

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

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18 **Summary:**

- 19 1. Cushion plants can have positive impacts on plant richness in severe environments and
20 possibly across trophic levels on arthropods, an under-studied topic.
- 21 2. This study examined whether soil communities under cushions of *Silene acaulis* and
22 *Diapensia lapponica* have higher richness and abundance of soil microarthropods
23 (Acari, Collembola) than adjacent non-cushion vegetation; and whether differences in
24 collembolan and mite abundance and species richness between *S. acaulis* cushions and
25 adjacent vegetation increase with elevation.
- 26 3. In total, 5199 individuals of Collembola (n=1392) and mites (n=3807) were identified
27 to order/species level in samples along an elevation transect (1000, 1100, 1200, 1320,
28 and 1400 m a.s.l.), and an exposed ridge above the treeline (1000 m a.s.l.) in northern
29 Sweden. Paired soil samples were taken within cushions of *Silene acaulis* (along the
30 elevation gradient) and *Diapensia lapponica* (on the exposed ridge) and adjacent non-
31 cushion plant vegetation.
- 32 4. *Silene acaulis* had a positive effect on species richness and abundance of Collembola,
33 with richness effects from 1100 m a.s.l. upwards. Oribatid mite abundance and richness
34 were also higher in *S. acaulis* compared with adjacent vegetation.
- 35 5. Species richness of Collembola and Oribatida declined with increasing elevation from
36 1200 m a.s.l. Collembola abundance peaked at mid-elevation (1200 m a.s.l.) in both *S.*
37 *acaulis* and adjacent vegetation, while oribatid mite abundance peaked at 1300 m a.s.l.
38 in both vegetation types.
- 39 6. Cushions of *D. lapponica* on the exposed ridge had a significant positive effect on
40 species richness, abundance and diversity of Collembola, and abundance of Oribatida.
- 41 7. Alpine cushion plants play an important role in supporting biodiversity of soil fauna in
42 severe alpine environments, with the positive effect of cushion plants increasing with
43 environment severity.

44

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

47

48

49 **Introduction**

50 Facilitation is defined as an interaction in which the presence of one species alters the
51 environment in a way that enhances growth, survival, or reproduction of a second, neighboring
52 species (Bronstein, 2009). Facilitation effects tend to occur in high-stress environments such as
53 Arctic and alpine ecosystems (Antonsson, Björk, & Molau, 2009), and the impact of facilitation
54 tends to increase with environmental stress (Brooker et al., 2008; Choler, Michalet, & Callaway,
55 2001). However, studies of positive interactions have been primarily focused on plant-plant
56 interactions (Brooker et al., 2008; Callaway & Walker, 1997; Choler et al., 2001).

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

66 Cushions-forming plant species are a common component of communities in alpine
67 locations around the world. Globally, 338 cushion plants have been recorded in 78 genera and
68 34 families, mainly in harsh alpine and other cold regions (Arredondo-Núñez, Badano, &
69 Bustamante, 2009; Hauri & Schröter, 1914). Cushion plants offer a broad scope of research
70 topics to study and the preliminary ecological evidence to date strongly suggests that cushion
71 plants can be keystone species in their ecosystems (A. M. Reid, Lamarque, & Lortie, 2010).
72 Predicted changes associated with a changing climate in regions with a high cushion plant
73 distribution make such plants very suitable for ecological observations and experiments.
74 Cushion plants act as foundation and nurse species in alpine ecosystems, providing structurally
75 unique microhabitats with more stable environmental conditions, and positively influencing the
76 diversity and abundance of other organisms (E. Badano & Cavieres, 2006; L. A. Cavieres,
77 Badano, Sierra-Almeida, & Molina-Montenegro, 2007; Molenda et al., 2012). (Bonanomi et
78 al., 2015). Soils under *Silene acaulis* cushions have been shown to have higher organic carbon
79 (C) content, salinity, total nitrogen (N), and C/N ratio, and lower pH compared with soil under
80 adjacent vegetation (Bonanomi et al., 2015). In a study in a rocky alpine meadow in British
81 Columbia, Canada, *S. acaulis* was found to have higher visitation rate and diversity of both
82 surface arthropods and pollinators relative to 11 species of non-cushion plants (Anya M. Reid

83 & Lortie, 2012). Higher richness, abundance, and diversity of ground arthropods and higher
84 richness and abundance, but not diversity, of plants have been observed in cushions of *S. acaulis*
85 in comparison with non-cushion adjacent vegetation in the same territory (Molenda et al.,
86 2012). Coulson *et al.* (2003) found higher soil microarthropod densities in *S. acaulis* cushions
87 than in five other vascular plants in a high-Arctic vegetation mosaic.

88 The aims of the present study were to: i) compare soil microarthropod communities
89 inhabiting two cushion plant species, *Silene acaulis* and *Diapensia lapponica*, with those
90 inhabiting adjacent non-cushion vegetation; and ii) evaluate the effect of elevation gradient and
91 facilitation by cushion plants on microarthropod communities under these two types of
92 vegetation. The hypotheses tested were that: 1) soil communities under cushions of *S. acaulis*
93 and *D. lapponica* have higher richness and abundance of the soil microarthropods (Acari,
94 Collembola) than soil communities under adjacent non-cushion vegetation; and that 2) a
95 facilitation effect, measured as the difference in collembolan and mite abundance and species
96 richness between *S. acaulis* cushions and adjacent vegetation, increases with increasing
97 elevation.

98

99 **Methods and study area**

100 The study was carried out in northernmost Sweden, at Latnjajaure Field Station (LFS) in the
101 Latnjavagge valley (68°21'N, 18°30'E). The valley is covered with snow for most of the year,
102 and the climate is classified as sub-Arctic (Alatalo & Molau, 1995; Polunin, 1951). It has cool
103 summers and relatively mild, snow-rich winters, with mean annual air temperature ranging from
104 -0.76 to -2.92 °C between 1993 and 2013 (Alatalo, Jägerbrand, Chen, & Molau, 2017). Mean
105 annual precipitation since 1993 is 846 mm, but in individual years it ranged from 607 mm
106 (1996) to 1091 mm (2003). July is the warmest month, with mean temperature ranging from
107 5.9 °C in 1995 to 13.1 °C in 2013 (Alatalo, Jägerbrand, Chen, et al., 2017). The vegetation in
108 the valley comprises a wide range of communities, varying from dry to wet and poor and acidic
109 to base-rich (Molau & Alatalo, 1998).

110

111 **Cushion plants**

112 *Silene acaulis* L. (Caryophyllaceae) is a herbaceous cushion plant characteristic of alpine and
113 Arctic tundra habitats in Asia, Europe, Greenland, and North America. It has a disjunct
114 circumpolar distribution in sub-Arctic, Arctic, and alpine locations and a gap in the Siberia
115 region (Gussarova et al., 2015; Junntila & Robberecht, 1993). In Europe, the southernmost
116 populations of *S. acaulis* are found in the Alps, Balkans, British Isles, Carpathian mountains,

117 Cantabrian Mountains, and Pyrenees (Ferrarini, Dai, Bai, & Alatalo, 2019). *Silene acaulis* is
118 widespread in the Latnjavagge valley (1000 m a.s.l.) to the peak of Latnjačorru mountain (1446
119 m a.s.l.). As at other sites, the cushion morphology of *S. acaulis* changes with elevation, with
120 the cushions becoming smaller and more compact at higher elevation (Alatalo & Molau, 1995;
121 Bonanomi et al., 2015). It is a long-lived perennial that forms light-green, moss-like dwarf
122 cushions with pink flowers (Morris & Doak, 1998). *Silene acaulis* has high germination rates,
123 and the cushion growth form enables its seedlings to tolerate frost and drought (Milbau, Graae,
124 Shevtsova, & Nijs, 2009). Its small seeds can be dispersed by wind (Gehring & Delph, 1999).
125 *Silene acaulis* is polymorphic, with reproductive systems and gender frequencies varying
126 between populations (Alatalo & Molau, 1995; Philipp, 1997).

127 *Diapensia lapponica* L. (Diapensiaceae) is another cushion-forming and long-lived
128 circumpolar Arctic-alpine evergreen perennial species, adapted to the harshest of environments
129 with exposed cold, windswept conditions (R. T. Day & Scott, 1984; Molau, 1997). *Diapensia*
130 *lapponica* is a long-lived (up to 400 years) (Molau, 1997). Its plants form cushion domes or
131 mats, radiating from a single, stout, woody tap-root, which act as solar heat traps and warm up
132 the soil beneath the cushions (R. T. Day & Scott, 1984; Molau, 1997). The leaves are glabrous,
133 and frost-resistance of the cushion is imparted by extremely dense leaf aggregation (Molau,
134 1997). *Diapensia lapponica* is common at exposed sites, such as windswept ridge crests, and is
135 indifferent to substrate acidity. In locations with active soil processes, e.g., solifluction, *D.*
136 *lapponica* can be found in microhabitats with longer duration of annual snow cover (Molau,
137 1996). It is a slow-growing species, e.g., at Latnjajaure the average age at which the plant
138 becomes reproductive is 18 years (Molau, 1997). Seed recruitment of *D. lapponica* typically
139 takes place during colder years, e.g., in the Latnjavagge valley there is a negative correlation
140 between seedling recruitment and mean annual temperature (Molau, 1997). Although *D.*
141 *lapponica* is a weak competitor, it can grow in adverse habitats, often on acid soils or low-
142 nutrient soils (R. T. Day & Scott, 1984; Molau, 1997). Where the climate and soil permit, *D.*
143 *lapponica* clumps can be invaded and overgrown by competing species (R. T. Day & Scott,
144 1984). Research to date on this plant species has focused on recruitment and persistence of *D.*
145 *lapponica* seedlings (Sutton, Hermanutz, & Jacobs, 2006), age-related growth and reproduction
146 (Molau, 1997), survival and genetic divergence (Ikeda, Senni, Fujii, & Setoguchi, 2008), and
147 pollen limitation of reproduction (Elberling, 2001). There is a lack of data on the influence of
148 *D. lapponica* cushions on soil fauna.

149

150 **Sampling and identification of soil fauna**

151 In peak summer (25 July) 2013, five soil cores were extracted from individual cushions of *S.*
152 *acaulis* and five from adjacent non-cushion vegetation (50-100 cm distance from *S. acaulis*
153 cushions), in a pairwise design (at each elevation) along an elevation gradient from the bottom
154 of the Latnjavagge valley (above treeline) along the south-west facing slope to the peak of
155 Latnjačorru mountain (1446 m a.s.l.). Sampling was carried out at (m a.s.l.): 1000
156 (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,
157 18°30'27.36"E), 1300 (68°21'33.78"N, 18°30'46.57"E), and 1400 (68°21'45.80"N,
158 18°31'13.27"E), along the same elevation transect as in a previous study on the facilitation
159 effect of *S. acaulis* on plants (Antonsson et al., 2009).

160 On 27 July 2013, 14 soil cores were taken from cushions of *D. lapponica* and 14 from
161 adjacent non-cushion vegetation in a pairwise design along a ridge at 1000 m a.s.l.
162 (68°21'23,7"N, 18°29' 41.16"E) in the Latnjavagge valley (Molau, 1996). Photo documentation
163 of the vegetation along the elevation gradient and the exposed ridge is provided in
164 supplementary electronic materials to this paper (Figs. S1-S6). The samples comprised soil
165 cores 3.6 cm in diameter (10 cm² in area) and with a maximum depth of 6-12 cm (depending
166 on soil depth) (Figs. S7-S8). The samples were stored in plastic bags in coolboxes until
167 extraction of soil fauna, which was performed within five days of field sampling using a
168 modified high-gradient extraction apparatus applied over seven days (Crossley & Blair, 1991).

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

175

176 **Statistical analyses**

177 To characterize Collembola and Oribatida communities at the sites, abundance (A), dominance
178 (D), and species richness (S) were analyzed as community parameters. The dominance of an
179 individual species was expressed as $D = N_i/N \times 100$ (%), where N_i = total number of individuals
180 of species i and N = total number of individuals at each site. Diversity indices were calculated,
181 namely Shannon diversity index (H') and Pielou evenness index (J'), to document the character
182 of the microarthropod communities. Species dominance rank curves with a comparison of trend
183 lines between *Silene* cushions and adjacent vegetation along the elevation gradient were

184 constructed, to assess the differences in structure of soil microarthropod communities (MS
185 Excel 2016).

186 Repeated-measure ANOVA was used to test the significance of abundance variance of
187 soil microarthropods between vegetation types along the elevation gradient. When the data were
188 not normally distributed, Box-Cox transformation was applied. Species of Collembola with
189 more than 100 specimens and species of Oribatida more than 50 specimens in the total material
190 were tested to detect significant differences in ecological parameters between *S. acaulis*
191 cushions and adjacent vegetation along the elevation gradient. The Wilcoxon matched pairs test
192 was used to confirm significant differences between *S. acaulis* cushions and adjacent vegetation
193 for mean abundance, species richness, and diversity indices of Collembola and Oribatida, and
194 mean abundance of dominant Collembola and Oribatida species for every elevation separately.

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

200 Non-metric multidimensional scaling (NMDS) ordination was used to display patterns
201 of soil microarthropod distribution in *S. acaulis* cushions and adjacent vegetation. A two-
202 dimensional solution was generated without data transformation in the autopilot mode, with the
203 slow and thorough option and Sørensen (Bray-Curtis) distance (appropriate for community
204 data). NMDS was performed using PC-ORD version 7.2 (McCune: & Mefford, 2016), using a
205 data matrix of the abundance of selected Collembola and Oribatida species (Collembola with
206 more than 100 specimens and Oribatida more than 50 specimens in total material) calculated
207 for every vegetation type and elevation.

208

209 **Results**

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

211 In total, 3807 individuals of soil mites and 1392 individuals of Collembola were recorded along
212 the elevation gradient with *S. acaulis* cushions and adjacent vegetation. Within the mites,
213 Oribatida (2835 individuals), Prostigmata (745 individuals), and Gamasina (193 individuals)
214 were the most numerous groups. Astigmatina represented only a negligible proportion of the
215 total Acari numbers, and were therefore excluded from statistical analyses. Recorded
216 Collembola individuals belonged to 41 species, 30 genera, and 10 families. Oribatida,

217 the dominant group in soil mites, were identified to species level, with 107 species belonging
218 to 52 genera and 28 families.

219 Abundances of total Acari and dominant Acari groups were higher in *S. acaulis* cushions
220 than in adjacent vegetation at all elevations, but only total Acari at 1100 m a.s.l. showed a
221 significant difference (Table 1). Oribatida had the highest abundance of all Acari across the
222 elevation transect (Table 1), representing more than 70% of all mite individuals collected.
223 Oribatid abundance in *Silene* cushions increased with elevation to 1400 m a.s.l., at which there
224 was a decrease. The abundance of the mites in adjacent vegetation plots showed no distinct
225 trend. The predatory groups Prostigmata and Gamasina had different abundance distributions
226 between the two vegetation types at different elevation levels. Gamasina showed higher
227 abundance in adjacent vegetation at 1000 and 1100 m a.s.l., but appeared in distinctly higher
228 abundance in *Silene* cushions at higher elevations, with a significant difference ($p<0.05$) only
229 at the highest elevation (Table 1). Prostigmata showed the opposite abundance distribution
230 trend. These mites were distinctly more abundant in *Silene* plots up to 1200 m a.s.l., while their
231 abundances at higher elevations were similar within both vegetation types. Similarly to
232 Oribatida, Collembola showed higher abundances in *Silene* cushions, except at 1400 m a.s.l.,
233 where the abundance was higher in adjacent vegetation. A statistically significant effect
234 ($p<0.01$) of vegetation type on total Acari, Collembola, and the Oribatida, and Gamasina groups
235 was obtained (Table 2). A significant effect of elevation or a combined effect of elevation and
236 vegetation type on these microarthropod groups was not observed.

237 Total species richness of Collembola in *Silene* cushions along the whole elevation
238 transect was slightly higher ($S=34$) than in adjacent vegetation ($S=31$). Species richness within
239 all *Silene* cushions at the different elevations studied was also higher than in adjacent
240 vegetation, except at 1000 m a.s.l. (Table 1). Total species richness of Collembola at elevation
241 levels and mean species richness per sample in both vegetation types decreased continuously
242 towards the highest elevation, with a significant difference at 1300 m a.s.l. ($p<0.05$). For
243 Oribatida, differences in total species richness between *Silene* cushions ($S=87$) and adjacent
244 vegetation ($S=67$) across the elevation transect were much more noticeable than in Collembola.
245 At all elevation levels studied except 1100 m a.s.l., *Silene* cushions showed higher per plot
246 species richness than adjacent vegetation (Table 1). Mean species richness of Oribatida was
247 significantly higher in *Silene* cushions at 1300 and 1400 m a.s.l. ($p<0.05$).

248 Diversity and equitability indices of Oribatida and Collembola in *Silene* cushions
249 compared with adjacent vegetation showed higher mean values at all elevation levels. For
250 Collembola, Shannon diversity index was significantly different for elevation at level 1300 m

251 a.s.l. ($p < 0.05$), while for Oribatida the index was significantly different at elevation 1400 m
252 a.s.l. ($p < 0.05$) (Table 1). A significant effect of elevation and vegetation type on Collembola
253 diversity and vegetation type on equitability index was detected (Table 2). Oribatida diversity
254 was significantly affected by elevation and vegetation type.

255 In NMDS ordination, the best three-dimensional solution, for which the first two
256 dimensions are shown in (Fig. 1), had final stress of 17.12 ($p < 0.001$) after 500 iterations. This
257 was confirmed by a Monte Carlo permutation test with $p < 0.005$, and mean stress of 17.45 for
258 real data and 250 runs for both real and randomized data. The first three axes explained 38.1%,
259 20.3%, and 16.5% of the variance, respectively. The NMDS results confirmed the impact of
260 higher elevations on community composition. The diagram revealed the similarity of
261 communities at lower elevations (1000 to 1200 m), and more different communities at the two
262 highest elevations (Fig. 1). Using species dominance rank curves revealed greater differences
263 in Collembola and Oribatida community structure between *Silene* cushions and adjacent
264 vegetation at two highest elevations (Fig. 2 and Fig. 3).

265 Species of Collembola and Oribatida were divided into three groups depending on their
266 preference for vegetation types. The first group, with the majority of species, preferred *Silene*
267 cushions (Collembola: *Ceratophysella scotica*, *Desoria violacea*, *Folsomia palearctica*, *F.*
268 *quadrioculata*, *Friesea mirabilis*, *F. truncata*, *Isotomiella minor*, *Parisotoma notabilis*;
269 Oribatida: *Ceratozetes thienemanni*, *Dissorhina ornata*, *Eupelops plicatus*, *Nothrus* aff.
270 *silvestris*, *Oribatula tibialis*, *Platynothrus peltifer*) (Table S1). The second group, which
271 showed higher abundances in adjacent vegetation, comprised a few Collembola species, namely
272 *Desoria olivacea*, *Folsomia brevicauda* and *Tetracanthella wahlgreni*, and the oribatid mite
273 *Tectocepheus velatus velatus*. The third group of species showed no distinct preference for
274 vegetation type along the elevation gradient (Collembola: *Isotoma viridis*, *Pseudanurophorus*
275 *binoculatus*, *Pseudisotoma sensibilis*; Oribatida: *Oppiella neerlandica*).

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

279

280 **Comparison of *Diapensia lapponica* and adjacent vegetation**

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

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

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

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

304

305 **Discussion**

306 Nurse plants modify the conditions in stressful environments by providing a microclimate
307 within their canopies. Thus they can increase species richness (Arroyo & Cavieres, 2003; E. I.
308 Badano & Marquet, 2009; Nuñez, Aizen, & Ezcurra, 1999), abundance (E. I. Badano,
309 Villarroel, Bustamante, Marquet, & Cavieres, 2007; L. Cavieres & Arroyo, 2002; Sklenář,
310 2009), phylogenetic diversity (Butterfield et al., 2013), and survival of other plant species (E.
311 I. Badano et al., 2007; L. A. Cavieres et al., 2007; L. A. Cavieres, Quiroz, & Molina-
312 Montenegro, 2008). In this study in an alpine region in Sweden, we observed a positive effect
313 of cushion plants upon soil microarthropods. As hypothesized, we found that the cushion plants
314 *Silene acaulis* and *Diapensia lapponica* had higher species richness of Collembola and
315 Oribatida than adjacent vegetation. The positive facilitation effect of *S. acaulis* was found to
316 increase with increasing elevation. In contrast, a study in high-elevation New Zealand only
317 found a positive impact of cushion plants on abundance and richness of mites, while Collembola

318 abundance was higher in adjacent vegetation (Minor et al., 2016). Those authors suggested that
319 the difference between organisms groups may have been due to mites being more sensitive to
320 disturbances. Collembola are more mobile and more generalist feeders, are more opportunist,
321 and colonize new patches between cushion plants (Minor et al., 2016).

322 Soils under *S. acaulis* and other cushion plants have been shown to have higher soil
323 moisture, organic C content, salinity, total N, and C/N ratio, and lower pH than soils under
324 adjacent vegetation (Antonsson et al., 2009; Bonanomi et al., 2015; L. A. Cavieres et al., 2007;
325 Minor et al., 2016). As bacterial and fungal communities are frequently positively associated
326 with higher soil moisture and organic C and N, soils under cushions could potentially have
327 larger biomass of bacteria and fungi, both of which are important food sources for Collembola
328 and Acari (Zumsteg, Bååth, Stierli, Zeyer, & Frey, 2013). The morphology of *S. acaulis*
329 changes along the elevation gradient, with looser and flatter cushions at lower elevation and
330 more dense and tight dome-shaped cushions at higher elevation (Bonanomi et al., 2015). More
331 dense *Silene* cushions might retain moisture and stabilize temperature more effectively, thus
332 supporting richer bacterial and fungal communities.

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

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

345 A study examining *S. acaulis* and its role as a facilitator species in the Canadian Rocky
346 Mountains found that *S. acaulis* had higher visitation rate and diversity of both ground
347 arthropods and pollinators than all non-cushion plants (Anya M. Reid & Lortie, 2012).
348 Similarly, arthropod richness, abundance, and diversity of above-ground invertebrates were all
349 higher in cushions of *S. acaulis* compared with adjacent vegetation in a study in the same
350 territory (Molenda et al., 2012). Another study at Latnjajaure, covering the same transect as in

351 the present study, found that cushions of *S. acaulis* had a facilitator effect on other plants at
352 higher elevations (Antonsson et al., 2009).

353 Rank – abundance (relative abundance) diagrams are widely used to document a complex
354 community structure (Begon *et al.*, 1990). Steeper curves indicate more unbalanced community
355 structure with high portion of recedent species and greater changes in local environment (e.g.
356 Lindberg *et al.*, 2002; Camann *et al.*, 2008; Luptáček *et al.*, 2012). In the species dominance
357 rank curves obtained in the present study, collembolan and oribatid mite communities displayed
358 more visible differences between *Silene* cushions and adjacent vegetation at the two highest
359 elevations with harsher microclimate conditions, while communities with more similar
360 structure were observed at lower elevations with a milder microclimate.

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

373 While Collembola and Acari in alpine and Arctic areas are not likely to be directly
374 negatively affected by increased temperatures due to climate change, mites are under severe
375 threat globally due to habitat destruction and degradation (Sullivan & Ozman-Sullivan, 2020).
376 However, both experimental (Alatalo & Little, 2014; Villellas, García, & Morris, 2019) and
377 monitoring studies (Doak & Morris, 2010) suggest that *S. acaulis* may be vulnerable to climate
378 change. In addition, recent modeling studies have estimated that more than 50% current
379 locations of *S. acaulis* are likely to be outside the future species climatic hypervolume in North
380 America (Ferrarini, Dai, et al., 2019). In the British Islands, the majority of its current locations
381 will likely become unsuitable in the future (Ferrarini, Alsafran, Dai, & Alatalo, 2019).
382 Similarly, *D. lapponica* is vulnerable to climate change, as earlier onset of snowmelt will
383 expose it to increased risk of early frost events, which increase mortality when the plant is not
384 protected by snow cover (Molau, 1996). In this study, the species richness of both collembolans

385 and mites was higher in cushions of *S. acaulis* and *D. lapponica* than in adjacent vegetation. If
386 the abundance of these cushion plants declines in the future, this could have adverse effects on
387 microarthropod diversity in alpine and Arctic regions.

388

389 **Conclusions**

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

398

399 **Author contributions**

400 The study was designed by J.M.A. Fieldwork was performed by J.M.A., P.C., and P.L. Micro-
401 arthropod identification was made by P.C, P.J., and P.L. D.M performed statistical analyses.
402 J.M.A., P.L. and L.K. were the main authors of the paper. All co-authors contributed to
403 manuscript revisions and agree with the final version.

404

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408 during fieldwork.

409

410 **Conflict of interests**

411 The authors declare no conflict of interests.

412

413 **Supplementary materials**

414 Electronic supplementary materials accompany this article at ...

415

416 **References**

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598

599 **Figure legends**

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

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

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

610

611 **Table legends**

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

618 Tab. 2 Statistical parameter estimates from repeated measure ANOVA analyses testing the
619 effect of vegetation type, elevation and their interaction on microarthropod groups abundance,
620 species richness, diversity and equitability. Legend: p - probability value, df - degrees of
621 freedom, A - abundance, S - species richness, H' - Shannon's diversity index, J' - Pielou's
622 evenness index. Data Box Cox transformed to normalized distribution. Significant differences

623 provided in bold. Oribatida evenness could not be tested due to not normal data distribution
624 even after above mentioned transformation.

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

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

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

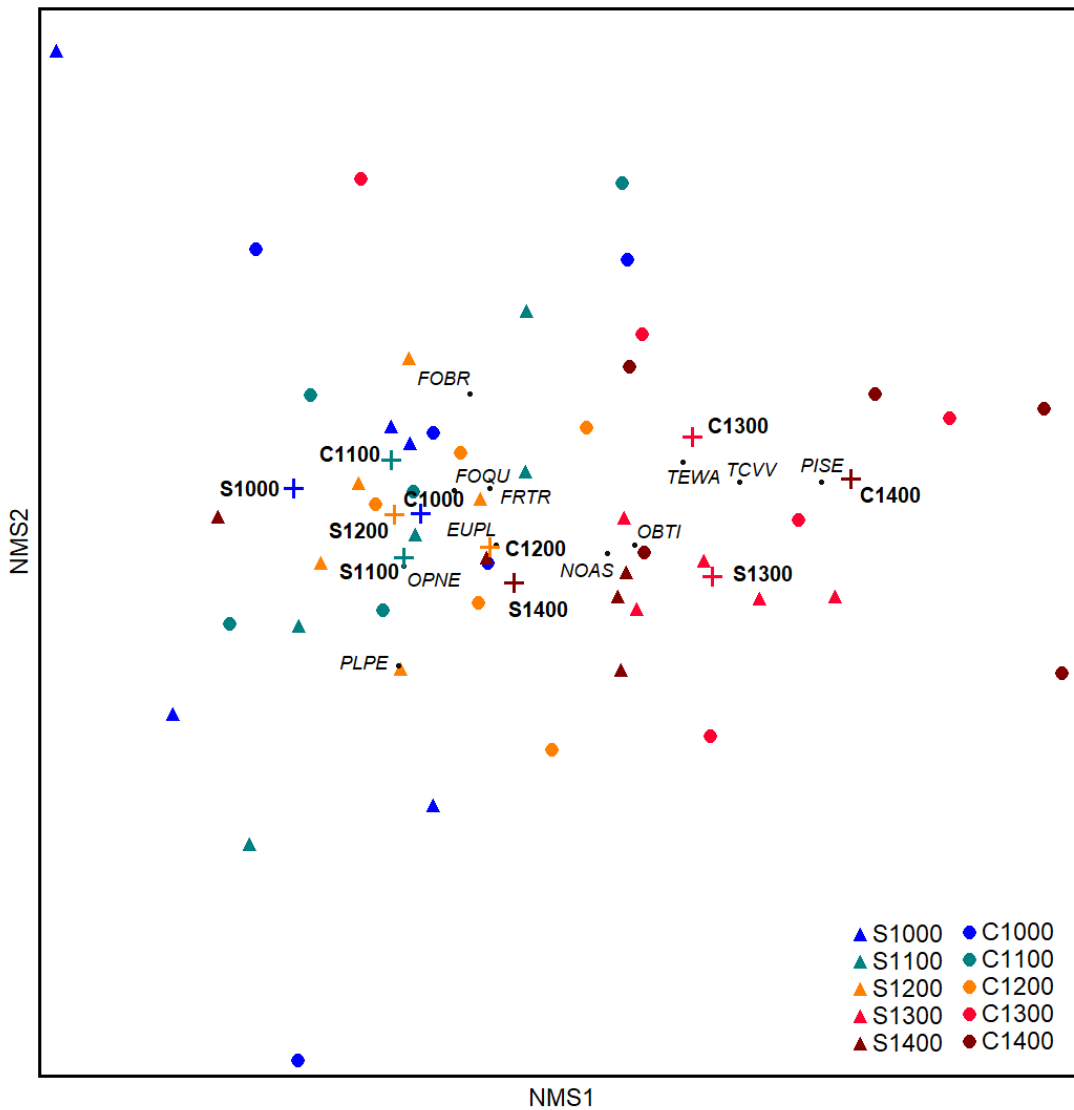
637

638 In electronic supplementary materials:

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

642 Table S2 Mean abundance [ind.m⁻²] of Collembola and Oribatida species in *Diapensia*
643 *lapponica* cushions and adjacent vegetation.

644



645

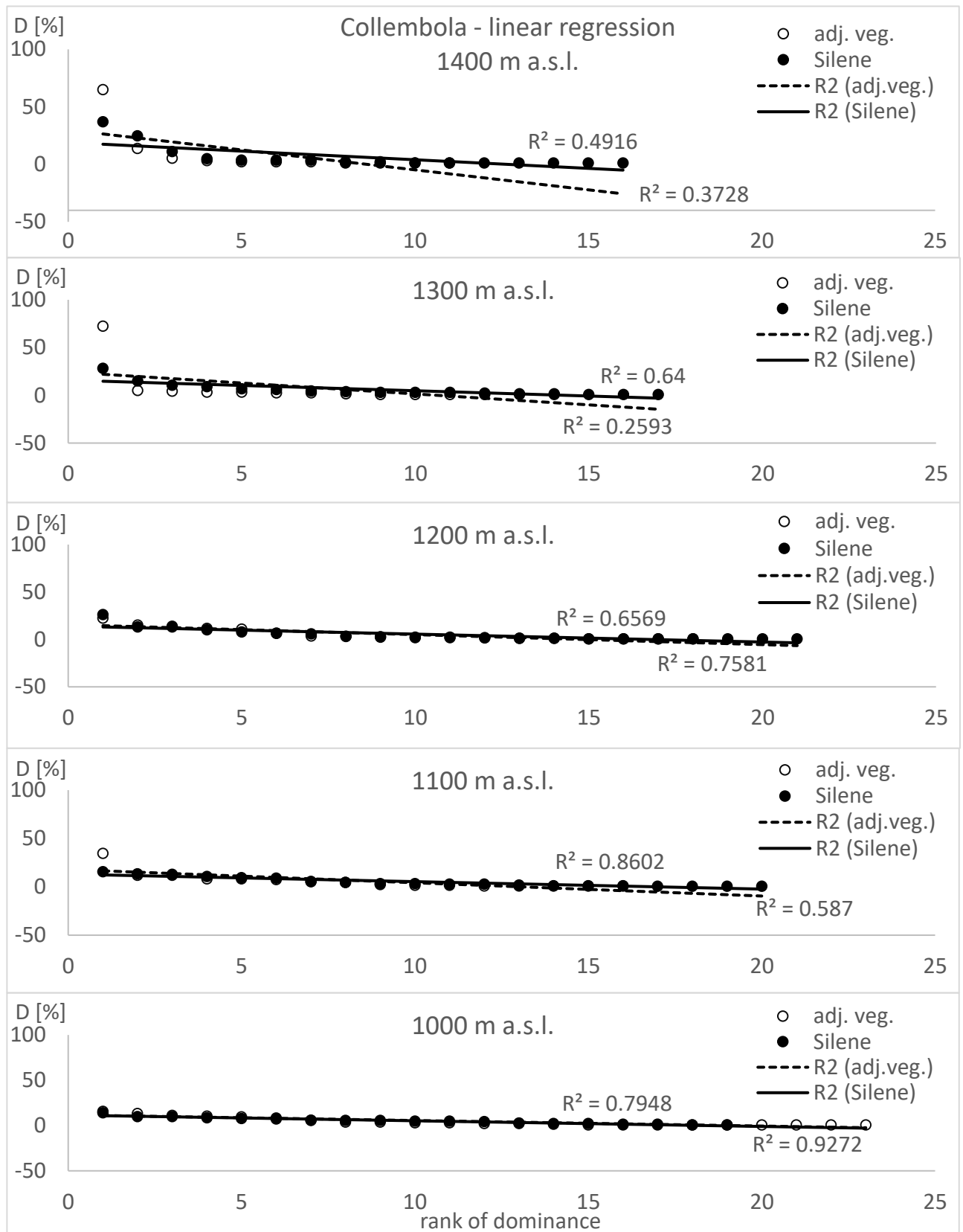
646 Fig. 1. Non-metric multidimensional scaling (NMDS) ordination plot of Collembola and
 647 Oribatida communities in *Silene acaulis* cushions and adjacent vegetation along an elevation
 648 gradient in an alpine region in northern Sweden. S – *Silene* cushions centroids, C – adjacent
 649 vegetation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

650

651

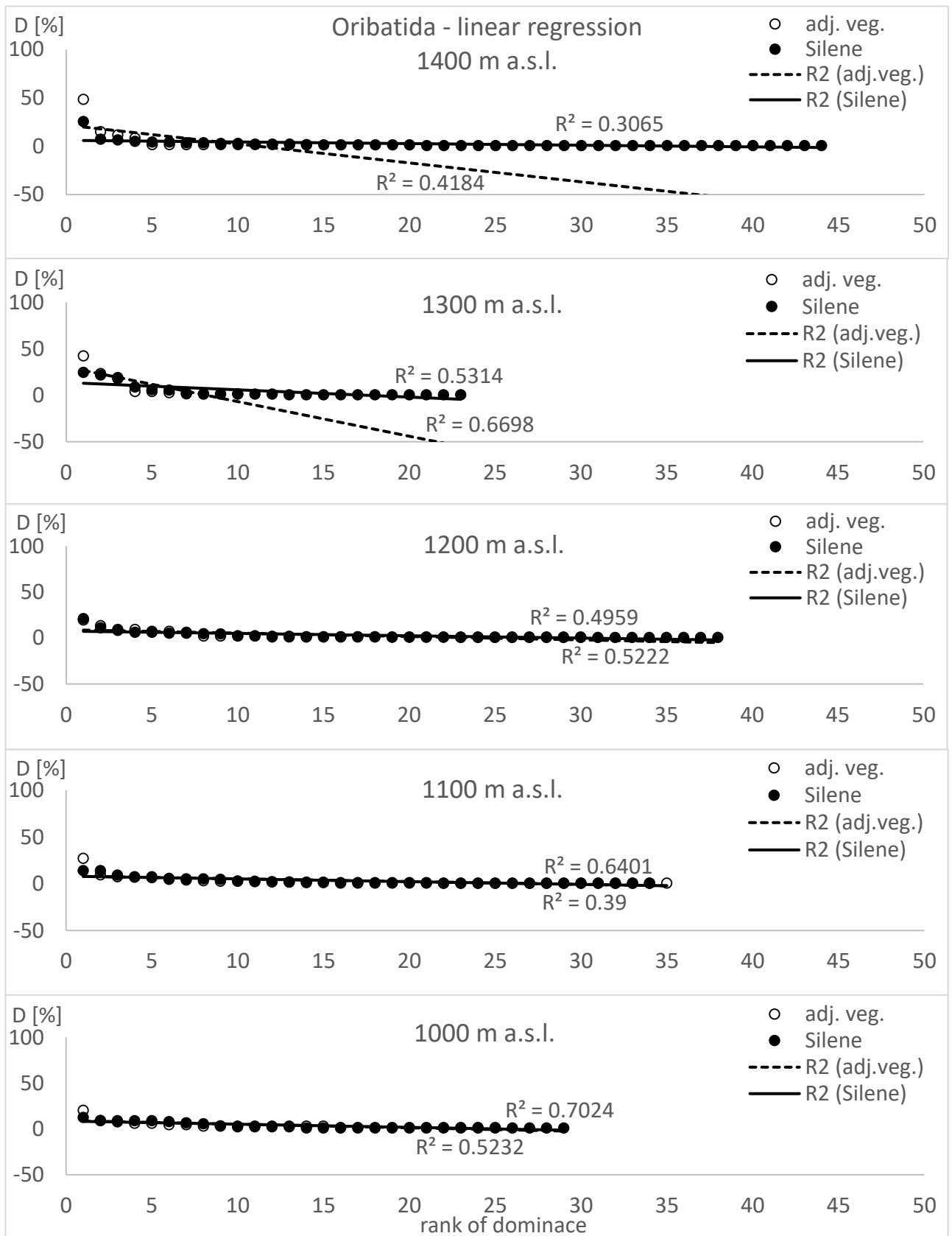
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654

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



659 Fig. 3. Rank of Oribatida species dominance in *Silene acaulis* cushions and adjacent
660 vegetation along an elevation gradient. Silene - dominance of species observed in *Silene*
661 *acaulis* cushions, ad. 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 evenness 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.

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											
<i>Folsomia quadrioculata</i>	FOQU	2752	3539	4718	3145	10616	4423	1769	786	5898	2556
S.D.		4683	4318	4631	1758	4418	3260	1282	822	4285	3651
<i>Tetracanthella wahlgreni</i>	TEWA	590	2752	983	0	2359	4522	7470	16906	197	983
S.D.		879	590	1390	0	1786	6652	5586	17016	440	1390
<i>Folsomia brevicauda</i>	FOBR	1573	2949	3735	9240	5308	4915	786	1180	590	0
S.D.		1319	3260	4734	11068	4895	5604	1282	1758	879	0
<i>Friesea truncata</i>	FRTR	2752	2162	5504	2162	3145	0	3932	393	197	197
S.D.		5126	3139	6317	2899	3503	0	4662	538	440	440
<i>Pseudisotoma sensibilis</i>	PISE	0	0	0	0	197	393	2359	983	3932	11992
S.D.		0	0	0	0	440	879	2038	983	3993	13977
Oribatida											
<i>Oppiella neerlandica</i>	OPNE	2162	2556	4718	7863	8650	3735	1966	393	6881	1769
S.D.		2131	2656	2728	8982	5706	1282	2305	879	6739	3956
<i>Tectocephus velatus velatus</i>	TCVV	0	393	2162	2752	590	1769	6684	6094	1769	5701
S.D.		0	538	3433	4579	538	1282	5079	8524	1891	6498
<i>Oribatula tibialis</i>	OBTI	1180	393	786	197	590	1769	8650	3342	786	197
S.D.		1758	879	822	440	538	2014	7136	1645	822	440
<i>Nothrus cf. borussicus</i>	NOAS	393	983	1769	1376	983	0	7667	2556	0	0
S.D.		538	1702	822	1645	983	0	7068	5183	0	0
<i>Platynocheilus peltifer</i>	PLPE	1573	393	4718	983	2556	2556	2162	197	0	0

S.D.		2467	538	7876	983	3376	2263	2544	440	0	0
<i>Eupelops plicatus</i>	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 microarthropod 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**.

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

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

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

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

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

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

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

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

Collembola	<i>Diapensia lapponica</i>	adjacent vegetation
<i>Ceratophysella scotica</i>	70	0
<i>Desoria neglecta</i>	211	0
<i>Entomobrya nicoleti</i>	351	70
Entomobryidae juv.	70	70
<i>Folsomia brevicauda</i>	3440	3651
<i>Folsomia manolachei</i>	843	0
<i>Folsomia quadrioculata</i>	5055	1755
<i>Friesea mirabilis</i>	140	0
<i>Friesea truncata</i>	1896	140
<i>Hypogastrura cf. sensilis</i>	211	0
<i>Isotomiella minor</i>	351	70
<i>Lepidocyrtus lignorum</i>	211	0
<i>Mesaphorura tenuisensillata</i>	70	0
<i>Micranurida forsslundi</i>	70	0
<i>Parisotoma notabilis</i>	1334	421
<i>Protaphorura pseudovanderdrifti</i>	140	0
<i>Pseudanurophorus binoculatus</i>	70	0
<i>Tetracanthella wahlgreni</i>	632	632
Oribatida	<i>Diapensia lapponica</i>	adjacent vegetation
<i>Berniniella bicarinata</i>	0	70
Camisiidae juv.	70	140
<i>Carabodes labyrinthicus</i>	0	70
<i>Ceratozetes thienemanni</i>	3791	1053
Ceratozetidae juv.	2598	772
<i>Dissorhina ornata</i>	1194	140
<i>Mycobates sarakensis</i>	351	983
<i>Neonothrus humicolus</i>	70	0
Nothrus juv.	70	70
<i>Oppiella acuminata</i>	1545	70
<i>Oppiella hauseri</i>	70	0
<i>Oppiella neerlandica</i>	70	140
<i>Oppiella nova</i>	0	140
<i>Oppiella subpectinata</i>	281	70
Oribatida indet. juv.	913	0
<i>Oribatula tibialis</i>	140	0
<i>Phthiracarus</i> sp.	0	70
<i>Punctoribates punctum</i>	70	0

<i>Suctobelba trigona</i>	281	0
<i>Suctobelbella acutidens</i>	70	0
<i>Tectocepheus juv.</i>	983	913
<i>Tectocepheus velatus velatus</i>	2949	2036
<i>Trichoribates cf. trimaculatus</i>	70	0

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