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

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Summary:

1. Cushion plants can have positive impacts on plant richness in severe environments and possibly across trophic levels on arthropods, an under-studied topic.
2. This study examined whether soil communities under cushions of *Silene acaulis* and *Diapensia lapponica* have higher richness and abundance of soil microarthropods (Acari, Collembola) than adjacent non-cushion vegetation; and whether differences in collembolan and mite abundance and species richness between *S. acaulis* cushions and adjacent vegetation increase with elevation.
3. In total, 5199 individuals of Collembola (n=1392) and mites (n=3807) were identified to order/species level in samples along an elevation transect (1000, 1100, 1200, 1300, and 1400 m a.s.l.), and an exposed ridge above the treeline (1000 m a.s.l.) in northern Sweden. Paired soil samples were taken within cushions of *Silene acaulis* (along the elevation gradient) and *Diapensia lapponica* (on the exposed ridge) and adjacent non-cushion plant vegetation.
4. *Silene acaulis* had a positive effect on species richness and abundance of Collembola, with richness effects from 1100 m a.s.l. upwards. Oribatid mite abundance and richness were also higher in *S. acaulis* compared with adjacent vegetation.
5. Species richness of Collembola and Oribatida declined with increasing elevation from 1200 m a.s.l. Collembola abundance peaked at mid-elevation (1200 m a.s.l.) in both *S. acaulis* and adjacent vegetation, while oribatid mite abundance peaked at 1300 m a.s.l. in both vegetation types.
6. Cushions of *D. lapponica* on the exposed ridge had a significant positive effect on species richness, abundance and diversity of Collembola, and abundance of Oribatida.
7. Alpine cushion plants play an important role in supporting biodiversity of soil fauna in severe alpine environments, with the positive effect of cushion plants increasing with environment severity.

Keywords: alpine tundra, cushion plants, facilitation, plant animal facilitation, plant animal interaction, soil fauna, soil mites, springtails

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, Björk, & Molau, 2009), and the impact of facilitation tends to increase with environmental stress (Brooker et al., 2008; Choler, Michalet, & Callaway, 2001). However, studies of positive interactions have been primarily focused on plant-plant interactions (Brooker et al., 2008; Callaway & Walker, 1997; Choler et al., 2001).

Binding of various organisms to certain plant species within terrestrial habitats is relatively well-known, in particular for pollinators and phytophagous larvae of insects or phytoparasites. Data on plant-arthropod interactions in natural alpine habitats are generally scarce. Such important interactions within alpine environments have been studied, but mainly for pollinators and benthic or soil surface species (Cardinale, Palmer, & Collins, 2002; Molenda, Reid, & Lortie, 2012; Molina-Montenegro, Badano, & Cavieres, 2006; A. N. Reid & Lortie, 2012; Sieber et al., 2011), with fewer studies on cushion plant-soil arthropod interactions (Coulson, Hodkinson, & Webb, 2003; Minor, Babenko, Ermilov, Khaustov, & Makarova, 2016).

Cushions-forming plant species are a common component of communities in alpine locations around the world. Globally, 338 cushion plants have been recorded in 78 genera and 34 families, mainly in harsh alpine and other cold regions (Arredondo-Núñez, Badano, & Bustamante, 2009; Hauri & Schröter, 1914). Cushion plants offer a broad scope of research topics to study and the preliminary ecological evidence to date strongly suggests that cushion plants can be keystone species in their ecosystems (A. M. Reid, Lamarque, & Lortie, 2010). Predicted changes associated with a changing climate in regions with a high cushion plant distribution make such plants very suitable 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 diversity and abundance of other organisms (E. Badano & Cavieres, 2006; L. A. Cavieres, Badano, Sierra-Almeida, & Molina-Montenegro, 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* was found to have higher visitation rate and diversity of both surface arthropods and pollinators relative to 11 species of non-cushion plants (A. N. Reid &

Lortie, 2012). Higher richness, abundance, and diversity 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 territory (Molenda et al., 2012). Coulson, Hodkinson & Webb (2003) found higher soil microarthropod densities in *S. acaulis* cushions than in five other vascular plants in a high-Arctic vegetation mosaic.

The aims of the present study were to: i) compare soil microarthropod communities inhabiting two cushion plant species, *Silene acaulis* and *Diapensia lapponica*, with those inhabiting 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 the soil microarthropods (Acari, Collembola) than soil communities under adjacent non-cushion vegetation; and that 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

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 (Alatalo & Molau, 1995; Polunin, 1951). 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, Jägerbrand, Chen, & Molau, 2017). Mean annual precipitation since 1993 is 846 mm, but in individual years it 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, Jägerbrand, Chen, et al., 2017). The vegetation in the valley comprises a wide range of communities, varying from dry to wet and poor and acidic to base-rich (Molau & Alatalo, 1998).

Cushion plants

Silene acaulis L. (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 (Gussarova et al., 2015; Junttila & Robberecht, 1993). In Europe, the southernmost populations of *S. acaulis* are found in the Alps, Balkans, British Isles, Carpathian mountains, Cantabrian Mountains, and Pyrenees (Ferrarini, Dai, Bai, & Alatalo, 2019). *Silene 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 & Molau, 1995; Bonanomi et al., 2015). It is a long-lived perennial that forms light-green, moss-like dwarf cushions with pink flowers (Morris & Doak, 1998). *Silene acaulis* has high germination rates, and the cushion growth form enables its seedlings to tolerate frost and drought (Milbau, Graae, Shevtsova, & Nijs, 2009). Its small seeds can be dispersed by wind (Gehring & Delph, 1999). *Silene acaulis* is polymorphic, with reproductive systems and gender frequencies varying between populations (Alatalo & Molau, 1995; Philipp, 1997).

Diapensia lapponica L. (Diapensiaceae) is another cushion-forming and long-lived circumpolar Arctic-alpine evergreen perennial species, adapted to the harshest of environments with exposed cold, windswept conditions (R. T. Day & Scott, 1984; Molau, 1997). *Diapensia lapponica* is a long-lived (up to 400 years) (Molau, 1997). Its plants form 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 (R. T. Day & Scott, 1984; Molau, 1997). The leaves are glabrous, and frost-resistance of the cushion is imparted by extremely dense leaf aggregation (Molau, 1997). *Diapensia 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). Seed 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 (R. T. Day & Scott, 1984; Molau, 1997). Where the climate and soil permit, *D. lapponica* clumps can be invaded and overgrown by competing species (R. T. Day & Scott, 1984). Research to date on this plant species has focused on recruitment and persistence of *D. lapponica* seedlings (Sutton, Hermanutz, & Jacobs, 2006), age-related growth and reproduction (Molau, 1997), survival and genetic divergence (Ikeda, Senni, Fujii, & Setoguchi, 2008), and pollen limitation of reproduction (Elberling, 2001). 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, five soil cores were extracted from individual cushions of *S. acaulis* and five from adjacent non-cushion vegetation (50-100 cm distance from *S. acaulis* cushions), in a pairwise design (at each elevation) 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).

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). The samples comprised soil cores 3.6 cm in diameter (10 cm^2 in area) and with 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 applied over seven days (Crossley & Blair, 1991).

Collembola and Acari were sorted under a binocular stereomicroscope and identified under a phase-contrast microscope (Leica DM2500). Collembola were identified to species level using basic taxonomic keys (Bretfeld, 1999; Fjellberg, 1998, 2007; Janssens & Christiansen, 2011; Potapov, 2001; Thibaud, Schulz, & da Gama Assalino, 2004; Zimdars & Dunger, 1994). Within Acari, Oribatida were identified to species level using taxonomic keys (Olszanowski, 1996; Walter & Proctor, 1999; Weigmann, 2006).

Statistical analyses

To characterize Collembola and Oribatida 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 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 *Silene* cushions and adjacent vegetation along the elevation gradient were constructed, to assess the differences in structure of soil microarthropod communities (MS Excel 2016).

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 Collembola with more than 100 specimens and species of Oribatida more than 50 specimens in the total material were tested to detect 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 Collembola and Oribatida, and mean abundance of dominant Collembola and Oribatida species for every elevation separately.

Significance of variance in mean abundance of soil microarthropod groups, species richness of Collembola and Oribatida, and mean abundance of dominant collembolan and oribatid mite species (species with more than 15 specimens in total material) between *Diapensia lapponica* and adjacent vegetation was tested using the Mann-Whitney test. All tests were performed using Statistica for Windows, version 12 (*Statistica*, 2013).

Non-metric multidimensional scaling (NMDS) ordination was used to display patterns of soil microarthropod distribution in *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: & Mefford, 2016), using a data matrix of the abundance of selected Collembola and Oribatida species (Collembola with more than 100 specimens and Oribatida more than 50 specimens in total material) calculated for every vegetation type and elevation.

Results

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

In total, 3807 individuals of soil mites and 1392 individuals of Collembola were recorded along the elevation gradient with *S. acaulis* cushions and adjacent vegetation. Within the mites, Oribatida (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 were excluded from statistical analyses. Recorded Collembola individuals belonged to 41 species, 30 genera, and 10 families. Oribatida, the dominant group in soil mites, were identified to species level, with 107 species belonging to 52 genera and 28 families.

Abundances of total Acari and dominant Acari groups were higher in *S. acaulis* cushions than in adjacent vegetation at all elevations, but only total Acari at 1100 m a.s.l. showed a significant difference (Table 1). Oribatida had the highest abundance of all Acari across the elevation transect (Table 1), representing more than 70% of all mite individuals collected. Oribatid abundance in *Silene* cushions increased with elevation to 1400 m a.s.l., at which there was a decrease. The abundance of the mites in 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 showed higher abundance in adjacent vegetation at 1000 and 1100 m a.s.l., but appeared in distinctly higher abundance in *Silene* cushions at higher elevations, with a significant difference ($p<0.05$) only at the highest elevation (Table 1). Prostigmata showed the opposite abundance distribution trend. These mites were distinctly more abundant in *Silene* plots up to 1200 m a.s.l., while their abundances at higher elevations were similar within both vegetation types. Similarly to Oribatida, Collembola showed higher abundances in *Silene* cushions, except at 1400 m a.s.l., where the abundance was higher in adjacent vegetation. A statistically significant effect ($p<0.01$) of vegetation type on total Acari, Collembola, and the Oribatida, and Gamasina groups was obtained (Table 2). 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 Collembola in *Silene* cushions along the whole elevation transect was slightly higher (S=34) than in adjacent vegetation (S=31). Species richness within all *Silene* cushions at the different elevations studied was also higher than in adjacent vegetation, except at 1000 m a.s.l. (Table 1). Total species richness of Collembola at elevation levels and mean species richness per sample in both vegetation types decreased continuously towards the highest elevation, with a significant difference at 1300 m a.s.l. ($p<0.05$). For Oribatida, differences in total species richness between *Silene* cushions (S=87) and adjacent vegetation (S=67) across the elevation transect were much more noticeable than in Collembola. At all elevation levels studied except 1100 m a.s.l., *Silene* cushions showed higher per plot species richness than adjacent vegetation (Table 1). Mean species richness of Oribatida was significantly higher in *Silene* cushions at 1300 and 1400 m a.s.l. ($p<0.05$).

Diversity and equitability indices of Oribatida and Collembola in *Silene* cushions compared with adjacent vegetation showed higher mean values at all elevation levels. For Collembola, Shannon diversity index was significantly different for elevation at level 1300 m a.s.l. ($p<0.05$), while for Oribatida the index was significantly different at elevation 1400 m a.s.l. ($p<0.05$) (Table 1). A significant effect of elevation and vegetation type on Collembola diversity and vegetation type on equitability index was detected (Table 2). Oribatida diversity was significantly affected by 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 higher elevations on community composition. The diagram revealed the similarity of communities at lower elevations (1000 to 1200 m), and more different communities at the two highest elevations (Fig. 1). Using species dominance rank curves revealed greater differences in Collembola and Oribatida community structure between *Silene* cushions and adjacent vegetation at two highest elevations (Fig. 2 and Fig. 3).

Species of Collembola and Oribatida were divided into three groups depending on their preference for vegetation types. The first group, with the majority of species, preferred *Silene* cushions (Collembola: *Ceratophysella scotica*, *Desoria violacea*, *Folsomia palearctica*, *F. quadrioculata*, *Friesea mirabilis*, *F. truncata*, *Isotomiella minor*, *Parisotoma notabilis*; Oribatida: *Ceratozetes thienemanni*, *Dissorhina ornata*, *Eupelops plicatus*, *Nothrus* aff. *silvestris*, *Oribatula tibialis*, *Platynothrus peltifer*) (Table S1). The second group, which showed higher abundances in adjacent vegetation, comprised a few Collembola 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 along the elevation gradient (Collembola: *Isotoma viridis*, *Pseudanurophorus binoculatus, Pseudisotoma sensibilis*; Oribatida: *Oppiella neerlandica*).

Variance of abundance between *Silene* cushions and adjacent vegetation was tested for the most abundant Collembola and Oribatida species (Table 3), but no significant differences were observed.

Comparison of *Diapensia lapponica* and adjacent vegetation

In total, 313 individuals of Collembola and 341 individuals of soil mites were collected in *D. lapponica* and adjacent vegetation on the exposed mountain ridge (1000 m a.s.l.). Collembola belonged to 17 species, 14 genera, and six families. More than 90% of total Acari consisted of

Oribatida, represented by 18 species, 14 genera, and nine families. Astigmatina were not detected in *Diapensia* cushions or in adjacent vegetation.

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

Per-plot species richness was higher in *Diapensia* cushions than in adjacent vegetation in both main microarthropod groups (Collembola and Oribatida). Mean species richness (per sample) also showed higher values in *Diapensia* cushions than in adjacent vegetation, but only Collembola showed a significant difference (Table 4). All Collembola species recorded in adjacent vegetation also appeared in *Diapensia* cushions. The majority of Oribatida and Collembola species common to both treatments were more abundant in *Diapensia* cushions (Table S2). Only the oribatid mite *Mycobates sarakensis* showed higher abundance in adjacent vegetation. Tests on variance of abundance were performed on more than 15 species in total. Significantly higher abundances of the springtails *Friesea truncata* and *Folsomia quadrioculata* and the oribatid mite *Ceratozetes thienemanni* were observed in *Diapensia* cushions (Table 5). Within the dominant microarthropod groups, only Collembola showed significantly higher diversity indices in *Diapensia* cushions compared with the adjacent vegetation (Table 4).

Discussion

Nurse plants modify the conditions in stressful environments by providing a microclimate within their canopies. Thus they can increase species richness (Arroyo & Cavieres, 2003; E. I. Badano & Marquet, 2009; Nuñez, Aizen, & Ezcurra, 1999), abundance (E. I. Badano, Villarroel, Bustamante, Marquet, & Cavieres, 2007; L. Cavieres & Arroyo, 2002; Sklenář, 2009), phylogenetic diversity (Butterfield et al., 2013), and survival of other plant species (E. I. Badano et al., 2007; L. A. Cavieres et al., 2007; L. A. Cavieres, Quiroz, & Molina-Montenegro, 2008). In this study in an alpine region in Sweden, we observed a positive effect of cushion plants upon soil microarthropods. As hypothesized, we found that the cushion plants *Silene acaulis* and *Diapensia lapponica* had higher species richness of Collembola and Oribatida than adjacent vegetation. The positive facilitation effect of *S. acaulis* was found to increase 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, while Collembola abundance was higher in adjacent vegetation (Minor et al., 2016). Those authors suggested that the difference between organisms groups may have been due to mites being more sensitive to disturbances. Collembola are more mobile and more generalist feeders, are more opportunist, and colonize new patches between cushion plants (Minor et al., 2016).

Soils under *S. acaulis* and other cushion plants have been shown to have higher soil moisture, organic C content, salinity, total N, and C/N ratio, and lower pH than soils under adjacent vegetation (Antonsson et al., 2009; Bonanomi et al., 2015; L. A. Cavieres et al., 2007; 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, both of which are important food sources for Collembola and Acari (Zumsteg, Bååth, Stierli, Zeyer, & Frey, 2013). 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 *Silene* cushions might retain moisture and stabilize temperature more effectively, thus supporting richer bacterial and fungal communities.

A previous study on the microscale distribution of microarthropods in high-Arctic Svalbard found that Collembola, but not mites, showed higher abundance in cushions of *S. acaulis* than in five other plant species in the adjacent vegetation, with no difference in species richness of Collembola or mites between the other plant species (Coulson et al., 2003). However, high-Arctic Svalbard encompasses more extreme environments, with markedly diminished species diversity (6 Collembola species, 7 mite species) compared with our alpine sub-Arctic site in Sweden (41 Collembola species, 107 Oribatida species).

Similarly, a study carried out in high-alpine Chile found that ladybird beetle abundance was higher in cushion plants than in the surrounding habitat, while a greenhouse experiment showed that, under milder temperature, the beetles did not prefer cushions (Molina-Montenegro et al., 2006). Thus, the facilitation effect was only expressed under harsher microclimate conditions.

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 (A. N. Reid & Lortie, 2012). Similarly, arthropod richness, abundance, and diversity of above-ground invertebrates were all higher in cushions of *S. acaulis* compared with adjacent vegetation in a study in the same territory (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 facilitator effect on other plants at higher elevations (Antonsson et al., 2009).

Rank – abundance (relative abundance) diagrams are widely used to document a complex community structure (Begon, Townsend, & Harper, 2006). Steeper curves indicate more unbalanced community structure with high portion of recedent species and greater changes in local environment (Camann, Gillette, Lamoncha, & Mori, 2008; Lindberg, Engtsson, & Persson, 2002; L'uptáčik, Miklisová, & Kováč, 2012). In the species dominance rank curves obtained in the present study, collembolan and oribatid mite communities displayed more visible differences between *Silene* cushions and adjacent vegetation at the two highest elevations with harsher microclimate conditions, while communities with more similar structure were observed at lower elevations with a milder microclimate.

A previous study in the Latnjajaure valley found that Collembola in three different plant communities were resistant to two decades of experimental warming (Alatalo, Jägerbrand, & Čuchta, 2015). However, juvenile mites declined with long-term warming (Alatalo, Jägerbrand, Juhanson, Michelsen, & Ľuptáčik, 2017), most likely because they are more soft-bodied than adults and thus more vulnerable to desiccation (Bokhorst et al., 2012; T. A. Day et al., 2009). However, it should be noted that the sampling in those studies was not focused on cushion plants, but performed randomly in the vegetation within experimental plots. Similarly, experimental warming in laboratory and field environment in high-Arctic Svalbard had no direct negative effect on Collembola and Acari, while warming combined with decreased moisture levels in the field had a large negative impact on Collembola (Hodkinson, Coulson, Webb, & Block, 1996). Mites were unaffected in that study, suggesting that Collembola are more vulnerable to desiccation than mites.

While Collembola and Acari in alpine and Arctic areas are not likely to be directly negatively affected by increased temperatures due to climate change, mites are under severe threat globally due to habitat destruction and degradation (Sullivan & Ozman-Sullivan, 2020). However, both experimental (Alatalo & Little, 2014; Villellas, García, & Morris, 2019) and monitoring studies (Doak & Morris, 2010) suggest that *S. acaulis* may be vulnerable to climate change. In addition, recent modeling studies have estimated that more than 50% current locations of *S. acaulis* are likely to be outside the future species climatic hypervolume in North America (Ferrarini, Dai, et al., 2019). In the British Islands, the majority of its current locations will likely become unsuitable in the future (Ferrarini, Alsafran, Dai, & Alatalo, 2019). 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 in cushions of *S. acaulis* and *D. lapponica* than in adjacent vegetation. If the abundance of these cushion plants declines in the future, this could have adverse effects on microarthropod diversity in alpine and Arctic regions.

Conclusions

Abundance, species richness, and diversity indices of soil microarthropods were all higher in *Silene* and *Diapensia* cushions than in adjacent vegetation, suggesting that cushion plants facilitate soil microarthropod communities. A significant impact of elevation and vegetation type on Collembola and soil mites was demonstrated. NMDS analysis and species rank curves revealed the differing microarthropod communities in two different vegetation types at high-elevation sites (above 1300 m a.s.l.). This indicates that facilitation of soil microarthropods by cushion plants increases with elevation and plays a more critical role in harsher environmental conditions.

Author contributions

The study was designed by J.M.A. Fieldwork was performed by J.M.A., P.C., and P.L. Micro-arthropod identification was made by P.C, P.J., and P.L. D.M performed statistical analyses. J.M.A., 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.

Acknowledgements

This study was funded by Carl Tryggers stiftelse för vetenskaplig forskning and Qatar Petroleum (through J.M.A). We thank the Abisko Scientific Research Station for hospitality during fieldwork.

Conflict of interests

The authors declare no conflict of interests.

Supplementary materials

Electronic supplementary materials accompany this article at ...

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Figure legends

Fig. 1. Non-metric multidimensional scaling (NMDS) ordination plot of Collembola and Oribatida communities in *Silene acaulis* cushions and adjacent vegetation along an elevation gradient in an alpine region in northern Sweden. S – *Silene* cushions centroids, C – adjacent vegetation centroids, 1000-1400 – elevation levels; for species abbreviations see Table 3.

Fig. 2. Rank of Collembola species dominance in *Silene acaulis* cushions and adjacent vegetation along an elevation gradient. Silene - dominance of species observed in *Silene acaulis* cushions, adj.veg. - dominance of species observed in adjacent vegetation.

Fig. 3. Rank of Oribatida species dominance in *Silene acaulis* cushions and adjacent vegetation along an elevation gradient. Silene - dominance of species observed in *Silene acaulis* cushions, adj.veg. - dominance of species observed in adjacent vegetation.

Table legends

Tab. 1 Mean abundance [ind.m^{-2}], species richness, diversity and equitability indices of microarthropod groups in *Silene acaulis* cushions and adjacent vegetation along an elevation gradient. Legend: A - abundance, St - total species richness, Sm - mean species richness per sample, H´ - Shannon´s diversity index, J´ - Pielou´s evenness index, Silene - *Silene acaulis,* adj.veg. - adjacent vegetation. Significance of variance was tested using Wilcoxon's matched pairs test. Significant differences provided in bold.

Tab. 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 equitability. Legend: p - probability value, df - degrees of freedom, A - abundance, S - species richness, H´ - Shannon´s diversity index, J´ - Pielou´s evenness index. Data Box Cox transformed to normalized distribution. Significant differences provided in bold. Oribatida eveness could not be tested due to not normal data distribution even after above mentioned transformation.

Tab. 3 Mean abundance [ind.m^{-2}] of dominant collembolan and oribatid mite species in *Silene acaulis* cushions and adjacent vegetation along an elevation gradient. Legend: Silene - *Silene acaulis*, adj.veg. - adjacent vegetation.

Table 4. Mean abundance [ind.m^{-2}] of soil microathropod groups, species richness and diversity indices of Collembola and Oribatida in *Diapensia lapponica* cushions and adjacent vegetation. Legend: A - abundance, St - total species richness, Sm - mean species richness per sample, H´ - Shannon´s diversity index, J´ - Pielou´s evenness index. Astigmatina were not tested due to high number of zero values. Significance of variance tested using Mann-Whitney's test. Significant results provided in bold.

Tab. 5 Mean abundance [ind.m^{-2}] of dominant collembolan and oribatid mite species in *Diapensia lapponica* cushions and adjacent vegetation. Significance of variance estimated using Mann-Whitney's test. Significant differences provided in bold.

In electronic supplementary materials:

Table S1 Mean abundance [ind.m^{-2}] of Collembola and Oribatida species in *Silene acaulis* cushions and adjacent vegetation along an elevation gradient. Legend: Silene - *Silene acaulis*, adj.veg. - adjacent vegetation

Table S2 Mean abundance [ind.m^{-2}] of Collembola and Oribatida species in *Diapensia lapponica* cushions and adjacent vegetation.

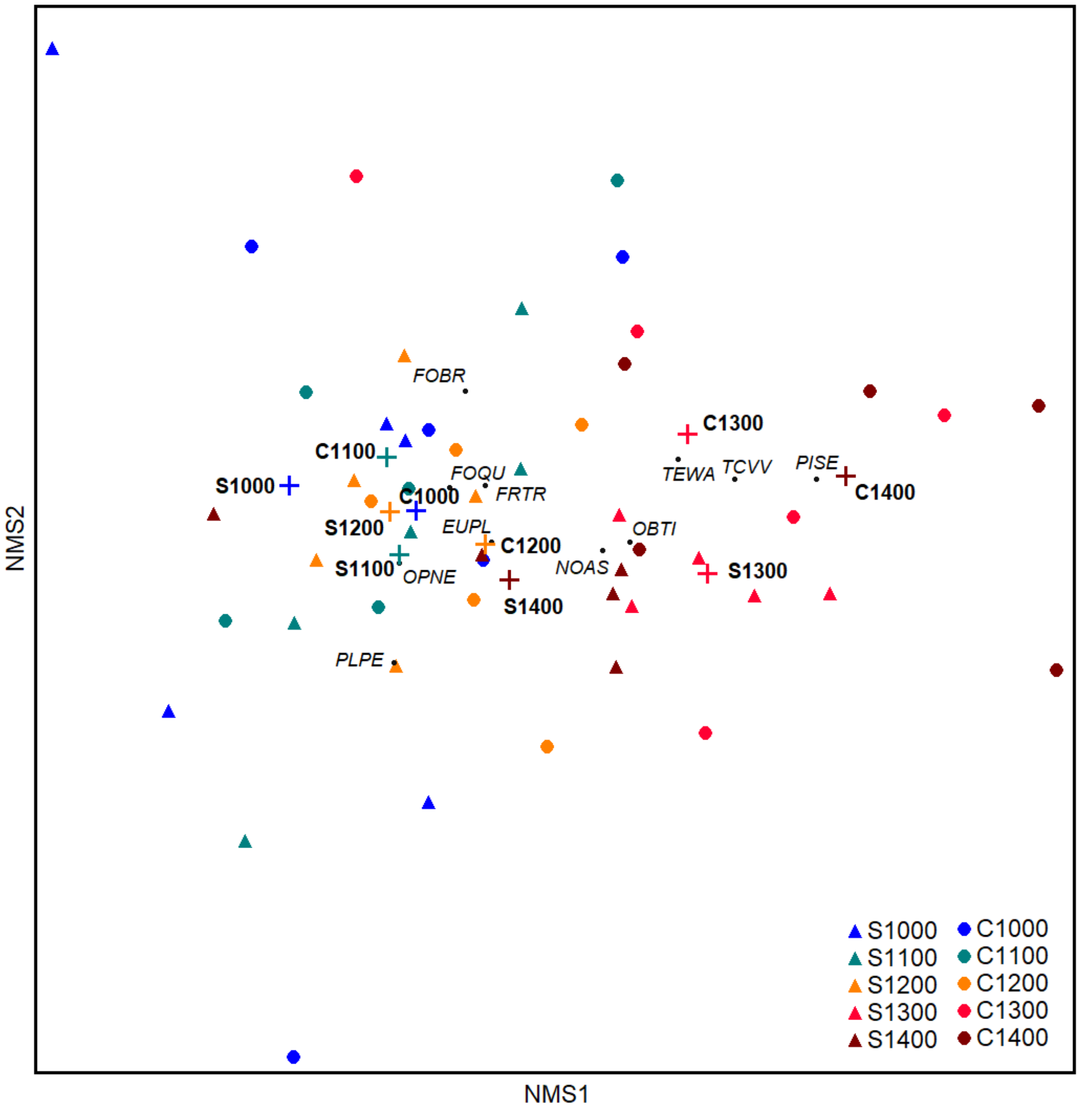

Fig. 1. Non-metric multidimensional scaling (NMDS) ordination plot of Collembola and Oribatida communities in *Silene acaulis* cushions and adjacent vegetation along an elevation gradient in an alpine region in northern Sweden. S – *Silene* cushions centroids, C – adjacent vegetation centroids, 1000-1400 – elevation levels; for species abbreviations see Table 3.

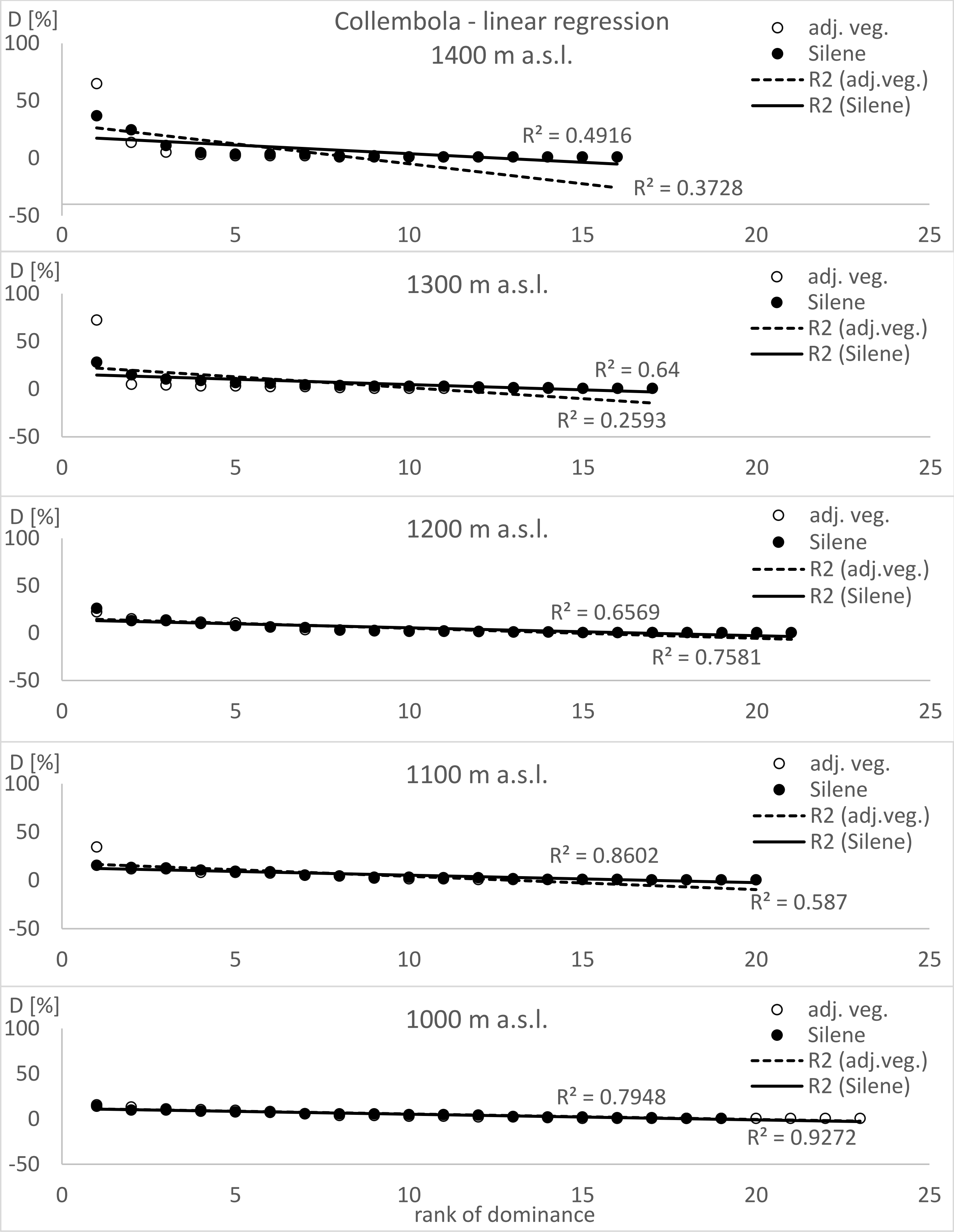

Fig. 2. Rank of Collembola species dominance in *Silene acaulis* cushions and adjacent vegetation along an elevation gradient. Silene - dominance of species observed in *Silene acaulis* cushions, adj.veg. - dominance of species observed in adjacent vegetation.

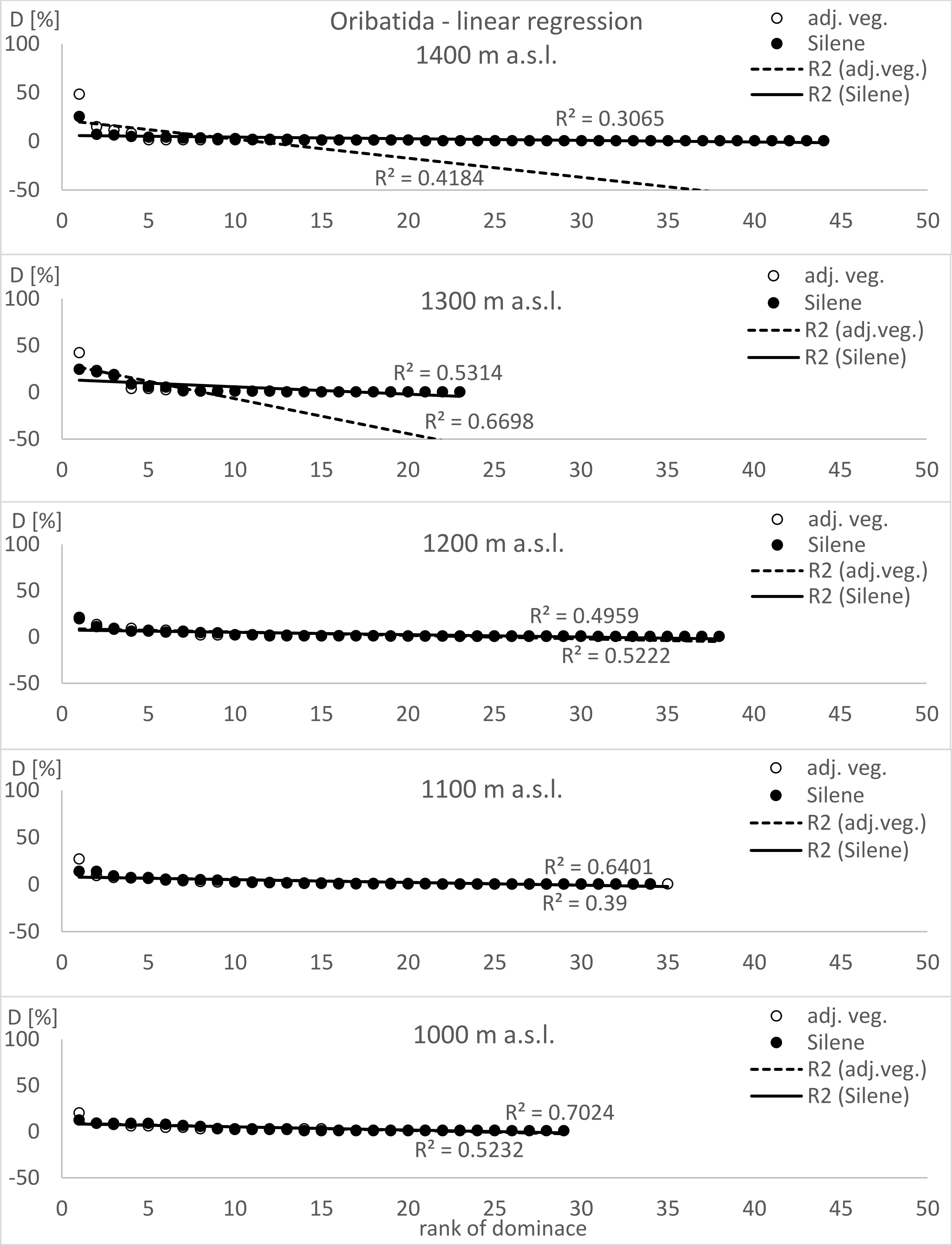
Oribatida - linear regression
1400 m a.s.l.
1300 m a.s.l.
1200 m a.s.l.
1100 m a.s.l.
1000 m a.s.l.
D [%]
100
50
0
-50
0
5
10
15
20
25
30
35
40
45
50
rank of dominace
○ adj. veg.
● Silene
R2 (adj.veg.)
R2 (Silene)
R² = 0.3065
R² = 0.4184
R² = 0.5314
R² = 0.6698
R² = 0.4959
R² = 0.5222
R² = 0.6401
R² = 0.39
R² = 0.7024
R² = 0.5232

Fig. 3. Rank of Oribatida species dominance in *Silene acaulis* cushions and adjacent vegetation along an elevation gradient. Silene - dominance of species observed in *Silene acaulis* cushions, adj.veg. - dominance of species observed in adjacent vegetation.

Tab. 1 Mean abundance [ind.m^{-2}], species richness, diversity and equitability indices of microarthropod groups in *Silene acaulis* cushions and adjacent vegetation along an elevation gradient.

Legend: A - abundance, St - total species richness, Sm - mean species richness per sample, H´ - Shannon´s diversity index, J´ - Pielou´s evenness index, Silene - *Silene acaulis*, adj.veg. - adjacent vegetation. Significance of variance was tested using Wilcoxon's matched pairs test. Significant differences provided in **bold**.

	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	80208	46788	**97311**	**70771**	109892	48360	123064	66446	75883	29685
S.D.	*48982*	*16070*	*42363*	*12549*	*115491*	*22126*	*83805*	*50646*	*14668*	*35823*
A - Prostigmata	28898	8060	30668	10812	25163	6881	8060	8453	10812	8650
S.D.	*30213*	*9985*	*51091*	*7156*	*38746*	*5247*	*6035*	*5672*	*9951*	*17739*
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	46001	34206	62711	52292	77849	39317	108909	56224	59369	20445
S.D.	*22771*	*8352*	*12748*	*11926*	*75050*	*22089*	*76550*	*48101*	*18397*	*17548*
A - Collembola	27719	26539	35386	26736	40694	32437	26343	23394	15924	18479
S.D.	*20914*	*11463*	*19174*	*9257*	*21497*	*20299*	*11151*	*16917*	*9790*	*14268*
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
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*

Tab. 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 equitability.

Legend: p - probability value, df - degrees of freedom, A - abundance, S - species richness, H´ - Shannon´s diversity index, J´ - Pielou´s evenness index. Data Box Cox transformed to normalized distribution. Significant differences provided in **bold**. Oribatida eveness could not be tested due to not normal data distribution even after above mentioned transformation.

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

Tab. 3 Mean abundance [ind.m^{-2}] of dominant collembolan and oribatid mite species in *Silene acaulis* cushions and adjacent vegetation along an elevation gradient.

Legend: Silene - *Silene acaulis*, adj.veg. - adjacent vegetation.

		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.	
Species	Abbreviation	Silene	adj.veg.	Silene	adj.veg.	Silene	adj.veg.	Silene	adj.veg.	Silene	adj.veg.
Collembola											
Folsomia quadrioculata	FOQU	2752	3539	4718	3145	10616	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	16906	197	983
S.D.		*879*	*590*	*1390*	*0*	*1786*	*6652*	*5586*	*17016*	*440*	*1390*
Folsomia brevicauda	FOBR	1573	2949	3735	9240	5308	4915	786	1180	590	0
S.D.		*1319*	*3260*	*4734*	*11068*	*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	11992
S.D.		*0*	*0*	*0*	*0*	*440*	*879*	*2038*	*983*	*3993*	*13977*
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*

Table 4. Mean abundance [ind.m^{-2}] of soil microathropod groups, species richness and diversity indices of Collembola and Oribatida in *Diapensia lapponica* cushions and adjacent vegetation.

Legend: A - abundance, St - total species richness, Sm - mean species richness per sample, H´ - Shannon´s diversity index, J´ - Pielou´s evenness index. Astigmatina were not tested due to high number of zero values. Significance of variance tested using Mann-Whitney's test. Significant results provided in **bold**.

	Diapensia lapponica	adjacent vegetation
A - total Acari	**16569**	**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	**15587**	**6740**
S.D.	*9372*	*4078*
A - Collembola	**15165**	**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*

Tab. 5 Mean abundance [ind.m^{-2}] of dominant collembolan and oribatid mite species in *Diapensia lapponica* cushions and adjacent vegetation.

Significance of variance estimated using Mann-Whitney's test. Significant differences provided in **bold**.

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*

Table S1. Mean abundance [ind.m^{-2}] of Collembola and Oribatida species in *Silene acaulis* cushions and adjacent vegetation along an elevation gradient.

Legend: Silene - *Silene acaulis*, adj.veg. - adjacent vegetation

	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.	
Collembola	Silene	adj.veg.	Silene	adj.veg.	Silene	adj.veg.	Silene	adj.veg.	Silene	adj.veg.
Ceratophysella scotica	1573	197	0	0	1376	590	590	197	0	0
Desoria neglecta	590	197	197	393	2556	983	1573	0	197	590
Desoria olivacea	0	983	983	1376	197	3735	197	0	590	0
Desoria violacea	786	197	197	197	1180	2162	2752	590	0	0
Deuterosminthurus sp.	0	0	0	197	0	0	0	0	0	0
Entomobrya corticalis	0	0	0	0	0	0	0	0	197	0
Entomobryidae juv.	393	197	0	197	393	197	0	0	197	0
Folsomia brevicauda	1573	2949	3735	9240	5308	4915	786	1180	590	0
Folsomia inoculata	0	0	0	0	393	0	0	0	0	0
Folsomia palearctica	1573	590	4522	1180	4128	1180	0	0	0	0
Folsomia quadrioculata	2752	3539	4718	3145	10616	3539	1769	786	5898	2556
Folsomides marchicus	1376	0	393	0	0	0	0	0	0	0
Friesea mirabilis	1180	197	1180	197	983	0	393	197	0	0
Friesea truncata	2752	2162	5504	2162	3145	0	3932	393	197	197
Heterosminthurus sp.	0	0	0	0	197	0	0	0	0	0
Hypogastrura cf. *sensilis*	3932	0	393	590	0	0	0	0	0	0
Isotoma viridis	0	4128	1966	197	590	7274	983	197	0	393
Isotomiella minor	1376	590	1573	2162	983	786	786	0	1769	393
Lepidocyrtus lanuginosus	0	0	590	0	0	0	0	0	0	0
Lepidocyrtus lignorum	197	197	0	0	197	197	0	0	590	0

Megalothorax minimus	0	0	197	0	0	0	0	0	0	0
Mesaphorura jirii	0	0	0	0	0	0	0	197	0	0
Mesaphorura tenuisensillata	0	0	0	0	0	0	0	0	0	197
Micranurida forsslundi	0	0	197	0	0	197	0	0	0	0
Micranurida pygmaea	0	0	0	0	0	0	393	0	0	0
Neanura muscorum	0	0	0	0	0	0	0	197	0	0
Parisotoma notabilis	2162	983	3145	393	5308	590	1180	590	197	393
Pogonognathellus flavicornis	0	197	0	0	197	0	0	0	0	0
Proisotoma minuta	0	197	0	0	0	0	0	0	0	0
Protaphorura armata	393	393	0	0	0	0	0	0	0	0
Protaphorura pseudovanderdrifti	2359	786	3342	3145	197	393	786	786	786	393
Pseudachorutes subcrassus	0	0	0	0	0	197	0	0	0	0
Pseudanurophorus binoculatus	1966	1573	1180	1966	0	590	197	0	197	0
Pseudisotoma sensibilis	0	0	0	0	197	393	2359	983	3932	11992
Scutisotoma subarctica	0	2556	0	0	0	0	197	0	0	0
Sphaeridia pumilis	0	0	0	0	197	0	0	0	0	0
Tetracanthella wahlgreni	590	2752	983	0	2359	4522	7470	16906	197	983
Tomocerina minuta	0	197	0	0	0	0	0	197	197	0
Willemia anophthalma	0	0	0	0	0	0	0	0	197	0
Willowsia nigromaculata	197	0	393	0	0	0	0	0	0	0
Xenylla maritima	0	786	0	0	0	0	0	0	0	393
	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.	
Oribatida	Silene	ad.veg.	Silene	ad.veg.	Silene	ad.veg.	Silene	ad.veg.	Silene	ad.veg.
Adoristes ovatus	0	0	197	0	197	197	0	0	197	0
Achipteria nitens	0	0	393	0	0	0	0	0	0	0
Banksinoma cf. *borealis*	197	0	0	0	2162	1376	0	0	0	0
Banksinoma lanceolata	0	0	0	0	0	0	0	0	1180	0
Belba compta	197	197	0	197	983	0	197	197	0	0
Berniniella bicarinata	393	0	0	0	0	0	0	0	0	0

Berniniella sigma	0	197	0	0	2556	0	0	0	393	0
Brachychochthonius sp.	0	0	0	0	197	0	0	0	0	0
Ceratoppia sphaerica	0	0	0	197	0	0	0	0	197	0
Ceratozetes thienemanni	1573	786	2359	1180	197	0	0	0	0	0
Conchogneta dalecarlica	0	0	0	0	0	0	0	0	393	197
Cultroribula bicultrata	0	0	0	197	786	0	0	0	0	0
Dissorhina ornata	1573	0	1966	197	197	393	197	197	1966	0
Edwardzetes edwardsi	197	0	0	0	0	197	0	0	0	0
Eobrachychthonius latior	393	197	0	0	0	0	0	0	0	0
Eueremaeus valkanovi	0	0	0	0	0	0	0	0	197	0
Eupelops plicatus	1573	393	3145	786	3342	1180	3145	590	0	197
Eupelops strenzkei	197	0	0	0	0	0	0	0	0	0
Euzetes globulus	0	0	0	0	197	0	0	0	197	0
Fuscozetes setosus	0	393	0	0	0	393	0	0	0	0
Fuscozetes sp.	0	0	0	786	0	0	0	0	0	0
Galumna obvia	0	0	0	0	0	0	393	0	0	0
Haplozetes sp.	0	0	0	197	0	0	0	0	0	0
Heminothrus longisetosus	0	0	0	0	0	0	393	0	0	197
Chamobates birulai	0	0	0	0	0	0	0	0	0	983
Chamobates borealis	197	197	0	0	0	0	0	0	197	0
Chamobates cuspidatus	0	0	0	0	197	0	0	0	197	0
Chamobates sp.	0	197	197	0	0	197	0	0	0	0
Chamobates voigtsi	0	0	0	393	786	0	0	0	197	0
Liochthonius brevis	0	0	983	0	0	0	0	0	0	0
Liochthonius sellnicki	0	0	393	197	0	0	0	0	0	0
Liochthonius simplex	393	0	0	0	0	0	0	0	0	0
Liochthonius strenzkei	197	0	393	0	0	0	0	0	393	0
Malaconothrus monodactylus	0	0	0	0	0	0	393	0	0	0
Malaconothrus sp.	0	0	0	0	0	0	0	0	197	0

Melanozetes meridianus	0	0	0	0	197	0	0	0	0	0
Metabelba pulverosa	0	0	0	0	197	0	0	0	0	0
Microppia minus	197	0	393	197	2162	197	0	0	197	0
Minunthozetes pseudofusiger	0	0	0	197	0	0	0	0	0	0
Multioppia glabra	0	0	0	0	0	0	197	0	197	0
Mycobates sarekensis	0	0	0	0	0	0	0	590	983	1376
Nanhermannia comitalis	0	0	0	0	0	0	197	0	0	0
Nanhermannia cf. *coronata*	0	0	0	0	0	0	0	0	197	0
Neotrichoppia confinis	0	0	0	0	197	0	0	0	0	0
Nothrus cf. *borussicus*	393	983	1769	1376	983	0	7667	2556	0	0
Ophidiotrichus vindobonensis	0	0	0	0	393	0	0	0	0	0
Oppiella cf. *propinqua*	0	0	0	0	0	0	786	0	0	0
Oppiella cf. *splendens*	0	0	0	0	393	1376	0	0	0	0
Oppiella falcata	0	0	197	0	4522	197	0	0	197	0
Oppiella marginedentata	0	0	0	0	0	0	0	0	393	0
Oppiella neerlandica	2162	2556	4718	7863	8650	3735	1966	393	6881	1769
Oppiella nova	197	197	590	0	197	197	393	197	1376	197
Oppiella sp.	0	0	0	197	197	197	0	0	197	0
Oppiella subpectinata	197	393	393	2162	590	197	197	0	590	0
Oppiella unicarinata	983	0	0	0	0	0	0	0	0	0
Oribatella calcarata	197	0	0	0	0	0	197	0	0	0
Oribatula interrupta	0	786	0	0	1769	0	0	0	983	197
Oribatula tibialis	1180	393	786	197	590	1769	8650	3342	786	197
Oromurcia sudetica	0	0	0	0	0	197	0	0	0	0
Pantelozetes paolii	0	0	197	197	0	0	0	0	0	0
Pantelozetes sp.	0	0	0	0	0	197	0	0	786	0
Pergalumna nervosa	197	0	0	0	0	0	0	0	197	0
Phauloppia sp.	197	0	0	0	0	0	0	0	0	0
Phthiracarus sp.	0	0	0	0	0	0	0	0	393	197

Platynothrus peltifer	1573	393	4718	983	2556	2556	2162	197	0	0
Protoribates capucinus	0	0	0	197	0	0	0	0	0	0
Punctoribates punctum	0	197	590	0	393	393	197	0	590	0
Quadroppia galaica	0	0	0	2162	0	0	0	0	0	0
Quadroppia hammerae	0	0	0	0	197	0	0	0	197	0
Quadroppia maritalis	0	0	197	0	0	0	197	0	0	0
Quadroppia monstruosa	0	0	197	0	0	0	0	0	0	0
Quadroppia quadricarinata	1376	1180	1573	0	197	197	0	0	197	0
Rhysotritia ardua	0	0	0	197	0	0	0	0	0	0
Scheloribates initialis	197	0	0	197	197	197	0	0	0	0
Scheloribates laevigatus	0	0	197	0	0	0	0	0	393	0
Scheloribates latipes	0	0	197	0	0	197	0	0	0	0
Scheloribates pallidulus	0	0	197	0	0	0	0	0	0	0
Steganacarus spinosus	0	0	0	0	0	197	0	0	0	0
Suctobelba altvateri	0	0	0	0	0	0	0	0	197	0
Suctobelba discrepans	0	0	0	0	0	0	0	0	197	0
Suctobelba granulata	0	0	0	0	0	197	0	0	197	0
Suctobelba reticulata	0	0	0	0	0	0	0	0	197	0
Suctobelba secta	0	0	0	197	0	0	0	0	0	0
Suctobelba trigona	0	393	197	0	0	0	393	0	197	0
Suctobelbella acutidens	197	197	590	0	0	0	197	0	0	197
Suctobelbella cf. *arcana*	0	0	786	0	0	0	0	0	0	0
Suctobelbella arcana	0	0	393	590	197	0	0	0	197	0
Suctobelbella cf. *forsslundi*	0	0	0	0	393	0	0	0	1180	0
Suctobelbella cf. *perforata*	0	0	0	0	0	197	0	0	0	0
Suctobelbella falcata	0	197	197	0	0	197	0	0	590	0
Suctobelbella longirostris	0	0	197	786	0	0	197	0	0	0
Suctobelbella palustris	0	0	0	0	0	0	0	0	0	197
Suctobelbella perforata	197	0	0	0	0	0	0	0	0	197

Suctobelbella sarekensis	590	393	1769	2162	197	0	197	0	0	0
Suctobelbella similis	0	0	0	0	0	0	0	0	197	0
Suctobelbella sp.1	0	0	0	197	0	0	0	0	0	0
Suctobelbella sp.2	0	0	0	590	0	0	0	0	0	0
Suctobelbella sp.3	0	0	0	197	0	0	0	0	0	0
Suctobelbella sp.4	0	0	0	197	0	0	0	0	0	0
Suctobelbella subcornigera	197	197	197	393	1966	0	0	0	393	0
Tectocepheus minor	0	0	0	0	590	0	0	0	0	0
Tectocepheus velatus knullei	0	0	0	0	590	0	0	0	0	0
Tectocepheus velatus sarekensis	0	590	0	197	0	197	0	0	197	0
Tectocepheus velatus velatus	0	393	2162	2752	590	1769	6684	6094	1769	5701
Trichoribates copperminensis	0	590	0	0	0	0	0	0	0	0
Trichoribates trimaculatus	0	0	0	0	0	393	0	0	0	0
Zygoribatula exilis	0	0	0	197	0	197	0	0	0	0

Table S2. Mean abundance [ind.m^{-2}] of Collembola and Oribatida species in *Diapensia lapponica* cushions and adjacent vegetation.

Collembola	*Diapensia lapponica*	adjacent vegetation
Ceratophysella scotica	70	0
Desoria neglecta	211	0
Entomobrya nicoleti	351	70
Entomobryidae juv.	70	70
Folsomia brevicauda	3440	3651
Folsomia manolachei	843	0
Folsomia quadrioculata	5055	1755
Friesea mirabilis	140	0
Friesea truncata	1896	140
Hypogastrura cf. *sensilis*	211	0
Isotomiella minor	351	70
Lepidocyrtus lignorum	211	0
Mesaphorura tenuisensillata	70	0
Micranurida forsslundi	70	0
Parisotoma notabilis	1334	421
Protaphorura pseudovanderdrifti	140	0
Pseudanurophorus binoculatus	70	0
Tetracanthella wahlgreni	632	632

Oribatida	*Diapensia lapponica*	adjacent vegetation
Berniniella bicarinata	0	70
Camisiidae juv.	70	140
Carabodes labyrinthicus	0	70
Ceratozetes thienemanni	3791	1053
Ceratozetidae juv.	2598	772
Dissorhina ornata	1194	140
Mycobates sarakensis	351	983
Neonothrus humicolus	70	0
Nothrus juv.	70	70
Oppiella acuminata	1545	70
Oppiella hauseri	70	0
Oppiella neerlandica	70	140
Oppiella nova	0	140
Oppiella subpectinata	281	70
Oribatida indet. juv.	913	0
Oribatula tibialis	140	0
Phthiracarus sp.	0	70
Punctoribates punctum	70	0

Suctobelba trigona	281	0
Suctobelbella acutidens	70	0
Tectocepheus juv.	983	913
Tectocepheus velatus velatus	2949	2036
Trichoribates cf. *trimaculatus*	70	0