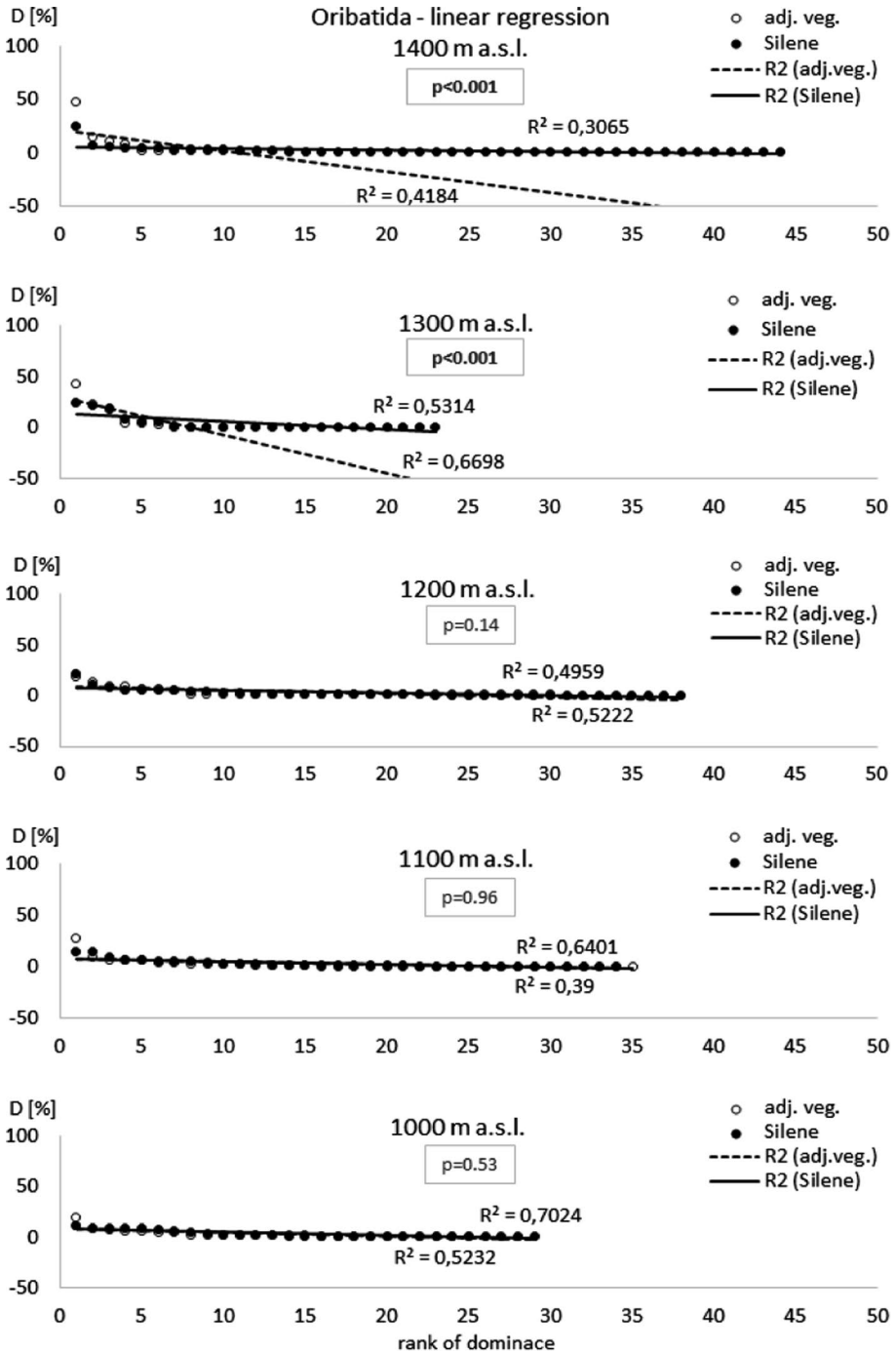
Fig. 3 Ranking of oribatid species dominance under *S. acaulis* cushions and adjacent vegetation along an elevation gradient. Silene—dominance of species observed under *S. acaulis* cushions, adj.veg.—dominance of species observed under adjacent vegetation

Table 3 Mean abundance [ind.m^{-2}] of dominant *collembolan* and *oribatid* mite species under *S. accaulis* cushions and adjacent vegetation along an elevation gradient

Species	Abbreviation	1000 m a.s.l		1100 m a.s.l		1200 m a.s.l		1300 m a.s.l		1400 m a.s.l	
		Silene	adj.veg	Silene	adj.veg	Silene	adj.veg	Silene	adj.veg	Silene	adj.veg
Collembola											
Folsomia quadrioculata	FOQU	2752	3539	4718	3145	10,616	4423	1769	786	5898	2556
S.D		4683	4318	4631	1758	4418	3260	1282	822	4285	3651
Tetracanthella wahlgreni	TEWA	590	2752	983	0	2359	4522	7470	16,906	197	983
S.D		879	590	1390	0	1786	6652	5586	17,016	440	1390
Folsomia brevicauda	FOBR	1573	2949	3735	9240	5308	4915	786	1180	590	0
S.D		1319	3260	4734	11,068	4895	5604	1282	1758	879	0
Friesea truncata	FRTR	2752	2162	5504	2162	3145	0	3932	393	197	197
S.D		5126	3139	6317	2899	3503	0	4662	538	440	440
Pseudisotoma sensibilis	PISE	0	0	0	0	197	393	2359	983	3932	11,992
S.D		0	0	0	0	440	879	2038	983	3993	13,977
Oribatida											
Oppiella neerlandica	OPNE	2162	2556	4718	7863	8650	3735	1966	393	6881	1769
S.D		2131	2656	2728	8982	5706	1282	2305	879	6739	3956
Tectocepheus velatus velatus	TCVV	0	393	2162	2752	590	1769	6684	6094	1769	5701
S.D		0	538	3433	4579	538	1282	5079	8524	1891	6498
Oribatula tibialis	OBTI	1180	393	786	197	590	1769	8650	3342	786	197
S.D		1758	879	822	440	538	2014	7136	1645	822	440
Nothrus cf. borussicus	NOAS	393	983	1769	1376	983	0	7667	2556	0	0
S.D		538	1702	822	1645	983	0	7068	5183	0	0
Platynothrus peltifer	PLPE	1573	393	4718	983	2556	2556	2162	197	0	0
S.D		2467	538	7876	983	3376	2263	2544	440	0	0
Eupelops plicatus	EUPL	1573	491	3145	786	3342	1180	3145	590	0	197
S.D		1491	983	3362	822	3077	1282	3362	1319	0	440

Silene: *S. accaulis*, *adj. veg*: adjacent vegetation

Comparison of *Diapensia lapponica* and adjacent vegetation

In total, 313 collembolans and 341 soil mite individuals were collected under *D. lapponica* and adjacent vegetation on the exposed mountain ridge (1000 m a.s.l.). The collembolans belonged to six families, 14 genera, and 17 species. More than 90% of Acari consisted of oribatids, represented by 18 species, 14 genera, and nine families. Astigmatina were not detected under *D. lapponica* cushions or under adjacent vegetation.

Total mites, saprophagous oribatids, and collembolans showed significantly ($p < 0.05$) higher abundance under *D. lapponica* cushions than under adjacent vegetation (Table 4). Predatory Gamasina mites showed higher abundance under *D. lapponica* cushions, but this relationship was not significant ($p > 0.1$). The abundance of mostly predaceous Prostigmata did not differ between vegetation types.

Table 4 Mean abundance [ind. m^{-2}] of soil microarthropod groups and species richness and diversity indices of collembolans and oribatids under *D. lapponica* cushions and adjacent vegetation

	Diapensia lapponica	adjacent vegetation
A—total Acari	**16,569**	**7372**
S.D	9139	4606
A—Prostigmata	351	351
S.D	623	828
A—Gamasina	562	211
S.D	743	419
A—Uropodina	70	70
S.D	263	263
A—Oribatida	**15,587**	**6740**
S.D	9372	4078
A—Collembola	**15,165**	**6810**
S.D	9048	4713
St—Collembola	17	7
Sm—Collembola	4.6	2.4
S.D	2.1	1.3
H´—Collembola	1.2	0.6
S.D	0.3	0.4
J´—Collembola	0.8	0.7
S.D	0.1	0.4
St—Oribatida	14	11
Sm—Oribatida	3.9	2.8
S.D	1.4	1.4
H´—Oribatida	1.1	0.8
S.D	0.4	0.5
J´—Oribatida	0.9	0.7
S.D	0.2	0.4

Astigmatina were not tested due to high number of zero values. Significance of variance tested using Mann–Whitney Test. Significant results shown in bold

A: abundance, *St*: total species richness, *Sm*: mean species richness per sample, *H´*: Shannon diversity index, *J´*: Pielou evenness index

* $p < 0.01$

Total species richness was higher under *D. lapponica* cushions than under adjacent vegetation in both main microarthropod groups (collembolans and oribatids). Mean species richness per sample was also higher under *D. lapponica* cushions than under adjacent vegetation, but only collembolans showed a significant difference (Table 4). All collembolan species recorded under adjacent vegetation also appeared under *D. lapponica* cushions. The majority of oribatid and collembolan species common to both treatments were more abundant under *D. lapponica* cushions (Table S2). Only the oribatid mite *Mycobates sarakensis* showed higher abundance under adjacent vegetation. Testing of the variance of abundance was performed on 11 species in total. Significantly higher abundances of the springtails *Friesea truncata* and *Folsomia quadrioculata* and the oribatid mite *Ceratozetes thienemanni* were observed under *Diapensia* cushions (Table 5). Of the two dominant microarthropod groups, only collembolans showed significantly higher diversity indices under *D. lapponica* cushions compared with the adjacent vegetation (Table 4).

Table 5 Mean abundance [ind. m⁻²] of dominant collembolan and oribatid mite species under *D. lapponica* cushions and adjacent vegetation

Species	Abbreviation	*Diapensia lapponica*	adjacent vegetation
Collembola			
Folsomia brevicauda	FOBR	3440	3651
S.D		2719	4453
Folsomia quadrioculata	FOQU	**5055**	**1755**
S.D		2856	1598
Friesea truncata	FRTR	**1896**	**140**
S.D		1701	357
Parisotoma notabilis	PSNO	1334	421
S.D		3099	922
Tetracanthella wahlgreni	TEWA	632	632
S.D		2364	1131
Oribatida			
Tectocephaeus velatus velatus	TCVV	2949	2036
S.D		2726	2452
Ceratozetes thienemanni	CZTH	**3791**	**1053**
S.D		3948	980
Oppiella acuminata	OPAC	1545	70
S.D		2239	263
Dissorhina ornata	DIOR	1194	140
S.D		2118	357
Mycobates sarekensis	MYSA	351	983
S.D		489	944

Significance of variance estimated using Mann–Whitney Test. Significant differences shown in bold

* p<0.01

Discussion

Nurse plants modify the conditions in stressful environments by providing a microclimate under their canopies. Thus they can increase species richness (Nuñez et al. 1999; Arroyo and Cavieres 2003; Badano and Marquet 2009), abundance (Cavieres and Arroyo 2002; Badano et al. 2007; Sklenář 2009), phylogenetic diversity (Butterfield et al. 2013), and survival of other plant species (Cavieres et al. 2007, 2008; Badano et al. 2007). In this study in an alpine region in Sweden, we observed a positive effect of cushion plants on soil microarthropods. As hypothesized, we found that the cushion plants *S. acaulis* and *D. lapponica* had higher species richness of collembolans and oribatids than adjacent vegetation. The positive facilitation effect of *S. acaulis* increased with increasing elevation. In contrast, a study in high-elevation New Zealand only found a positive impact of cushion plants on abundance and richness of mites (Oribatida, Mesostigmata, Prostigmata), while collembolan abundance was higher in adjacent vegetation (Minor et al. 2016). Those authors suggested that the difference between organism groups may have been due to mites being more sensitive to disturbances; collembolans are more mobile and more generalist feeders, are more opportunistic, and colonize new patches between cushion plants.

Soils under *S. acaulis* and other cushion plants have been shown to have higher moisture, organic C, salinity, total N, and C/N ratio, and lower pH than soils under adjacent vegetation (Cavieres et al. 2007; Antonsson et al. 2009; Bonanomi et al. 2015; Minor et al. 2016). As bacterial and fungal communities are frequently positively associated with higher soil moisture and organic C and N, soils under cushions could potentially have larger biomass of bacteria and fungi (Zumsteg et al. 2013), both of which are important food sources for collembolans and mites. The morphology of *S. acaulis* changes along the elevation gradient, with looser and flatter cushions at lower elevation and more dense and tight dome-shaped cushions at higher elevation (Bonanomi et al. 2015). More dense *S. acaulis* cushions might retain moisture and stabilize temperature more effectively, thus supporting richer bacterial and fungal communities.

There is a lack of information on soil properties under *D. lapponica* cushions compared with adjacent vegetation. *D. lapponica* is a long-lived plant and forms dome-shaped dense cushions (Day and Scott 1981) similar to those of *S. acaulis* and other cushion-forming species. It is often found in areas with cool summer temperatures (Damman 1976) and on acid, low-nutrient, or toxic soils (Day and Scott 1981), conditions which exclude many of its potential competitors. Cushions of *Diapensia* also act as heat traps and can considerably increase the soil temperature at night (Day and Scott 1981). These reports suggest that *D. lapponica* can influence soil properties under cushions, which could explain the distinct facilitation effect of *D. lapponica* on soil fauna observed in our study. There is likely to be a more stable and favourable microclimate for fauna in terms temperature and humidity.

A previous study on the microscale distribution of microarthropods in high-Arctic Svalbard found that collembolans, but not mites, showed higher abundance under cushions of *S. acaulis* than under five other plant species in the adjacent vegetation, with no difference in species richness of collembolans or mites between the other plant species (Coulson et al. 2003). However, that study was not carried out along an elevation gradient, unlike the present study in northern Sweden. Moreover, high-Arctic Svalbard encompasses more extreme environments, with markedly diminished species diversity (6 collembolan species, 7 mite species) compared with our alpine sub-Arctic site in Sweden (41 collembolan species, 107 oribatid species).

Similarly, a study carried out in high-alpine Chile found that ladybird beetle abundance was higher under cushion plants than under the surrounding vegetation, while a greenhouse experiment showed that, under milder temperatures, the beetles did not prefer cushions (Molina-Montenegro et al. 2006). Thus, the facilitation effect was only expressed under harsher microclimatic conditions. An association between facilitation effect and harsher microclimatic conditions could also explain why we observed more distinct differences in species richness, abundance, and diversity and evenness indices between cushions, compared with adjacent vegetation, at sites at the highest elevations (*S. acaulis*, 1300 and 1400 m a.s.l.) and on the exposed ridge (*D. lapponica*) in alpine Sweden examined in this study.

A study examining *S. acaulis* and its role as a facilitator species in the Canadian Rocky Mountains found that *S. acaulis* had higher visitation rate and diversity of both ground arthropods and pollinators than all non-cushion plants (Reid and Lortie 2012). Similarly, richness, abundance, and diversity index of above-ground arthropods were all higher under cushions of *S. acaulis* compared with adjacent vegetation in a study in the same area (Molenda et al. 2012). Another study at Latnjajaure, covering the same transect as in the present study, found that cushions of *S. acaulis* had a facilitation effect on other plants at higher elevations (Antonsson et al. 2009).

Rank-abundance (relative abundance) diagrams are widely used to document complex community structure (Begon et al. 2006). Steeper curves indicate more unbalanced community structure, with a few dominant and a high number of recedent species (Lindberg et al. 2002; Camann et al. 2008; Ľuptáčik et al. 2012). In the species dominance rank curves obtained in the present study, collembolan and oribatid mite communities displayed more visible differences between *S. acaulis* cushions and adjacent vegetation at the two highest elevations with harsher microclimatic conditions, while communities with more similar structure were observed at lower elevations with a milder microclimate. The vegetation that closely surrounded *S. acaulis* cushions at lower elevations (1000, 1100, 1200 m a.s.l.) (Antonsson et al. 2009) probably created more similar microclimatic conditions to those under *Silene* cushions, thus enabling movement of microarthropods between *S. acaulis* cushions and adjacent vegetation. At the highest elevations (1300, 1400 m a.s.l.), *S. acaulis* cushions and adjacent vegetation formed more or less isolated patches on the bedrock, and thus movement of microarthropods between *S. acaulis* cushions and adjacent vegetation more difficult. The adjacent vegetation consisted mainly of lichens and mosses, which likely also offered different soil conditions compared with those under *S. acaulis* cushions and had different community properties and structure.

Harsh microclimatic conditions on the exposed ridge, similar to those at the highest elevations (1300, 1400 m a.s.l.) of the gradient with *S. acaulis*, probably resulted in more favorable soil conditions under *D. lapponica* cushions compared with under poor adjacent vegetation (Molau 1996, 1997), explaining the significant differences in total Acari, oribatid, and collembolan abundance.

A previous study in the Latnjajaure valley found that collembolans under three different plant communities were resistant to two decades of experimental warming (Alatalo et al. 2015). However, abundance of juvenile mites, but not adults, declined with long-term warming (Alatalo et al. 2017b), most likely because juveniles are more soft-bodied than adults and thus more vulnerable to desiccation (Day et al. 2009; Bokhorst et al. 2012). That means there was a lower survival rate of juveniles to adulthood at higher temperatures. In addition, the warmed plots had no barriers within the soil, so adult soil mites could have re-colonized the warmed plots even when the conditions were unfavorable for juveniles (Alatalo et al. 2017b). Additionally, warmed plots could potentially

have allowed mites to reproduce and hatch earlier and grow faster than those in the control plots, so at the time of sampling many of them may have already developed into adults, decreasing the number of juveniles in the samples (Alatalo et al. 2017b).

However, it should be noted that the sampling in those studies was not focused on cushion plants, but performed randomly under the vegetation within experimental plots. Similarly, experimental warming in laboratory and field environment in high-Arctic Svalbard had no direct negative effect on collembolans and mites, while warming experiments combined with decreased moisture levels in the field had a large negative impact on collembolans (Hodkinson et al. 1996). Mites were unaffected in that study, suggesting that collembolans are more vulnerable to desiccation than mites.

Mites are under severe threat globally due to habitat destruction and degradation, with climate change likely to exacerbate the effects of the other drivers at an increasing rate (Sullivan and Ozman-Sullivan, 2021), although the mites and collembolans in alpine and Arctic areas are not likely to be directly negatively affected by increased temperatures due to climate change. However, experimental (Alatalo and Little 2014; Villellas et al. 2019) and monitoring studies (Doak and Morris 2010) suggest that *S. acaulis* may be vulnerable to climate change. Therefore, also collembolan and mite communities inhabiting soil under *S. acaulis* cushions could be indirectly vulnerable. In addition, recent modeling studies have estimated that more than 50% of current locations of *S. acaulis* are likely to be outside its future climatic hypervolume in North America (Ferrarini et al. 2019b). In the British Isles, the majority of its current locations will likely become unsuitable in the future (Ferrarini et al. 2019a). Similarly, *D. lapponica* is vulnerable to climate change, as earlier onset of snowmelt will expose it to increased risk of early frost events, which increase mortality when the plant is not protected by snow cover (Molau 1996). In this study, the species richness of both collembolans and mites was higher under cushions of *S. acaulis* and *D. lapponica* than under adjacent vegetation. If the abundance of these cushion plants declines in the future due to climate change, this is likely to have adverse effects on microarthropod diversity in alpine and Arctic regions.

Conclusions

In the subarctic study area, abundance, species richness and diversity indices of two major groups of soil microarthropods were all higher under *S. acaulis* and *D. lapponica* cushions than under adjacent vegetation, suggesting that cushion plants facilitate soil microarthropod communities. Significant impacts of elevation and vegetation type on collembolans and soil mites were demonstrated. NMDS analysis and species rank curves revealed differing microarthropod communities under the two different vegetation types at high-elevation sites (above 1300 m a.s.l.). This indicates that the level of facilitation of soil microarthropods by cushion plants increases with elevation and therefore plays a more critical role under harsher environmental conditions.

P.L. and L.K. were the main authors of the paper. All co-authors contributed to manuscript revisions and agree with the final version.

Data availability Data used for analysis accompany this article as electronic supplementary material.

Declarations

Conflict of interests The authors declare no conflict of interests.

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