Effects of reindeer grazing and recovery after cessation of grazing on the ground-dwelling spider assemblage in Finnish Lapland

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The effect of reindeer *Rangifer tarandus* L. grazing on the ground-dwelling spider assemblage in Northern Finland was studied. Changes in species richness, abundance and evenness of spider assemblages were analyzed in relation to changes in vegetation and environmental factors in long term grazed and ungrazed sites as well as sites that had recently switched from grazed to ungrazed and vice versa. Grazing was found to have a significant impact on height and biomass of lichens and other ground vegetation. However, it seemed not to have an impact on the total abundance of spiders. This is likely caused by opposing family and species level responses of spiders to the grazing regime. Lycosid numbers were highest in grazed and linyphiid numbers in ungrazed areas. Lycosidae species richness was highest in ungrazed areas whereas Linyphiidae richness showed no response to grazing. Four Linyphiidae, one Thomisidae and one Lycosidae species showed strong preference for specific treatments. Sites that had recovered from grazing for nine years and the sites that were grazed for the last nine years but were previously ungrazed resembled the long term grazed sites. The results emphasize the importance of reindeer as a modifier of boreal forest ecosystems but the impact of reindeer grazing on spiders seems to be family and species specific. The sites with reversed grazing treatment demonstrate that recovery from strong grazing pressure at these high latitudes is a slow process whereas reindeer can rapidly change the conditions in previously ungrazed sites similar to long term heavily grazed conditions.

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2   **spider assemblage in Finnish Lapland**

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14 **Abstract**

15 The effect of reindeer *Rangifer tarandus* L. grazing on the ground-dwelling spider assemblage in

16 Northern Finland was studied. Changes in species richness, abundance and evenness of spider

17 assemblages were analyzed in relation to changes in vegetation and environmental factors in

18 long term grazed and ungrazed sites as well as sites that had recently switched from grazed to

19 ungrazed and vice versa. Grazing was found to have a significant impact on height and biomass

20 of lichens and other ground vegetation. However, it seemed not to have an impact on the total

21 abundance of spiders. This is likely caused by opposing family and species level responses of

22 spiders to the grazing regime. Lycosid numbers were highest in grazed and linyphiid numbers in

23 ungrazed areas. Lycosidae species richness was highest in ungrazed areas whereas Linyphiidae

24 richness showed no response to grazing. Four Linyphiidae, one Thomisidae and one Lycosidae

25 species showed strong preference for specific treatments. Sites that had recovered from grazing

26 for nine years and the sites that were grazed for the last nine years but were previously ungrazed

27 resembled the long term grazed sites. The results emphasize the importance of reindeer as a

28 modifier of boreal forest ecosystems but the impact of reindeer grazing on spiders seems to be

29 family and species specific. The sites with reversed grazing treatment demonstrate that recovery

30 from strong grazing pressure at these high latitudes is a slow process whereas reindeer can

31 rapidly change the conditions in previously ungrazed sites similar to long term heavily grazed

32 conditions.

Introduction

38 Wild reindeer have been a natural part of the northern boreal ecosystems in Eurasia since the last

39 ice age, but in northern Fennoscandia and many parts of northern Russia they have been replaced

40 by reindeer husbandry with a sustained high density of semi-domesticated reindeer. Contrary to

41 the reindeer herding practices in Norway and Sweden, in Finland, semi-domesticated reindeer

42 herds can no longer have the traditional long migration between their separate summer and

43 winter ranges. The Finnish reindeer herding area is divided into 57 herding districts defined by

44 legislation (Suominen & Olofsson 2000). These districts are relatively small (about 1 000 to

45 5 000 km^2) compared to the herding areas in Norway and Sweden and prevent long term

46 migration. At present, modern herding practices force reindeer herds in Finland to graze in

47 restricted areas. It is especially detrimental to the lichen dominated winter pastures, if reindeer

48 are forced to use them at summertime since that leads to strong trampling impact. Kumpula et al.

49 2000 showed that the condition of lichen rich winter pastures is not explained by reindeer density

50 in relation to the total land area of a herding district but by the density of reindeer in relation to

51 the area of lichen ranges. Nowadays with the inclusion of supplementary feeding which prevents

52 natural mortality owing to shortage of food, the grazing pressure in relation to the carrying

53 capacity of pastures can rise excessively high (Kojola et al. 1991, Helle & Kojola 1993; Evans

54 1996; Kumpula et al. 1997; Suominen & Olofsson 2000). Local herders' cooperatives are trying

55 to save their best winter grazing areas from overgrazing by a system of pasture rotation system

56 (Kumpula et al. 1999), but the success of this is limited.

57   In the boreal ecosystem, the semi-domesticated reindeer (*Rangifer tarandus tarandus L.*)

58 can be seen as an ecosystem engineer or modifier as well as a disturbance. The ecosystem

59 engineer concept (Jones et al. 1994; 1997) implies that, in addition to impacts of reindeer

60 through trophic interactions, they control the physical properties of the ecosystem as well. The

61 concept of disturbance, according to the intermediate disturbance hypothesis (IDH) (Connel

62 1978), implies that the species diversity is at its peak when the level of disturbance is

63 intermediate. IDH has often been applied to the impact of herbivores on vegetation diversity.

64 Both roles stem from grazing behavior and are not mutually exclusive.

65   Sustained high density of deer has been shown to have a negative impact on vegetation

66 and this impact is further cascades to the whole ecosystem including animal assemblages (Côté

67 et al. 2004). Several studies have demonstrated that the changes caused by large herbivores can

68 have an impact on species composition and abundance of several other animal taxa through

69 various direct and indirect mechanisms (reviewed in Suominen & Danell 2006 and Foster et al.

70 2014). At the current constantly high densities reindeer herds have substantial influence on the

71 environment; irrespective of whether reindeer considered to be a native part of the ecosystem or

72 a disturbance due to high densities and lack of natural pasture rotation migration. For instance,

73 grazing can change, sustain and create habitats (Putman 1994), accelerate (Kielland et al. 1997;

74 Augustine & McNaughton 1998; Stark et al. 2000; 2002; Olofsson et al. 2004) and even

75 decelerate nutrient flux by affecting the detritus food web via changes in microclimate (Väre et

76 al. 1996; Pastor & Cohen 1997; Augustine & McNaughton 1998; Olofsson et al. 2001). In

77 addition, grazing has an impact on the community structure and species diversity of vegetation

78 (e.g. Väre et al. 1996; Pastor & Naiman 1992; Pastor & Cohen 1997; Milchunas et al. 1998;

79 Suominen 1999) and can influence the post-disturbance succession rate of vegetation (Oksanen

80 et al. 1995; Kielland et al. 1997; Helle et al. 1998). The impacts of reindeer on vegetation and

81 soil properties as well as on the interaction between soils, vegetation and climate change have

82   been studied a lot in recent years (e.g. Eskelinen et al. 2017; Kaarlejärvi et al. 2017; Ylänne et

83   al. 2017; Egelkraut et al. 2018; Maliniemi et al. 2018). Especially in winter ranges of reindeer in

84   boreal forests, which are typically dry pine forests with *Cladonia*-lichen dominated bottom layer

85   vegetation, it has been shown that the main impact of reindeer is a strong sift from thick lichen

86   carpets to much less bottom and field layer vegetation (e.g. Väre et al. 1996, Suominen &

87   Olofsson 2000, Köster et al. 2013). In addition to biomass and composition of forest floor

88   vegetation this then has cascading impacts on other ecosystem properties such as tree

89   recruitment, fungal communities, litter decomposition (Köster et al. 2013, 2015, Santalahti et al.

90   2018). Variation observed in vegetation can subsequently mediate the impact of grazing on

91   invertebrate partners in a community (Owen-Smith 1987; DeCalesta 1994; Baines et al. 1994;

92   Bromham et al. 1999; Suominen 1999; Wardle et al. 2001; Suominen et al. 2003; Suominen &

93   Danell 2006; Foster et al. 2014).

94   The forest floor spider community is greatly influenced by the habitat's abiotic

95   conditions, such as moisture, light and temperature (Uetz 1991) as well as by the structure of the

96   vegetation and other three dimensional habitat microhabitat features (Colebourn 1974, Hatley &

97   Macmahon 1980, Koponen 1995), and the presence of reindeer can change these conditions and

98   these changes can have an impact on the availability of prey for spiders. Since spiders act both as

99   abundant predators in the invertebrate community and as important prey for numerous forest

100   animals, the changes in spider assemblage can further cascade through the food web via

101   numerous direct and indirect ways.

102   In this study, we show the impact of reindeer grazing and trampling on the ground-

103   dwelling spider fauna in a special area with four different types of reindeer grazing history. It is

104   also unique in the way that moose (*Alces alces*) is present in both sites with and without reindeer

105 grazing. Our hypothesis is that reindeer through the changes caused in vegetation height,

106 structure and biomass as well as in the abiotic conditions has an impact on the assembly structure

107 of spiders. More specifically, we hypothesize that sites with recently reversed reindeer grazing

108 status would have intermediate environmental conditions and assembly structure compared long

109 term grazed and ungrazed sites. Following the IDH assumptions we expected a peak in diversity

110 of spider assemblages at intermediate grazing treatments compared to long term grazed or

111 ungrazed pastures.

112

113

114 **Study area and methods**

115

116 The study area (Fig. 1) was in eastern Finnish Lapland, in Raja-Jooseppi Inari (68°28'N, 28°

117 28'E) where semi-domesticated reindeer have been traditionally herded by tradition by Sámi

118 people for centuries on the Finnish territory. The study site was in dry lichen dominated pine

119 heath of typical reindeer winter pasture on Lappi reindeer herding district's eastern boarder. The

120 district has got an area of 4396 km^2, and its maximum number of overwintering reindeer is 8000

121 individuals. On the Russian side of the national border there are no wild or semi-domesticated

122 reindeer in the area close to the border. The study sites were in the restricted border zone on the

123 Finnish side of the border. We had a permission for the work from the Finnish Boarder Guard

124 (permit number 2717/2015).

125   A reindeer fence along the Finnish-Russian border was erected in the 1940s, and in 1997

126 a new fence crossing the old one was built in our study area. With time, the old fence was torn

127 down so that herds could enter untouched pastures. The junction of the new fence and the

128 position of the old fence forms a cross, where four different grazing regions are distinctly

129 present: i) UGraz - continuously ungrazed from 1940. ii) Graz - continuously grazed from at

130 least 1940. iii) (new ungrazed) NUGraz - ungrazed from 1997, but previously grazed. iiii) (new

131 grazed) NGraz - grazed from 1997 but previously ungrazed.

132   Reindeer fences prevent reindeer from entering the Russian side, where reindeer are

133 locally extinct due to historical causes. Moose, however, occur on both sides and are capable of

134 crossing the fences. This gives a unique opportunity to solely study the grazing effects of

135 reindeer.

136

137

138 **Pitfall trapping**

139

140 Spiders were collected using pitfall traps. The traps were plastic cups 170 ml in volume each

141 with a mouth diameter of 70 mm. The killing / preserving fluid was a mix of polypropylene

142 glycol (60%) and tap water, with a hint of detergent added. With pitfall traps it is possible to

143 passively collect a large proportion of actively moving fauna, and being abundant and actively

144 moving creatures, spiders are frequently encountered in pitfalls. A comparison of spider

145 sampling techniques has proved pitfall trapping to maintain its catching efficiency most

146 constantly in time (Churchill & Arthur 1999).

147

148 **Trapping design**

149

150   A total of 36 trap lines, each consisting of five traps positioned three meters apart, were placed in

151   six plots in the vicinity of the reindeer fence junction in an area of 150 x 500 meters. Each plot

152   included three treatments: the upper region of the fence crossing had Graz, NGraz and UGraz;

153   the lower region had Graz, NUGraz and UGraz. Each treatment within a plot had two trap lines

154   had two trap lines, one five meters from the fence and another 20 meters from the fence. All the

155   trap lines were parallel to the fence. Duo to the possible fence effect, i.e. packing of the deer

156   against the fence and thus higher grazing and trampling impact (e.g. Oksanen 1978, Olsofsson et

157   al. 2001), we tested prior to the further analyses whether the lines with different distance to the

158   fence differed from each other (paired t-test or Wilcoxon signed-ranks test).

159   The trapping period was two months from early June to early August 2005 and due to the

160   short summer of northern boreal regions it practically covered the entire growing season. The

161   emptying interval was one month.

162   Identification of mature specimens was done to species level. As juveniles often lack

163   distinctive species characters (Norris 1999) they were identified to family level.

164

165   ***Vegetation and environmental factors***

166
167   Species composition and height of field and bottom layer vegetation was evaluated with a 50 x

168   50 cm square situated in the middle of each trap line. Dry biomass of the vegetation and soil

169   moisture of soil samples were collected in mid-July, and measured in the laboratory. In each trap

170   line, temperature was measured at the depth of 5 cm in the soil (June 7th 2005, to nearest 0.1 ⁰C).

171   Since the impacts of reindeer on *Cladina* lichen dominated forest floor vegetation have been

172   documented in several other studies (e.g. reviews by Suominen & Olofsson 2000, Bernes et al.

173   2015), and the main focus of the present study is on the spider community, we present the

174   vegetation results here only as major functional groups pooled over species: lichens, mosses and

175   vascular plants. In our study sites, all other vascular plants than ericaceous dwarf shrubs, were

176   too rare to be statistically tested, and all these shrubs had similar response to treatments. Thus,

177   the result on vascular plants is in fact equal to the response of these shrubs.

178

179   ***Data analysis***
180
181   Data was analyzed using SAS Enterprise Guide 3.0, EcoSim (Gotelli & Entsminger 2001), and

182   Canoco for Windows 4.5 (ter Braak & Smilauer 1998). Equality of variances was tested with

183   Levene's test. Normality of residuals was tested with the Shapiro-Wilk test. Variables that were

184   not normally distributed were analyzed with the nonparametric Kruskal-Wallis χ^2-test or

185   Spearman rank correlation (see the table captions). Since many key variables such as spider

186   abundances and plant biomasses could not be analysed with parametric tests the effect of

187   treatments on even those response variables that fulfilled the requirements of parametric tests

188   were also tested with simple one-way ANOVA. In the statistical analyses we used trapping lines

189   as sampling units (observations) i.e. data over the individual traps on each line was combined.

190   The vegetation and physical variables were also measured at trapping line level.

191   Interactions between environmental variables and species were analyzed using linear

192   regression. The Detrended Correspondence Analysis (DCA) ordination method was used to

193   analyze community structure. The two options "downweighting of rare species" and "trend

194   correction by segments" of Canoco for Windows were turned on.

195   As the number of species and the number of individuals per sample are often strongly

196   correlated, the number of individuals caught in each trap line was adjusted by rarefaction (see

197   Gotelli & Colwell 2001) to make trap lines of dissimilar catch size comparable.

198

199

200 **Results**

201
202 The distance of the trap line from the fence, *i.e.* "fence effect", was found to have no effect on

203 spiders and vegetation (paired t-test or Wilcoxon signed-ranks test, p>0.1) and in the subsequent

204 analysis this classifying factor was removed.

205

206 *General abundance and species numbers*
207

208 A total of 4225 spider specimens were collected during the whole sampling period. Of these,

209 3426 specimens were collected from early June till early July and 804 from early July to early

210 August. Mature spiders that were identified to species level numbered 3241 individuals, and 984

211 specimens were juveniles and therefore identified to family level only (see Supplement for a

212 complete list of specimens). In total 73 spider species were caught, representing 11 families

213 (Table 1).

214   In terms of specimen numbers (number of spider individuals, abundance), the most

215 common families were wolf spiders (Lycosidae) and sheet weavers (Linyphiidae). Nearly one

216 third of the mature spiders were wolf spider *Pardosa eiseni* or *Alopecosa aculeata* individuals.

217 The twelve most common species comprised 76% of the total number of spiders (Table 2). Eight

218 species were encountered only once.

219

220 *Vegetation and environmental variables by treatment*
221

222   Total lichen dry biomass (Fig. 2) and lichen height differed significantly between treatments

223   (df=5, χ^2= 26,65, p<0.0001; df=5, χ^2=43,18, p<0.0001) Soil moisture did not differ between

224   treatments, but soil temperature did (df=5, F= 4.09 p= 0.0212) (Fig. 2). The impact of treatment

225   on response variables is shown in Table 3.

226   Dry biomasses of mosses or vascular plants were not significantly affected by grazing

227   (Table 3). Vegetation height differed significantly between treatments for all functional groups

228   i.e. lichens, mosses, and dwarf shrubs (practically all vascular plants in the field layer were dwarf

229   shrubs) all being highest in ungrazed plots (Table 3).

230   Most common vascular plants were dwarf shrubs ling (*Calluna vulgaris*), lingonberry

231   (*Vaccinium vitis-idaea*), crowberry (*Empetrum nigrum*) and bilberry (*V. myrtillus*). In addition

232   to those, some graminoids (Poaceae), willow (*Salix* spp.), bog bilberry (*Vaccinium uliginosum*)

233   and marsh Labrador tea (*Rhododendron tomentosum,* ex. *Ledum palustre*) grew on some sites.

234   Among these plants there were three, which typically characterize more moist or even marshy

235   sites, that were found only or almost exclusively in the long term ungrazed sites. Bog bilberry

236   and *Sphagnum*-mosses were found only in the ungrazed sites where their occurrence frequencies

237   were 36% and 20% of the studied plots. For marsh Labrador tea the occurrence frequency was

238   64% in ungrazed and 18% in grazed sites.

239   Soil moisture and soil temperature (df=16, F=8.18, p= 0.011), and lichen biomass and

240   soil temperature (df=16, F=8.93, p= 0.009) correlated negatively, whereas no correlation was

241   found between soil moisture and lichen biomass (Figs 3 a-c).

242   ***Impacts of grazing on spiders***

243

244 **Abundance**

245

246 The total number of all spider individuals was similar between treatments, but at the family level

247 there were differences (Table 3), correlations between spider families are shown in Table 4).

248 Wolf spiders (Lycosidae) were most numerous in long grazed and recently grazed treatments;

249 sheet weavers (Linyphiidae) were most abundant in ungrazed areas, while crab spiders

250 (Thomisidae) showed a more complex yet family specific pattern (Table 3, Fig. 4).

251 Sheet weavers *Palliduphantes antroniensis* and *Hilaira herniosa* clearly occurred most

252 often in ungrazed areas, whereas the sheet weaver *Agyneta gulosa* and the crab spider *Ozyptila*

253 *arctica* were as clearly restricted to grazed areas (Fig. 5).

254

255

256 **Species richness**

257

258 Rarefied trap line species richness (n=123 for each trap line) did not differ significantly between

259 treatments (Table 3). The rarefied wolf spider species richness (n=21) was affected by

260 treatments. The highest number of species (6, SD 0.4) was detected in ungrazed sites, the lowest

261 in sites with a long history of grazing (3.5, SD 0.2).

262 Species richness of Thomisidae was also affected (F=4.27, df=5, *p*=0.018) by treatments

263 so that the highest richness was found in grazed areas. In sheet weavers the species richness

264 showed no response to grazing.

265

266

267

268   *Impact of vegetation and environmental factors on spiders*

269

270   With increasing *Cladina* dry mass and height, the abundance of linyphiids and species richness

271   of lycosids increased but the abundance of thomisids decreased (Table 5). Biomass of vascular

272   plants did not correlate with the abundance or richness of any of the tested spider taxa (Spearman

273   correlation n=36, r<0.27, P>0.11). Moss biomass correlated negatively with Lycosidae richness

274   (Spearman correlation n=36, r=-0.460, P=0.005), but not with other spider variables.

275   Of the most common species *Ozyptila arctica* (Thomisidae) and *Agyneta gulosa*

276   (Linyphiidae) decreased in abundance with increasing lichen dry mass and height, whereas

277   *Palliduphantes antroniensis* (Linyphiidae) was clearly more abundant in areas with thick lichen

278   cover. Also, *Hilaira herniosa* (Linyphiidae) showed a similar pattern to *P. antroniensis*. Other

279   common species showed no response to changes in lichen dry mass or height (Table 5). With

280   increasing soil moisture, the abundance of Gnaphosidae and the total species richness of spiders

281   increased significantly. *Micrargus herbigradus* and *Pocadicnemis pumila* (Linyphiidae) were

282   more abundant in moister areas, whereas *A. gulosa* numbers decreased with increasing moisture.

283   The other common species did not respond significantly to soil moisture.

284   Higher soil temperature was connected to a decrease in linyphiid abundance, rarefied

285   lycosid species richness and the total rarefied species richness of the spider assemblage in each

286   treatment (Table 5). *M. herbigradus* and *P. antroniensis* decreased in abundance, while *A. gulosa*

287   abundance was significantly higher in sites with warmer soil.

288

289   **Correlations between spider families**

290

291   Correlations between abundances and species richnesses of spider the two most numerous spider

292   families, Lycosidae and Linyphiidae, are shown in Table 4. For the overall spider abundance and

293   richness we used the abundance and richness of all other spider families than the one that was

294   tested for, i.e. for Lycosidae all spiders except lycosids and for Linyphiidae all other spiders than

295   linyphids.   The abundance of wolf spider individuals correlates negatively with their own

296   rarefied species richness and positively with the abundance of other spiders and the richness of

297   linyphid spiders. The species richness of Lycosidae spiders correlated positively with the

298   abundance of Linyphiidae and negatively with the richness other spiders and especially that of

299   linyphids. High species richness of linyphids was associated with high abundance of spiders of

300   other families. Earlier, Marusik & Koponen (2002) have found that rich lycosid fauna correlates

301   with high overall species richness in the spider community as well analogous patterns. In our

302   case the opposite was found when the lycosids themselves were excluded from the overall spied

303   richness.

304

305   **Multidimensional scaling**
306

307   A DCA-ordination visualizing the effect of environmental factors and treatments on spider

308   communities is presented in Fig 6. Treatments are distinctly located on different sides of the

309   graph depending on grazing history. Recently grazed and recently ungrazed treatments are

310   grouped with long grazed areas on the first ordination axis, leaving the ungrazed area at the other

311   end of the gradient. On the second ordination axis, no clear differences are detectable, except a

312   more narrow distribution of ungrazed areas. Soil temperature and soil moisture varies between

313   trap lines fairly independently of lichen dry biomass, but covary with each other to some extent.

314   The position of spider species on ordination axis 1 and 2 is presented in Fig. 7. Axis 1

315   mainly represents lichen biomass as in Fig. 6. *Agyneta conigera* and *A. gulosa* (Linyphiidae) are

316   clearly detached from other species, indicating a preference for grazed areas over ungrazed. The

317   lichen rich end of the first axis is dominated by *H. herniosa* (Linyphiidae), *Robertus lividus*

318   (Theridiidae) and especially *P. antroniensis* (Linyphiidae).

319   On the second axis *Pardosa hyperborea* (Lycosidae) represents a distinct end point. *H.*

320   *herniosa* and *Minyriolus pusillus* (Linyphiidae) amongst others are found at the opposite end.

321   *Xysticus obscurus* (Thomisidae) is a species that did not react to the first axis, but reacted

322   strongly to the second, while other species were situated somewhere between.

323

324   **Discussion**

325

326   ***Impact of grazing on spiders***

327

328   Both family and species level responses to grazing were extensive in lycosids and linyphids,

329   even though the combined abundance or species richness of all spiders did not differ between

330   treatments.

331   As expected, wolf spiders were more abundant in grazed areas, and the response of sheet

332   weavers was entirely the opposite. Several explanations for this pattern can be found. Wolf

333   spiders chase their prey at ground level, thus making open habitat the optimal foraging ground.

334   Wolf spiders are also relatively large in body size, making it hard to exploit thick, porous lichen

335   carpet as a hunting ground. Also, because this group hunts actively by running, warmer and drier

336   ground may be more suitable for them. Lower numbers of lycosids in ungrazed areas can also be

337   explained by a lower number of suitable prey (Suominen 1999), in addition to physically more

338   demanding substrate. Linyphiidae spiders catch their prey by using webs, thus their habitat

339   should comprise suitable anchoring sites for web structures. The abundance of web-building

340   spiders has been found to be limited by both the availability of suitable web sites and prey

341   availability (Minoshima et al. 2013, and references therein). Grazing has been shown to decrease

342   both abundance and species richness of web-hunting spiders in Japan and in Kenya, by removing

343   suitable web-building sites (e.g. Miyashita et al. 2004; Warui et al. 2005; Takada et al. 2008;

344   Minoshima et al. 2013). Some studies have suggested that the impact of large herbivores could

345   also be mediated through the abundance of prey (Suominen et al. 2008; Takada et al. 2008) or

346   direct physical disturbance to the spider webs (Foster et al. 2015). In several of these studies the

347   method obtaining spider counts in the field has been based on direct observations of spider webs.

348   This partially circularly reasoning methodology might overemphasize the importance of web

349   building structures for the abundance of web-building spiders. Sweep net sampling in an area

350   close to the present study site during the same summer did not show significant differences in the

351   amount of insect prey (see supplementary material). Since the study area is typical winter pasture

352   for reindeer it is unlikely that there would be substantial direct disturbance of the webs by

353   reindeer during summer. A lack of suitable construction sites for webs and possibly also the

354   different microclimate conditions (i.e. humidity and temperature) seem feasible explanations in

355   this study.

356   Thomisidae abundance in both intermediate treatments strongly reflected the grazing

357   history of the intermediate treatments. The observed similarity between recently ungrazed and

358   continuously grazed sites could be explained by the slow recovery of vegetation. However, as

359 continuously ungrazed and recently grazed sites also showed a resemblance, this hypothesis of

360 prolonged succession seems incorrect.

361

362 **Species richness of spiders**

363

364 The response of rarefied wolf spider species richness to treatments was as expected. In the

365 presumably favourable sites species richness was low and abundance high, whereas in low

366 quality sites species richness was high and abundance low. This is well in line with the

367 competitive exclusion theory, according to which strong competitors in good quality habitats can

368 outcompete subdominants with a similar ecological niche, hence leading to lower species

369 richness (Gause 1934; Hardin 1960). In suboptimal, ungrazed habitats, competitive exclusion is

370 not effective as other factors than inter-species competition are more limiting. A high number of

371 species could be seen as a sign of a more heterogeneous habitat, where more species can live

372 together. However, a monotonous thick and dense carpet of lichen is not likely to be more

373 heterogeneous than grazed areas or provide more suitable environments for ground dwelling

374 wolf spiders.

375 Species richness within Linyphiidae family did not differ between treatments. As

376 linyphiids are highly efficient in their dispersal capacities (ballooning method), they can respond

377 efficiently to environmental changes. Yet, due to wind-driven and rather erratic dispersal,

378 linyphiids are also often dispersed to suboptimal habitats, hence the species present in one spot

379 might reflect chance only. Linyphiid abundance, however, can tell more about the actual quality

380 of the habitat.

381

382

383 **Spider species responses**
384
385 *A. gulosa* and *A. conigera,* linyphid species found in grazed areas in high numbers, typically

386 prefer areas in an early successional phase just after disturbance and are even considered pioneer

387 species (Koponen 2004; Koponen & Koneva 2006). Occurrence of pioneer species in an area

388 grazed continuously from at least the 1940s shows that grazing pressure is high enough to keep

389 an area constantly in its early stage of succession. Linyphiidae spiders. *P. antroniensis* and *H.*

390 *herniosa* are typical northern boreal bottom layer species (Koponen 1999), and here strictly

391 occurred in great abundance in ungrazed, reindeer-free areas.

392 Of the species that are not web-spinning*, Xysticus obscurus* (Thomisidae) was restricted

393 to humid areas, but was rather infrequent in abundance and was previously found in multiple

394 habitats (Koponen 1977). *P. hyperborea* also indicated predominantly lichen rich, humid areas,

395 but was also highly abundant in one site with low lichen biomass. The crab spider *O. arctica* was

396 exceptional in its abundance by being most common in long term grazed sites as well as in newly

397 ungrazed site.

398 Linear regression revealed the affinity of *Micrargus herbigradus* (Linyphiidae) to cool

399 and moist sites. However, its occurrence was not affected by lichen biomass.

400 DCA-ordination did not group species into families but instead showed greatly differing

401 environmental affinities, even within a genus. Hence, use of higher taxa than species to describe

402 changes in environmental attributes can be misleading if the responses of the species contradict

403 each other and the researcher is not utterly aware of the ecology of the focal species.

404

405

406

Importance of microclimate for spiders

408

409 In addition to causing differences in lichen biomass and height as well as other direct and

410 indirect impacts on vegetation, grazing induces differences in microclimate, which may also

411 explain the observed patterns in spider fauna (Koponen et al. 1975; Samu et al. 1999; Frick et al.

412 2007). Large, actively moving wolf spiders require a warmer habitat than small, relatively

413 motionless web-hunting spiders. Due to their small body size, linyphiids are also more

414 vulnerable to drying out. Inside and on top of the spongy, absorbent lichen carpet, the risk of

415 desiccation is probably less important. Also, Riechert and Tracy (1975) showed that by building

416 webs in physically optimal sites instead of sites maximizing prey catch, web-building spiders

417 could significantly increase their fitness.

418

Impact of grazing on vegetation and environmental variables

420

421 As expected and shown by numerous previous studies (e.g. Väre et al. 1996, Suominen &

422 Olofsson 2000, Köster et al. 2013), the main impact of reindeer on vegetation was a reduction in

423 reindeer lichens. Reindeer significantly reduced both the biomass and the height of their main

424 winter food, the *Cladina* lichens, that otherwise dominate ground layer vegetation in these

425 forests. Grazing also raised the soil temperature in summer by removing the isolating and

426 reflecting layer of white thick lichen. This differs from the results of the study by Köster et al.

427 (2015). They didi not find significant difference in soil temeprature in fairly similar conditions

428 not so far away from our study site. We did not detect significant differences in soil moisture

429 between treatments, and this is similar to the results of Köster et al. (2015). This may have been

430 a result of small-scale topographical differences at the study site. However, occurrence of typical

431 peatland species on the sandy soil of our study area like the spider *Pardosa sphagnicola* and

432 plants like peat moss (*Sphagnum* spp.) and bog bilberry in the long term ungrazed area implies

433 that there are actual differences in moisture levels between treatments. Also *Pardosa*

434 *hyperborea*, being relatively abundant in our samples in ungrazed areas, is known to prefer moist

435 conditions (Koponen 1977), even to the extent of being one of the dominant species in peatlands

436 of the boreal zone (Koponen 2002).

437   The DCA ordination of the spider community split the treatments along two gradients: a

438 first ordination axis that mainly represented lichen biomass and a second axis representing soil

439 moisture and temperature. The latter, however, could not divide the species as clearly as the first.

440 Most of the long grazed sites, along with intermediate treatments, were located at a relatively dry

441 section of the gradient. The first axis clearly separated the ungrazed sites from the others, while

442 variation within axis two was to some extent greater. Since the treatments with a recently altered

443 grazing regime were grouped with long grazed treatments, eight years of protection from grazing

444 appears not to be a long enough time to alter the composition of spider assemblage at the study

445 site. Furthermore, areas with only a decade of grazing already resembled the long grazed areas in

446 multiple ways.

447   Next to non-existent differences in vegetation between continuously grazed areas and

448 areas with a decade of recovery from grazing were in contrast to our hypothesis emphasizing the

449 importance of the level of grazing. Generally, harsh climatic conditions in northern boreal

450 forests, leading to a slow succession rate and therefore minute detectable changes in vegetation

451 in the time span of only one decade, may explain some of the findings. The study and modelling

452   by Kumpula et al. (2000) showed that if lichen has been grazed and trampled to extremely low

453   level its recovery is much lower than that of more moderately depleted lichen stand. This might

454   well be the case in our study area as well. Also, changing interspecific competition in the plant

455   community due to changes in microclimate may slow down recovery from grazing (Olofsson

456   2006). Patterns in Thomisidae abundance, however, imply that there might be real differences

457   also between long grazed and intermediate treatments.

458

459

460

461   **Conclusion**

462

463   Based on our results, we could not find evidence of the hypothesized increase in spider diversity

464   under intermediate grazing impact by reindeer in lichen dominated dry pine forests in the

465   northern boreal zone, but the hypothesis cannot be rejected based on our data. Our data, of

466   course, comes from only one year and a limited area, and as such is has some limitations.

467   However, it seems rather that instead of being intermediate in relation reindeer impact the

468   treatments where grazing impact had been reversed eight years ago were fairly similar to long

469   term grazed habitats.

470   Focal species, sexes or even life stages can experience the same disturbance in dissimilar

471   ways. However, in sites where one species was highly abundant, the species richness within that

472   family was always lower than the species richness in sites of more even species distribution. This

473   suggests active competitive exclusion.

474   Even though Linyphiidae and Lycosidae spiders responded to reindeer grazing in the

475 same way as to clear-cut forest management in Pajunen et al. (1995), oversimplification of the

476 detrimental effects of heavy grazing on the forest floor spider community should be avoided. The

477 findings only support the existence of substantial habitat quality differences between grazed and

478 ungrazed areas for spiders. Furthermore, it is vital to remember that foraging habits and thus the

479 impact on vegetation also differ between large herbivore grazers (Huntly 1991; Adler et al.

480 2001). The distinct differences in feeding habits of reindeer between seasons can lead to

481 completely different impacts of the same herbivore species, through winter grazing on ground

482 lichens and summer grazing on grasses and deciduous leaves. Moreover, even though the

483 responses to treatments showed clear family-level habitat preferences among linyphiids and

484 lycosids, certain species within these families showed opposite responses. Thus,

485 oversimplification of family-level habitat preferences should also be avoided.

486   What our results clearly demonstrate is an extremely slow recovery rate of the

487 community after heavy grazing, which extends from the lichens even to invertebrates such as

488 spiders. Both of our intermediate treatments with eight years of reindeer exclusion or eight years

489 of grazing were strikingly similar to each other and to the long term grazed treatment. Thus we

490 could not see signs of noticeable recovery from heavy grazing after eight years of protection

491 from grazing, but on the other hand formerly ungrazed habitat was very similar to habitat that

492 had been grazed for decades after eight years of grazing. The recovery of lichen pasture after

493 heavy grazing is a long process (Olofsson 2006; Hansen et al. 2007) and not only for slow-

494 growing lichens, but also for other vegetation, the physical environment, and for faunistic

495 components like the spiders studied here.

496

497

498

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502

503 **References**

504 Adler PB, Raff DA, Lauenroth, WK. 2001. The effect of grazing on the spatial

505 heterogeneity of vegetation. *Oecologia* 128:465–479.

506 Augustine DJ, McNaughton SJ. 1998. Ungulate effects on the functional species

507 composition of plant communities: herbivore selectivity and plant tolerance. *The Journal*

508 *of Wildlife Management* 62:1165–1183.

509 Baines D, Sage RB, Baines MM. 1994. The implications of red deer grazing to

510 ground vegetation and invertebrate community structure of Scottish native

511 pinewoods. *Journal of Applied Ecology* 31:776–783.

512 Bernes C, Bråthen KA, Forbes BC, Hofgaard A, Moen J, Speed JD. 2015. What are the impacts

513 of reindeer/caribou (*Rangifer tarandus* L.) on arctic and alpine vegetation? A systematic review.

514 *Environmental Evidence* 4:4.

515 ter Braak CJF, Smilauer P. 1998. CANOCO reference manual and user's guide to

516 Canoco for Windows –software for canonocal community ordination (version

517 4). Microcomputer Power, Ithaca. New York.

518 Bromham LM, Cardillo M, Bennett AF, Elgar MA. 1999. Effects of stock

519 grazing on the ground invertebrate fauna of woodland remnants. *Australian Journal of Ecology*

520   24:199–207.

521   Churchill TB, Arthur JM. 1999. Measuring spider richness: effects of different

522   sampling methods and spatial and temporal scales. *Journal of Insect Conservation* 3:287–

523   295.

524   Colebourn PH 1974. The Influence of Habitat Structure on the Distribution of Araneus

525   diadematus Clerck. *Journal of Animal Ecology* 43:401-409.

526   Connell JH. 1978. Diversity in Tropical Rain Forests and Coral Reefs. *Science* 199:1302–1310.

527   Côté SD, Rooney TP, Tremblay J-P, Dussault C, Waller DM. 2004. Ecological impacts of deer

528   overabundance. *The Annual Review of Ecology, Evolution, and Systematics* 35:113–47.

529   Decalesta DS. 1994. Effect of White-tailed Deer on songbirds within managed forests

530   in Pennsylvania. *The Journal of Wildlife Management* 41:711–718.

531   Egelkraut D, Kardol P, De Long JR, Olofsson J. 2018. The role of plant–soil feedbacks in

532   stabilizing a reindeer-induced vegetation shift in subarctic tundra. *Functional Ecology* 32:1959–

533   1971.

534   Eskelinen A, Kaarlejärvi E, Olofsson J 2017. Herbivory and nutrient limitation protect warming

535   tundra from lowland species' invasion and diversity loss. *Global Change Biology* 23:245–255..

536   Evans R. 1996. Some impacts of overgrazing by reindeer in Finnmark, Norway.

537   *Rangifer* 16:3–19.

538   Frick H, Nentwig W, Kropf C. 2007. Influence of stand-alone trees on epigeic spiders (Araneae)

539   at the alpine timberline. *Annales Zoologici Fennici* 44:43–57.

540   Foster CN, Barton PS, Lindenmayer DB. 2014. Effects of large native herbivores on other

541   animals. *Journal of Applied Ecology* 51:929–938.

542   Foster CN, Barton PS, Wood JT, Lindenmayer DB. 2015. Interactive effects of fire and large

543   herbivores on web-building spiders. *Oecologia* 179:237–248.

544   Gause GF (1934). Experimental analysis of Vito Volterra's mathematical theory of the struggle

545   for existence. *Science* 79(2036):16–17.

546   Gotelli NJ, Entsminger GL. 2001. EcoSim: Null models software for ecology.

547   Gotelli NJ, Colwell RK. 2001. Quantifying biodiversity: procedures and pitfalls in the

548   measurement and comparison of species richness. *Ecology Letters* 4:379–391.

549   Hansen BB, Henriksen S, Aanes R, Saether BE. 2007. Ungulate impact on

550   vegetation in a two-level trophic system. *Polar Biology* 30:549–558.

551   Hardin G. 1960. The competitive exclusion principle. *Science* 131(3409):1292–1297.

552   Hartley CL, Macmahon JA 1980. Spider community organization: Seasonal variation and the

553   role of vegetation architecture. *Environmental Entomology* 9:632-639.

554   Helle T, Kojola I. 1993. Reproduction and mortality of Finnish semi-domesticated

555   reindeer in relation to density and management strategies. *Arctic* 46:72–77.

556   Helle T, Kajala L, Niva A, Särkelä M. 1998. Poron laidunnuksen vaikutus

557   tunturikoivikoiden rakenteeseen. In: Hyppönen M, Penttinen T,

558   Poikajärvi H (eds.) Poron vaikutus metsä- ja tunturiluontoon.

559   Tutkimusseminaari Hetassa 1997. Metsäntutkimuslaitoksen tiedonantoja. 678:

560   132–141.

561   Huntly N. 1991. Herbivores and the dynamics of communities and ecosystems.

562   *The Annual Review of Ecology, Evolution, and Systematics* 22:477–503.

563   Jones CG, Lawton JH, Shachak M. 1994. Organisms as ecosystem engineers.

564   *Oikos* 69:373–386.

565 Jones CG, Lawton JH, Shachak M. 1997. Positive and negative effects of

566 organisms as physical ecosystem engineers. *Ecology* 78:1946–1957.

567 Kaarlejärvi E, Eskelinen A, Olofsson J 2017. Herbivores rescue diversity in warming tundra by

568 modulating trait-dependent species losses and gains. *Nature Communications* 8: 419.

569 Kielland K, Bryant JP, Ruess RW. 1997. Moose herbivory and carbon turnover

570 of early successional stands in interior Alaska. *Oikos* 80:25–30.

571 Kojola I, Helle T, Aikio P. 1991. Productivity of semi-domesticated reindeer in

572 Finland. *Rangifer* 11:53–64.

573 Kojola I, Helle T, Niskanen M, Aikio P. 1995. Effects of lichen biomass on

574 winter diet, body mass and reproduction of semi-domesticated reindeer

575 *Rangifer tarandus* in Finland. *Wildlife Biology* 1:33–38.

576 Koponen S. 1977. Spider fauna (Araneae) of Kevo area, northenmost Finland. *Reports from*

577 *the Kevo Subarctic Research Station* 13:48–62.

578 Koponen S. 1995. Ground-living spiders (Araneae) of old forests in eastern Finland.

579 *Memoranda Societatis pro Fauna et Flora Fennica* 71:57–62.

580 Koponen S. 1999. Common ground-living spiders in old taiga forests of Finland. *Journal of*

581 *Arachnology* 27:201–204.

582 Koponen S. 2002. Ground-living spiders in bogs in northern Europe. *Journal of*

583 *Arachnology* 30: 262–267

584 Koponen S. 2004. Effects of intensive fire on the ground-living spider (Araneae) fauna

585 of a pine forest. European Arachnology 2003, *Arthropoda Selecta* Special Issue

586 1:133–137.

587   Koponen S, Koneva GG. 2006. Spiders along a pollution gradient (Araneae). European

588   Arachnology 2005, *Acta Zoologica Bulgarica Supplement* 1:131–136.

589   Koponen S, Haukioja E, Iso-Iivari L. 1975. Comparison of spider catches and weather in

590   subarctic conditions. Proc 6th Int Arachn Congress, Amsterdam 1974:77–81.

591   Köster E, Köster K, Aurela M, Laurila T, Berninger F, Lohila A, Pumpanen J. 2013. Impact of

592   reindeer herding on vegetation biomass and soil carbon content: a case study from Sodankylä,

593   Finland. *Boreal Environmental Research* 18:35-42.

594   Köster K, Berninger F, Köster E, Pumpanen J. 2015. Influences of reindeer grazing on above-

595   and below-ground biomass and soil carbon dynamics. *Arctic, Antarctic and Alpine Research*

596   47:495-503.

597   Kumpula J, Colpaert A, Kumpula T, Nieminen M. 1997. Suomen

598   poronhoitoalueen talvilaidunvarat [The winter pasture resources of the Finnish

599   reindeer management area]. Kala- ja riistaraportteja, nro 93, Riista ja

600   kalatalouden tutkimuslaitos.

601   Kumpula J, Colpaert A, Nieminen M. 2000. Condition, potential recovery rate, and productivity

602   of lichen (*Cladonia* spp.) ranges in the Finnish reindeer management area. *Arctic* 53:152-160.

603   Kumpula J, Fielitz U, Colpaert A. 1999. Porojen laidunten käyttö Pohjois-Lapissa:

604   GPS-seuranta ja satelliitikuvatulkinnat laidunten käytön tutkimisessa [Pasture

605   use of reindeer in northernmost Lapland: GPS-tracking and satellite image

606   data as a study method]. Kala- ja Riistaraportteja nro 150. Riista- ja

607   kalatalouden tutkimuslaitos.

608   Maliniemi T, Kapfer J, Saccone P, Skog, A, Virtanen R 2018. Long-term vegetation changes of

609   treeless heath communities in northern Fennoscandia: Links to climate change trends and

610   reindeer grazing. *Journal of Vegetation Science* 29:469-479.

611   .

612   Marusik YM, Koponen S. 2002. Diversity of spiders in boreal and arctic zones. *Journal of*

613   *Arachnology* 30:205–210.

614   Milchunas DG, Lauenroth WK, Burke IC. 1998. Livestock grazing: animal and

615   plant biodiversity of shortgrass steppe and the relationship to ecosystem

616   function. *Oikos* 83:63–74.

617   Minoshima M, Takada MB, Agetsuma N, Hiura T. 2013. Sika deer browsing differentially

618   affects web-building spider densities in high and low productivity forest understories. *Ecoscience*

619   20:55–64.

620   Miyashita T, Takada M, Shimazaki A. 2004. Indirect effects of herbivory by deer

621   reduce abundance and species richness of web spiders. *Ecoscience* 11:74–79.

622   Nilsson SG, Nilsson IN. 1983. Are estimated species turnover rates on islands largely sampling

623   errors? *The American Naturalist* 595–597.

624   Norris KC. 1999. Quantifying change through time in spider assemblages: sampling

625   methods, indices and sources of error. *Journal of Insect Conservation* 3:309–325.

626   Oksanen L. 1978. Lichen grounds of Finnmarksvidda, northern Norway, in relation to

627   summer- and winter grazing by reindeer. *Reports from Kevo Subarctic Research Station* 14:64–

628   71.

629   Oksanen L, Moen J, Helle T. 1995. Timberline patterns in northernmost

630   Fennoscandia. Relative importance of climate and grazing. *Acta Botanica Fennica*

631   153:93–105.

632   Olofsson J, Kitti H, Rautiainen P, Stark S, Oksanen L. 2001. Effects of summer

633   grazing by reindeer on composition of vegetation, productivity and nitrogen

634   cycling. *Ecography* 24:13–24

635   Olofsson J, Stark S, Oksanen L. 2004. Reindeer influence on ecosystem

636   processes in the tundra. *Oikos* 105:386–396.

637   Olofsson J. 2006. Short- and long-term effects of changes in reindeer grazing pressure

638   on tundra vegetation. *Journal of Ecology* 94:431–440.

639   Owen-Smith N. 1987. Pleistocene Extinctions: The Pivotal Role of Megaherbivores.

640   *Paleobiology* 13:351–362.

641   Pajunen T, Haila Y, Halme E, Niemelä J, Punttila P. 1995. Forest fragmentation

642   and ground-dwelling spiders (Arachnida, Araneae) in the southern Finnish

643   taiga. *Ecography* 18:62–72.

644   Pastor J, Cohen Y. 1997. Herbivores, the functional diversity of plant species, and

645   the cycling of nutrients in ecosystems. *Theoretical Population Biology* 51:165–179

646   Pastor J, Naiman RJ. 1992. Selective Foraging and Ecosystem Processes in Boreal

647   Forests. *American Naturalist* 139:690–705.

648   Putman RJ (1994) Effects of grazing and browsing by mammals on woodlands. *British Wildlife*

649   5:205–213.

650   Riechert SE, Tracy CR. 1975. Thermal balance and prey availability: Bases for a

651   model relating web-site characteristics to spider reproductive success. *Ecology*

652   56:265–284.

653 Samu F, Sunderland KD, Szinetar C. 1999. Scale-dependent dispersal and distribution patterns of

654 spiders in agricultural systems: a review. *Journal of Arachnology* 27:325–332.

655 Santalahti M, Sund H, Sietiö O-M, Köster K, Berninger F, Laurila T, Pumpanen J, Heinonsalo J.

656 2018. Reindeer grazing alter soil fungal community structure and litter decomposition related

657 enzyme activities in boreal coniferous forests in Finnish Lapland. *Applied Soil Ecology* 132:74-

658 82.

659 Stark S, Wardle DA, Ohtonen R, Helle T, Yeates GW. 2000. The effect of

660 reindeer grazing on decomposition, mineralization and soil biota in a dry

661 oligotrophic Scots pine forest. *Oikos* 90:301–310.

662 Stark S, Strömmer R, Tuomi J. 2002. Reindeer grazing and soil microbial processes

663 in two suboceanic and two subcontinental tundra heaths. *Oikos* 97:69–78.

664 Suominen O. 1999. Mammalian herbivores, vegetation and invertebrate assemblages

665 in boreal forests: feeding selectivity, ecosystem engineering and trophic

666 effects. *Annales Universitatis Turkuensis* 122.

667 Suominen, O. & Danell, K. 2006. Effects of large herbivores on other fauna. Large Herbivore

668 Ecology, Ecosystem Dynamics and Conservation (eds K. Danell, R. Bergstrom, P. Duncan & J.

669 Pastor), pp. 383–412. Cambridge University Press, Cambridge.

670 Suominen O, Niemelä J, Martikainen P, Niemelä P, Kojola I 2003. Impact of reindeer grazing on

671 ground-dwelling Carabidae and Curculionidae assemblages in Lapland. *Ecography* 26:503-513.

672 Suominen O, Olofsson J. 2000. Impacts of semi-domesticated reindeer on structure

673 of tundra and forest communities in Fennoscandia: a review. *Annales Zoologici*

674 *Fennici* 37:233–249.

675 Suominen O, Persson I-L, Danell K, Bergström R, Pastor J. 2008. Impact of simulated moose

676 densities on abundance and richness of vegetation, herbivorous and predatory arthropods along a

677 productivity gradient. *Ecography* 31:636–645.

678 Takada M, Baba YG, Yanagi Y, Terada S, Miyashita T. 2008. Contrasting responses of web-

679 building spiders to deer browsing among habitats and feeding guilds. *Environmental Entomology*

680 37:938–946.

681 Uetz GW. 1991. Habitat structure and spider foraging. In: Bell SA,

682 McCoy ED, Mushinsky HR (Eds.). Habitat Structure: The Physical

683 Arrangement of Objects in Space. Chapman & Hall, London 325–348.

684 Väre H, Ohtonen R, Mikkola K. 1996. The effect and extent of heavy grazing by

685 reindeer in oligotrophic pine heaths in north eastern Fennoscandia. *Ecography*

686 19:245–253.

687 Wardle DA, Barker GM, Yeates GW, Bonner KI, Ghani A. 2001. Impacts of

688 introduced browsing mammals in New Zealand forests on decomposer

689 communities, soil biodiversity and ecosystem properties. *Ecological Monographs* 71:587–614.

690 Warui CM, Villet MH, Young TP, Jocque R. 2005. Influence of grazing by large

691 mammals on the spider community of a Kenyan Savanna biome. *Journal of Arachnology*

692 33:269–279.

693 Ylänne H, Olofsson J, |Oksanen L, Stark S. 2017. Consequences of grazer-induced vegetation

694 transitions on ecosystem carbon storage in the tundra. *Functional Ecology* 32:1091–1102.

695

696 **Figure and Table captions**

697

698   Figure 1. Map of Finland showing the study area.

699

700   Figure 2. The differences between treatments in soil temperature (°C at the depth of 5 cm), soil

701   moisture (top layer of mineral soil), and total lichen biomass (dry mass g/0.25 m^2) (mean ± SD).

702   The treatments are Graz – long term grazed area, UGraz – long term ungrazed, NGraz – grazed

703   last 9 years, but previously ungrazed, NUGraz – ungrazed last 9 years, but previously grazed (the

704   number (1) in treatments Graz and UGraz refers to sites that act as a reference to the NGraz

705   treatment and number (2) to those that act as reference to the NUGraz treatment).

706

707   Figure 3. The relationship between lichen biomass (dry mass g/0.25 m^2), soil moisture (% top

708   layer of mineral soil), and soil temperature (°C at the depth of 5 cm). Statistically significant

709   linear regressions are included into the figures.

710

711   Figure 4. Pooled family level abundances of spider individuals of the three most abundant spider

712   families in different treatments (mean number of individuals per trapping line ± SD). For the

713   abbreviations of treatments see the legend of figure 2.

714

715   Figure 5. Abundances of spider individuals of four common species between different treatments

716   (mean number of individuals per trapping line ± SD). For the abbreviations of treatments see the

717   legend of figure 2.

718

719   Figure 6. DCA-ordination visualizing the effect of environmental factors and treatments on

720   spider communities. The symbols for treatments: long term grazed = □, sites where grazing

721   status changed in 1997 = ◊, long term ungrazed = ○. The axes 1 and 2 explained 33.4 % and 16.7

722   % of the variation (relative eigenvalue portions 0.40 and 0.16 respectively).

723

724   Figure 7. The location of spider species on DCA-ordination axes 1 and 2. Only species with

725   more than 20% weight on the ordination are shown. The axes 1 and 2 explained 14.5 % and 9.3

726   % of the variation in the species data (relative eigenvalue portions 0.198 and 0.127 respectively).

727

728   Table 1. List of spider species found in the study.

729

730   Table 2. Twelve most common species and their specimen numbers.

731

732   Table 3. Impact of treatment on response variables (mean and SD, or estimate with 95%

733   confidence limits). Variables that fulfill the assumptions for a parametric test were tested with

734   ANOVA and the F-test (DF= 5). Spider abundances and lichen biomass were tested with the

735   non-parametric Kruskal-Wallis χ^2-test (DF=5). Species richness for pooled families, Lycosidae

736   and Linyphiidae, are rarefied values. Due to the low number of species and specimens, species

737   richnesses of Thomisiidae and Gnaphosidae are absolute values without rarefaction. Site-level

738   richness (α-diversity) is the rarefied number of species per trapping line. γ-diversity is the

739   rarefied number of species per treatment (with 95% confidence limit). Bold font indicates

740   variables with statistically significant (p<0.05) treatment impact.

741

742   Table 4. Spearman rank correlations of the abundances (n) and species richnesses (S) of spider

743   families. (* = p<0.05, **p<0.01)(n=18). Others n and Others S mean the abundance and richness

744   respectively of all other spider families than the one tested against.

745

746   Table 5. The responses of spider family species richnesses (s) and abundances (n), as well as the

747   abundances of the most numerous species to environmental variables. Linear regression results

748   are also included (* = p<0.05, **p<0.01)(df=16). S = number of species, n = number of

749   specimen.

750

Figure 1

Map of Finland showing the study area.

Norway

Russia

Sweden

Finland

N

0   75   150   300 Km

Figure 2

The differences between treatments in soil temperature (°C at the depth of 5 cm), soil moisture (top layer of mineral soil), and total lichen biomass (dry mass g/0.25 m^2) (mean ± SD).

The treatments are Graz – long term grazed area, Ugraz – long term ungrazed, NGraz – grazed last 9 years, but previously ungrazed, NUgraz – ungrazed last 9 years, but previously grazed (the number (1) in treatments Graz and Ugraz refers to sites that act as a reference to the NGraz treatment and number (2) to those that act as reference to the NUgraz treatment).

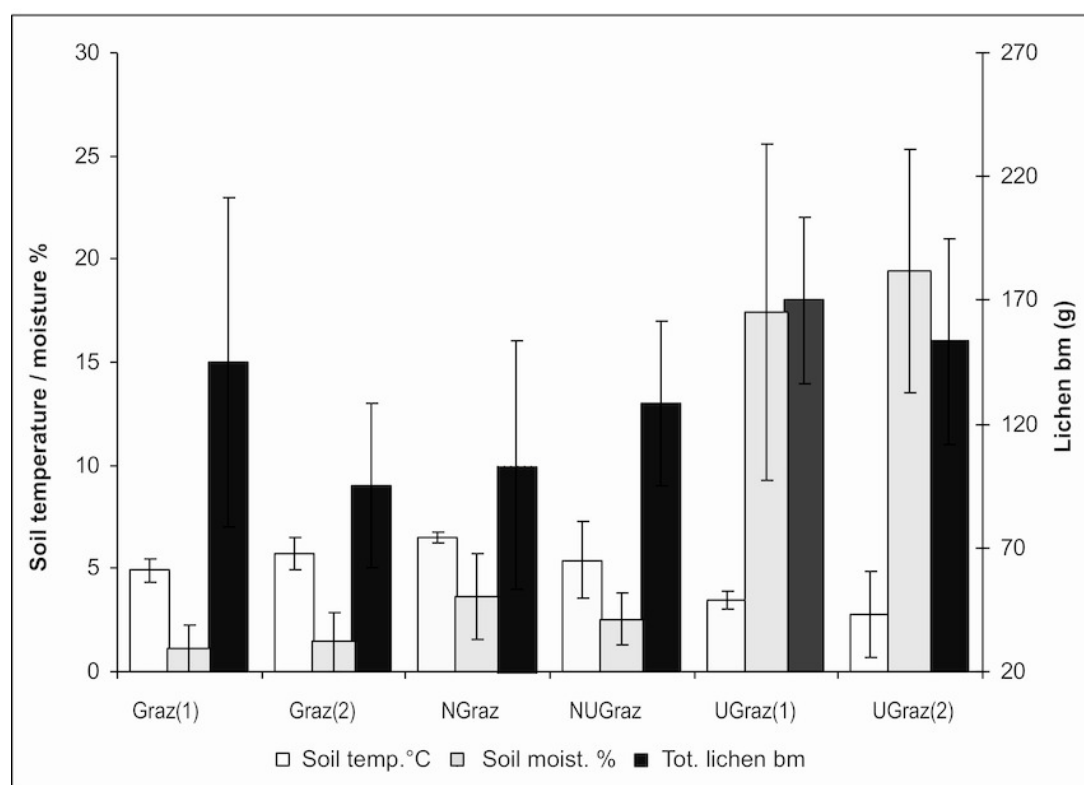
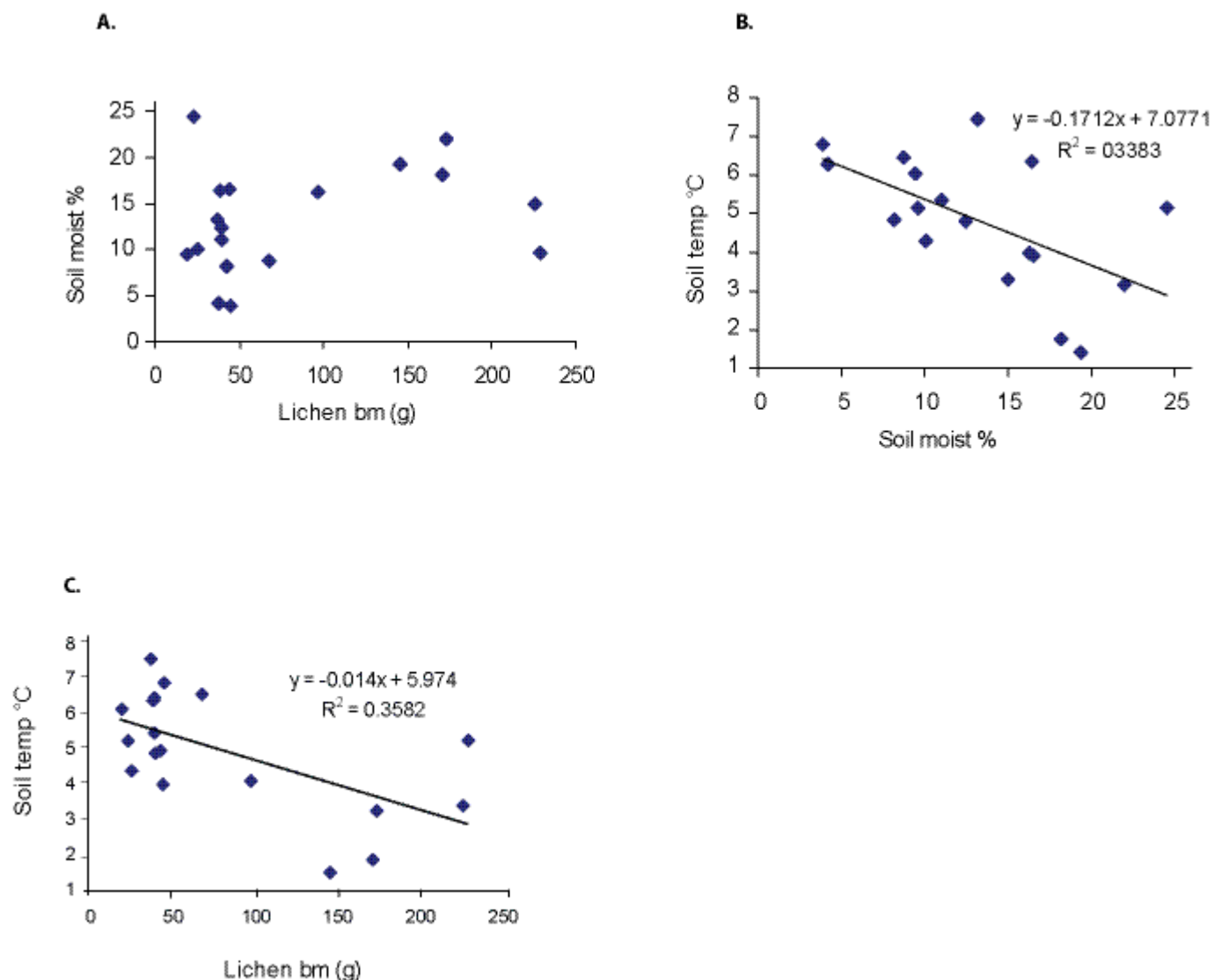



Figure 3

The relationship between lichen biomass (dry mass g/0.25 m^2), soil moisture (% top layer of mineral soil), and soil temperature (°C at the depth of 5 cm).

Statistically significant linear regressions are included into the figures.

A.

B.

C.

Figure 4

Pooled family level abundances of spider individuals of the three most abundant spider families in different treatments (mean number of individuals per trapping line ± SD).

For the abbreviations of treatments see the legend of figure 3.

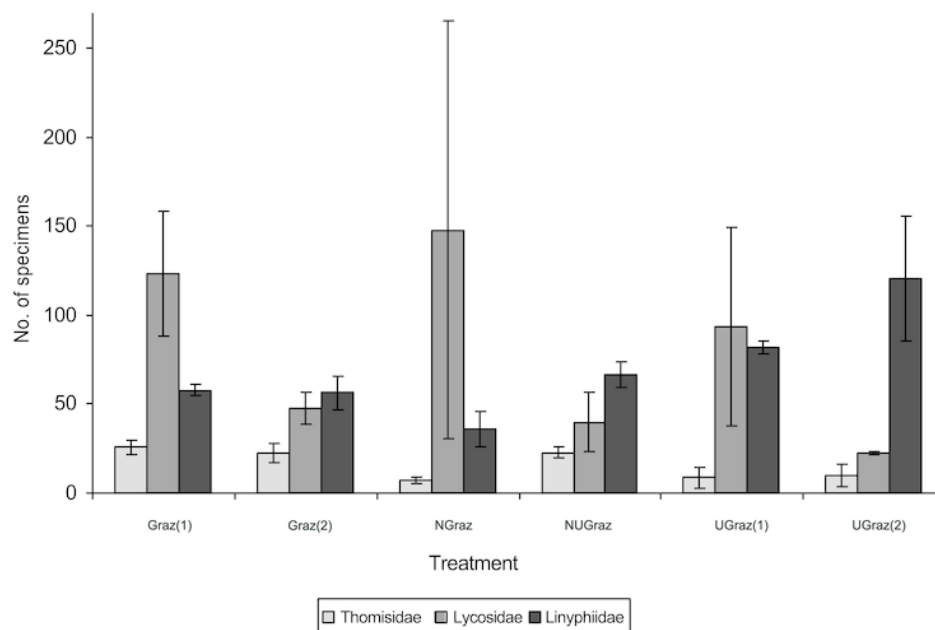



Figure 5

Abundances of spider individuals of four common species between different treatments (mean number of individuals per trapping line ± SD).

For the abbreviations of treatments see the legend of figure 3.

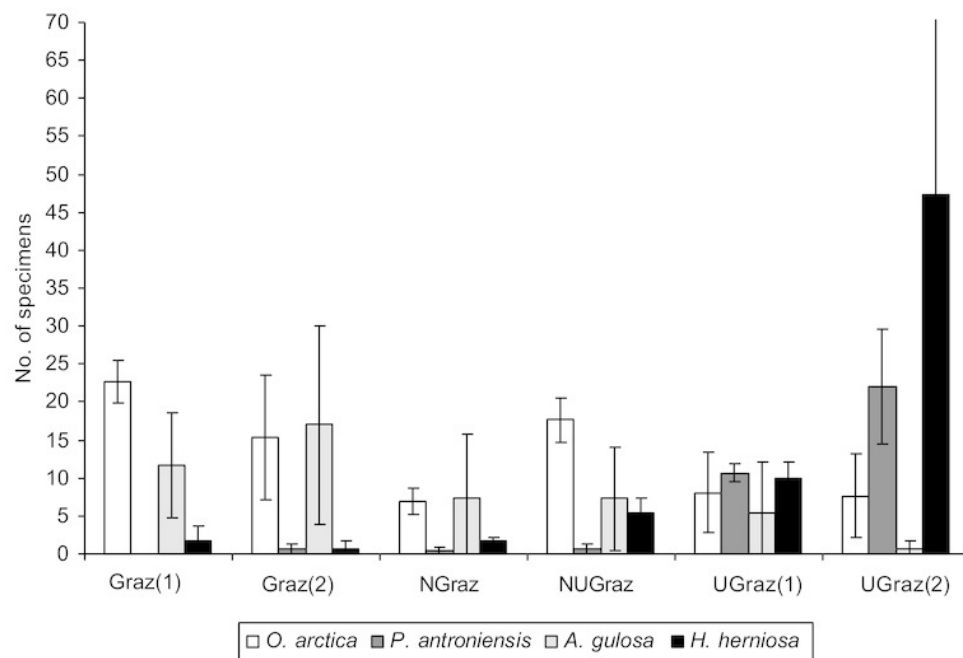



Figure 6

DCA-ordination visualizing the effect of environmental factors and treatments on spider communities.

The symbols for treatments: long term grazed = ☐, sites where grazing status changed in 1997 = ◊, long term ungrazed = ◯. The axes 1 and 2 explained 33.4 % and 16.7 % of the variation (relative eigenvalue portions 0.40 and 0.16 respectively).

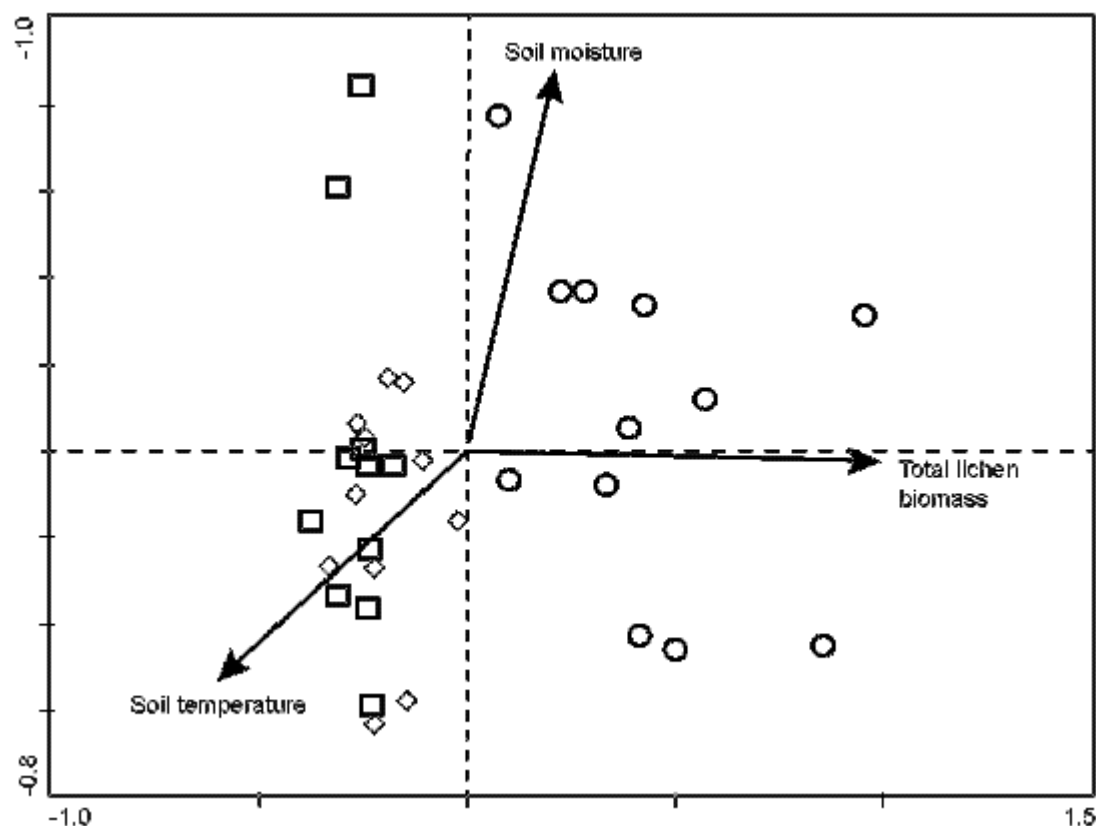



Figure 7

The location of spider species on DCA-ordination axes 1 and 2.

Only species with more than 20% weight on the ordination are shown. The axes 1 and 2 explained 14.5 % and 9.3 % of the variation in the species data (relative eigenvalue portions 0.198 and 0.127 respectively).

X. obscurus

H. hemiosa

M. pusillus

W. karpinskii

A. gulosa

P. antroniensis

O. arctica

A. conigera

P. pumila

R. lividus

A. aculeata

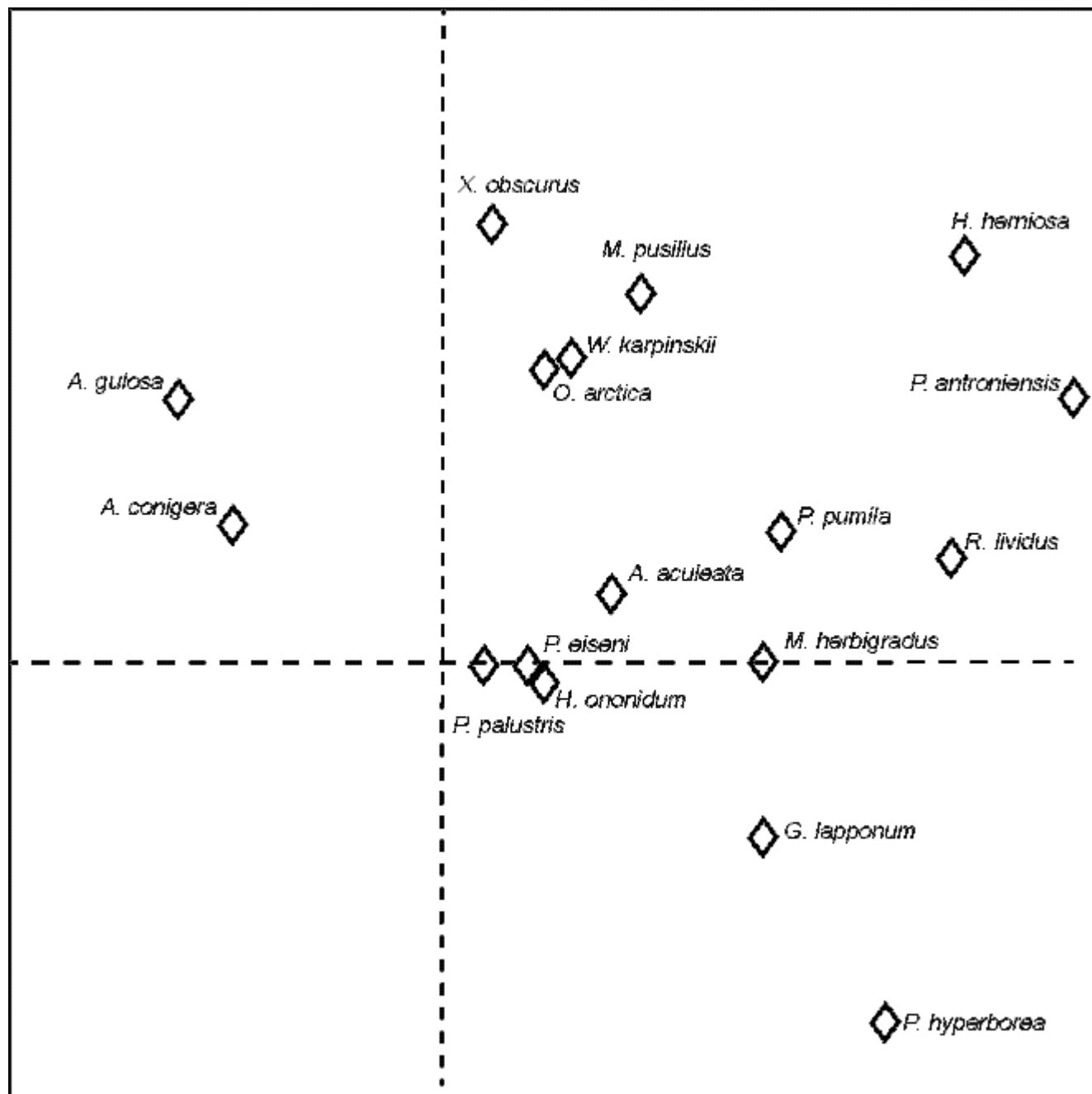
P. eiseni

M. herbigradus

H. ononidum

P. palustris

G. lapponum

P. hyperborea

List of species found in the study.

Araneidae
Hypsosinga albovittata (Westring, 1851)
Cercidia prominens (Westring, 1851)

Dictynidae
Hackmania prominula (Tullgren, 1948)

Gnaphosidae
Gnaphosa lapponum (L. Koch, 1866)
Gnaphosa montana (L. Koch, 1866)
Gnaphosa muscorum (L. Koch, 1866)
Gnaphosa sticta (Kulczynski, 1908
Haplodrassus signifer (C. L. Koch, 1839)
Haplodrassus soerenseni (Strand, 1900)
Micaria alpina (L. Koch, 1872
Zelotes subterraneus (C. L. Koch, 1833)

Hahnidae
Hahnia ononidum (Simon, 1875)

Linyphiidae
Agyneta cauta (O. P.-Cambridge, 1902)
Agyneta conigera (O. P.-Cambridge, 1863)
Agyneta gulosa (L. Koch, 1869)
Agyneta subtilis (O. P.-Cambridge, 1863)
Agyneta trifurcata (Hippa & Oksala, 1985)
Bolepthyphantes index (Thorell, 1856)
Ceratinella brevipes (Westring, 1851)
Centromerus arcanus (O. P.-Cambridge, 1873)
Cnephalocotes obscurus (Blackwall, 1834)
Decipiphantes decipiens (L. Koch, 1879)
Diplocentria bidentata (Emerton, 1882)
Diplocentria rectangulata (Emerton, 1915)
Hilaira herniosa (Thorell, 1875)
Macrargus rufus (Wider, 1834)
Maso sundevalli (Westring, 1851)
Micrargus herbigradus (Blackwall, 1854)
Minyriolus pusillus (Wider, 1834)
Moebelia penicillata (Westring, 1851)
Mughiphantes cornutus (Schenkel, 1927)
Neriene clathrata (Sundevall, 1830)
Oreoneta sinuosa (Tullgren, 1955)
Palliduphantes antroniensis (Schenkel, 1933)
Pocadicnemis pumila (Blackwall, 1841)

Porrhomma pallidum (Jackson, 1913)
Scandichrestus tenuis (Holm, 1943)
Semljicola latus (Holm, 1939)
Sisicus apertus (Holm, 1939)
Tapinocyba pallens (O. P.-Cambridge, 1872)
Tenuiphantes alacris (Blackwall, 1853)
Tenuiphantes mengei (Kulczynski, 1887)
Tenuiphantes tenebricola (Wider, 1834)
Tibioploides arcuatus (Tullgren, 1955)
Tibioplus diversus (L. Koch, 1879)
Walckenaeria antica (Wider, 1834)
Walckenaeria capito (Westring, 1861)
Walckenaeria cuspidata (Blackwall, 1833)
Walckenaeria dysderoides (Wider, 1834)
Walckenaeria karpinskii (O. P.-Cambridge, 1873)
Walckenaeria obtusa (Blackwall, 1836)
Walckenaeria unicornis (O. P.-Cambridge, 1861)
Zornella cultrigera (L. Koch, 1879)

Liocranidae
Agroeca proxima (O. P.-Cambridge, 1871)

Lycosidae
Acantholycosa lignaria (Clerck, 1757)
Alopecosa aculeata (Clerck, 1757)
Alopecosa pinetorum (Thorell, 1856)
Pardosa eiseni (Thorell, 1875)
Pardosa hyperborea (Thorell, 1872)
Pardosa lasciva (L. Koch, 1879)
Pardosa lugubris (Walckenaer, 1802)
Pardosa palustris (Linnaeus, 1758)
Pardosa sphagnicola (Dahl, 1908)

Philodromidae
Thanatus formicinus (Clerck, 1757)

Salticidae
Evarcha falcata (Clerck, 1757)
Neon reticulatus (Blackwall, 1853)

Theridiidae
Robertus lividus (Blackwall, 1836

92   *Theonoe minutissima* (O. P.-Cambridge,
93   1879)
94
95   **Thomisidae**
96   *Ozyptila arctica* (Kulczynski, 1908)
97   *Xysticus audax* (Schrank, 1803)
98   *Xysticus luctuosus* (Blackwall, 1836)
99   *Xysticus obscurus* (Collett, 1877)

100

Twelve most common species and their specimen numbers.

Species	*Pardosa eiseni*	*Alopecosa aculeata*	*Pardosa palustris*	*Ozyptila arctica*	*Hilaira herniosa*	*Pocadicnemis pumila*
n	622	344	276	235	200	159

Species	*Agyneta gulosa*	*Pardosa hyperborea*	*Walckenaeria karpinskii*	*Palliduphantes antroniensis*	*Hahnia ononidum*	*Micrargus herbigradus*
n	148	118	117	103	80	67

4

Impact of treatment on response variables (mean and SD, or estimate with 95% confidence limits).

Variables that fulfill the assumptions for a parametric test were tested with ANOVA and the F-test (DF= 5). Spider abundances and lichen biomass were tested with the non-parametric Kruskal-Wallis χ²-test (DF=5). Species richness for pooled families, Lycosidae and Linyphiidae, are rarefied values. Due to the low number of species and specimens, species richnesses of Thomisiidae and Gnaphosidae are absolute values without rarefaction. Due to the same reason the Pielou's evenness index J' could not be calculated for Gnaphosidae. Site-level richness (α-diversity) is the rarefied number of species per trapping line. γ-diversity is the rarefied number of species per treatment (with 95% confidence limit). JK-species no. is the first order jackknife estimate of the total number of species in each treatment (with 95% confidence limits). Bold font indicates variables with statistically significant (p<0,05) treatment impact.

	Mean (SD)						F(χ^2)	P
	UGraz (1)	UGraz (2)	Graz (1)	Graz (2)	NUGraz	NGraz		
SPIDER RICHNES								
α	26.8 (4.1)	28.5 (2.3)	23.13 (2.1)	27.12 (5.9)	28.8 (6.0)	21.4 (2.8)	1.53	0.251
γ	41.5 (3.1)	49.3 (1.5)	38.7 (4.1)	47.0 (0.2)	46.0 (0.5)	36.9 (2.5)	-	-
Lycosidae	4.1 (0.2)	6.1 (0.4)	3.6 (0.3)	4.5 (0.7)	4.7 (1.5)	3.6 (0.8)	4.37	**0.017**
Linyphiidae	11.5 (1.4)	9.8 (1.4)	11.2 (1.7)	10.2(3.1)	11.2 (1.7)	12.6 (2.0)	0.72	0.623
Thomisidae	1.7 (0.6)	2.3 (0.6)	2.3 (0.6)	3.3 (0.6)	2.3 (0.6)	1.3 (0.6)	4.27	**0.018**
Gnaphosidae	2.6 (0.6)	1.3 (0.6)	2.6 (0.6)	3.0 (1.7)	3.3 (1.5)	3.0 (1.0)	1.2	0.366
SPIDER ABUNDANCE								
Total	203.7 (66.0)	166.7 (37.3)	225.3 (41.4)	135.6 (14.2)	144.6 (13.7)	206.0 (121)	(5.63)	0.344
Lycosidae	93.3 (55.9)	22.3 (1.2)	123.3 (35.5)	47.7 (9.2)	40.0 (16.5)	147.7 (117.4)	(12.09)	**0.034**
Linyphiidae	81.7 (3.8)	120.2 (35.3)	58.0 (3.5)	56.3 (9.3)	67 (7.2)	35.7 (10.0)	(15.27)	**0.009**
Thomisidae	8.7 (7.6)	10.0 (6.1)	26.0 (4.0)	22.3 (5.5)	22.7 (3.1)	7.3 (2.1)	(12.74)	**0.026**
Gnaphosidae	9.0 (2.6)	2.0 (1.0)	6.3 (3.5)	4.7 (3.1)	6.3 (2.5)	7.7 (6.7)	(7.45)	0.189
P.antroniensis	10.7 (5.3)	22 (7.5)	0 (0)	0.7 (0.6)	0.7 (0.6)	0.3 (0.6)	24.41	**<0.0001**
H. herniosa	10 (2)	47.3 (27.1)	1.7 (2.1)	0.7 (1.2)	5.3 (2.1)	1.7 (0.6)	7.88	**0.002**
O. arctica	8 (5.3)	7.7 (5.5)	22.7 (2.9)	15.3 (8.1)	17.7 (2.9)	7 (1.7)	5.24	**0.009**
A. gulosa	5.3 (6.8)	0.7 (1.2)	11.7 (6.7)	17 (13.1)	7.3 (6.8)	7.3 (8.5)	1.46	0.273
ENV.VAR.								
Soil. °C	3.48 (0.45)	2.77 (2.07)	4.9 (0.56)	5.7 (0.80)	5.4 (1.84)	6.5 (0.24)	4.09	**0.0212**
Moist %	0.18 (0.04)	0.16 (0.05)	0.15 (0.08)	0.09 (0.04)	0.13 (0.04)	0.10 (0.06)	1.27	0.338
VEGET.HEIGHT								
Lichen	13.33 (1.32)	13.61 (0.78)	5.00 (1.12)	4.94(1.24)	7.22 (0.79)	5.10 (0.95)	(43.18)	**<0.0001**
Moss	3.89 (2.15)	4.89 (1.76)	1.63 (0.74)	1.88 (0.78)	3.00 (1.87)	1.13 (0.23)	8.49	**<0.0001**
Vascular plants	23.11 (8.08)	18.33 (3.84)	14.00 (2.35)	10.67 (3.31)	14.44 (4.25)	10.67 (2.35)	10.38	**<0.0001**
VEGET.BIOM.								
Lichen	165.29 (68.14)	181.62 (49.12)	29.09 (9.84)	31.96 (11.96)	41.17 (10.50)	50.50 (17.27)	(26.65)	**<0.0001**
Moss	8.36 (14.28)	11.23 (9.52)	4.29 (8.46)	8.62 (13.75)	21.40 (39.24)	2.38 (3.15)	0.77	0.580
Vascular plants	43.40 (16.39)	35.45 (18.82)	28.09 (12.11)	36.64 (20.37)	34.45 (19.20)	23.43 (6.94)	1.09	0.384

Spearman rank correlations of the abundances (n) and species richnesses (S) of spider families. (* = p<0.05, **p<0.01)(n=18).

	Lycosidae n	Lycosidae S	Linyphiidae n	Linyphiidae S
Lycosidae n	1			
Lycosidae S	**-0.842****	1		
Linyphiidae n	-0.418	**0.495***	1	
Linyphiidae S	**0.712****	**-0.628****	-0.203	1
Others n	-0.294	0.376	-0.362	**0.710****
Others S	**0.539***	**-0.602****	0.221	-0.005

The responses of spider family species richnesses (s) and abundances (n), as well as the abundances of the most numerous species to environmental variables.

Linear regression results are also included (* = p<0.05, **p<0.01)(df=16). S = number of species, n = number of specimen.

a)	Lichen bm	Soil moist. %	Soil temp. °C	b)	Lichen bm	Soil moist. %	Soil temp. °C
	F	F	F		F	F	F
Tot. species (S)	0,47	0,28	5,68 *	A.aculeata	1,06	0,65	1,38
Lycosidae S	3,64	0,33	10,71 **	O.arctica	4,92*	0,1	2,02
Linyphiidae S	0,41	2,31	0,02	H.ononidum	0,26	0,69	0,05
Thomisidae S	1,09	0,11	0,01	P.antroniensis	37,17**	1,96	11,98**
Gnaphosidae S	2,8	0,44	1,32	A . gulosa	6,28*	4,94*	6,52**
Tot. specimens (n)	0,43	3,32	0	P. pumila	2,11	4,42*	1,87
Lycosidae n	0,33	0,85	1,16	H.herniosa	17,7**	0,25	3,28
Linyphiidae n	20,69 **	1,09	8,09 *	W.karpinskii	0,86	0,02	0,35
Thomisidae n	6,54 **	0,25	2,42	M.herbigradus	0,27	12**	6,57**
Gnaphosidae n	0,11	3,954	0				