Red deer mediate spatial and temporal plant heterogeneity in boreal forests

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ABSTRACT

21

22   Selective herbivory can influence both spatial and temporal vegetation heterogeneity.

23 For example, many northern European populations of free-ranging ungulates have reached

24 unprecedented levels, which can influence plant species turnover, long-term maintenance of

25 biodiversity and the subsequent stability of boreal ecosystems. However, the mechanisms by

26 which large herbivores affect spatial and temporal vegetation heterogeneity remain poorly

27 understood. Here, we combined a 10-year exclusion experiment with a herbivore intensity

28 gradient to investigate how red deer (*Cervus elaphus*) acts as a driver of temporal and spatial

29 heterogeneity in the understory of a boreal forest. We measured the two dimensions of

30 heterogeneity as temporal and spatial species turnover and. We found that temporal

31 heterogeneity was positively related to herbivory intensity, and we found a similar trend for

32 spatial heterogeneity. Removing red deer (exclosure) from our study system caused a distinct

33 shift in species composition, both spatially (slow response) and temporally (quick response).

34 Vegetation from which red deer had been excluded for ten years showed the highest spatial

35 heterogeneity, suggesting that the most stable forest understory will occur where there are no

36 large herbivores. However, excluding red deer resulted in lower species diversity and greater

37 dominance by a low number of plant species. If both stable but species rich ecosystems are

38 the management goal, these findings suggest that naturally fluctuating, but moderate red deer

39 densities should be sustained.

40

KEY WORDS

INTRODUCTION

44 Vegetation heterogeneity has two broad functional roles in ecosystem stability: temporal

45 heterogeneity (i.e., temporal species turnover) destabilizes, whereas spatial heterogeneity (i.e.,

46 spatial species turnover) stabilizes ecosystems (May 1974). However, factors such as the

47 presence or absence of disturbance can determine the nature of these roles. For example,

48 severe disturbance often leads to high temporal species turnover in systems dominated by

49 pioneer species, butwhen long-lived and slower growing species dominate, species turnover is

50 low (Rydgren et al. 2004). Spatial species turnover is the difference in species composition

51 across both local and regional assemblages, with high values reflecting a patchy distribution

52 of plant species at various spatial scales (Koleff et al. 2003). High spatial heterogeneity can

53 make an ecosystem more robust to disturbances. It also facilitates important ecosystem

54 functions such as dispersal and recolonization, and by increasing resources and refugia

55 (Hovick et al. 2015). Therefore, spatial heterogeneity is also important for ecosystem

56 resilience (the ability to reorganize and renew itself following disturbance; Elmqvist et al.

57 2003).

58   Large herbivores can act as ecosystem engineers by trampling and feeding selectively

59 (Jones et al. 1994), thereby modifying plant species composition and dynamics. The influence

60 of herbivory on vegetation heterogeneity depends on ecosystem productivity (Proulx &

61 Mazumder 1998), herbivore selectivity (Adler et al. 2001) and intensity (Mackey & Currie

62 2001), as well as the species of herbivore, its use of habitat and how selectively it feeds (Côté

63 et al. 2004; DeGabriel et al. 2011). Some general patterns are apparent: strongly preferred or

64 herbivory-sensitive plant species become less abundant in the presence of herbivores, whereas

65 herbivory-tolerant and non-preferred species increase (Augustine & McNaughton 1998).

66 Herbivores can also increase vegetation heterogeneity when preferred plant species are

67 unevenly distributed in the landscape (Hester et al. 2000), or if they forage more patchily than

68 the vegetation pattern (Adler et al. 2001), for example, when external factors such as

69 disturbance or stress influence a herbivore's spatial use of habitat.

70   Few studies simultaneously address the effects of herbivores on spatial and temporal

71 vegetation heterogeneity (Adler et al. 2001), with most focussing on simple measures of

72 diversity such as species richness or alpha diversity (within-plot diversity). However, other

73 aspects of diversity are important in understanding how herbivory impacts vegetation. For

74 example, landscapes with several sites of low alpha diversity can still be heterogeneous if the

75 variation in diversity between sites is high. Large herbivores can contribute to this spatial

76 heterogeneity by feeding patchily (Adler et al. 2001; Koleff et al. 2003), and herbivory that

77 affects temporal heterogeneity can alter colonization opportunities for new plant species

78 (Bakker et al. 2003). Few studies have examined herbivory-induced changes in the vegetation

79 by conducting long-term monitoring across herbivory-intensity gradients (although see

80 Heckel et al. (2010)), but such studies are crucial for understanding how the intensity of

81 herbivory disturbs ecosystems (Hester et al. 2000; Nuttle et al. 2014).

82   Densities of red deer (*Cervus elaphus*) have reached unprecedented levels in Northern

83 Europe (Fuller & Gill 2001), causing management concerns for ecosystem stability and

84 biodiversity (Côté et al. 2004). In Fennoscandia, herbivore assemblages have changed from

85 livestock dominance to cervid dominance during the past 60 years, alongside a reduction in

86 total herbivory (Austrheim et al. 2011). However, cervid herbivory has increased most in

87 relatively resource-poor inland forest areas. Differences in both use-of-area and year-round

88 presence compared with past livestock herbivory can be expected (Austrheim et al. 2011).

89 The present intensity of herbivory by red deer may represent a disturbance regime to which

90 the plant species in the Fennoscandian boreal forests are not evolutionarily adapted.

91   In this paper we investigate how red deer herbivory mediates spatial and temporal

92 vegetation heterogeneity in the understory of a boreal forest ecosystem by combining a 10-

93 year red-deer exclosure experiment with a substantial natural gradient in herbivory intensity.

94 We monitored plant-species richness and abundance at 12 sites, each with one exclosure

95 macroplot paired with one macroplot open to red deer herbivory. The open macroplots

96 covered a range of intensities of herbivory, allowing us to examine the importance of

97 herbivory along gradients of intensity. Removing herbivory can reveal vegetation resilience in

98 relation to long-term disturbance (Elmqvist et al. 2003; Beschta & Ripple 2009). We

99 previously investigated the effect of herbivory intensity on species richness, and found that

100 overall species richness showed a unimodal peaked response to increasing herbivory, in

101 accordance with the intermediate disturbance hypothesis (Hegland et al. 2013). However, the

102 functional groups differed in their responses. The richness of forbs, graminoids and mosses

103 increased, while dwarf-shrubs and young trees decreased with increasing herbivory intensity

104 (Hegland et al. 2013). There was actually twice as many species benefitting from red deer

105 herbivory. However, how this translates into spatial and temporal heterogeneity remains

106 unclear.

107   We predicted that excluding red deer would lead to higher temporal species turnover

108 shortly after exclusion, but reduced turnover in the long term (Prediction 1a). As intense

109 herbivory can enhance light availability and opportunities for recruitment of new species

110 (Rydgren et al. 2004), we expected a positive relationship between the intensity of herbivory

111 and temporal species turnover (Prediction 1b). We also hypothesized that red deer reduce

112 species turnover spatially, because selective herbivory may depress highly digestible plant

113 species, enhance browse-tolerant and avoided ones (Augustine & McNaughton 1998), and aid

114 seed dispersal through zoochory (Steyaert et al. 2009). Therefore, we predicted that excluding

115 red deer would increase spatial species turnover (Prediction 2a), and expected a negative

116 relationship between the intensity of herbivory and spatial species turnover (Prediction 2b;

117 Rooney 2009).

118   **METHODS**

119   **Study area**

120   We conducted our study at Svanøy Island (61°30'N, 5°05'E), western Norway. The

121   island is situated in the boreo-nemoral zone and covered mainly by old-growth boreal forest

122   dominated by Scots pine (*Pinus sylvestris*). Mean annual precipitation and temperature are

123   2000 mm and 8 °C, respectively (Skogen & Lunde 1997, Florø airport,

124   http://www.eklima.met.no). The deer density is approximately 7.5 deer km^{-2}, which is

125   considered high in Norway (Hegland et al. 2013). The island includes a red-deer farm with

126   more than 30 deer km^{-2}, but wild and farmed deer are separated by a game fence. Some

127   domestic sheep (*Ovis aries*) are free-ranging, mainly during summer.

128

129   **Study design and sampling**

130   In 2001, we established 12 sites in pine-bilberry (*Vaccinium myrtillus*) forest. Each

131   site contained one exclosure macroplot and one open macroplot, both 9×9 m with seven

132   permanent 1×1 m plots inside (Fig. 1). All plots were in flat areas, randomly placed but

133   rejected and re-placed if adult trees were within 0.5 m. The exclosures were surrounded by 3

134   m tall fences with 10×10 cm wire mesh. To avoid edge effects, we left a 0.5 m zone between

135   the fence and the macroplot. Small herbivores could move freely into the exclosures, although

136   few or none were present. Common boreal herbivores such as the mountain hare (*Lepus

137   timidus*) have not been observed on the island, and we caught no rodents in 350 rodent trap-

138   nights during 2011. Henceforth, 'treatment' refers to exclosures and open plots. Two sites

139   were situated within the red deer farm, and these contained only six and three open plots,

140   respectively, because some plot positions were lost. We surveyed the vegetation in June 2001,

141   2006 and 2011. Each 1 x 1 m plot was divided into 100 subplots. We recorded the vascular

142   and bryophyte species in each plot and measured their abundance as frequency in these 100

143   subplots. In addition, the abundance and richness of young trees (50–400 cm in 2011) was

144   recorded at the macroplot scale.

145   The intensity of red deer herbivory varied among the 12 open macroplots. To quantify

146   this we estimated the intensity of herbivory on randomly selected bilberry ramets at each site

147   (see also; Hegland et al. 2013). Bilberry is widely distributed, abundant, intermediately

148   preferred by red deer, and therefore a good indicator species for monitoring the intensity of

149   red deer herbivory (Mysterud et al. 2010). In June 2001 and 2011, we measured five and three

150   randomly selected ramets, respectively, in all seven plots in each macroplot, and three ramets

151   in four randomly selected plots per macroplot in 2006. We calculated the intensity of

152 herbivory on each ramet as the percentage of annual shoots browsed, in five categories: 0, 1

153 (1–24%), 2 (25–49%), 3 (50–74%), 4 (75–100%), (*sensu* Frelich and Lorimer (1985)),

154 divided by ramet height. Hereafter we term this as 'herbivory intensity'. We used the mean

155 herbivory intensity of all ramets per macroplot per year as our measure of intensity when

156 analysing spatial heterogeneity statistically. To analyse temporal heterogeneity we compare

157 these mean values across the periods 2001–2006 and 2006–2011. Our herbivory-intensity

158 measure was strongly related to an independent fecal count survey (r = 0.94, N = 12, p <

159 0.001, Hegland et al. 2013).

Heterogeneity measures

161   To calculate alpha diversity we used the Shannon diversity index (H′) and evenness

162 (exp[H′]/S, where S is the number of species; (Kindt & Coe 2005)) for all species pooled and

163 repeated this for the bottom layer (bryophytes), field layer (all vascular plants, including trees

164 < 50 cm), and the understory tree layer (trees 50–400 cm). For temporal species turnover

165 (Predictions 1a and 1b), we calculated Bray-Curtis dissimilarity (per cent dissimilarity/100,

166 BC; Legendre & Legendre 1998) within each plot for the first five years (2001–2006) and the

167 last five years (2006–2011). For spatial species turnover (Predictions 2a and 2b), we

168 calculated BC between each plot and all other plots within each macroplot and year and used

169 the mean of these six values as the BC value for each plot. Prior to all BC calculations we

170 changed the range of the abundance scale for each species from 100 to 16 with a power

171 function (van der Maarel 1979), and thereby achieved a recommended intermediate weighting of

172 species (Økland 1990; Rydgren 1993).

Statistical analyses

174   We analysed all responses with linear mixed effects models (packages lme4 (Bates et

175 al. 2014) and lmerTest (Kuznetsova et al. 2015) in R version 3.1.1 (R Core Team 2014). We

176 started with full models, applied backward elimination of fixed effects, and validated the final

177 models as proposed by Crawley (2007, Table S1). Although species turnover is a proportion,

178 we specified all our models for Gaussian distribution, as the residuals showed normal

179 distributions, resulting in more conservative p-values. As the two sites in the red deer farm

180 had much higher red deer densities than the other sites, we ran all models with and without

181 'farm' as a factor.

182 **RESULTS**

183 Across the three sampling years, we recorded 70 plant species, 52 of which occurred in both

184 treatments. Overall, the mean number of species per plot was 16 (± 0.2 SE). *Vaccinium*

185 *myrtillus*, *Avenella flexuosa* and *Hylocomium splendens* were common, and occurred in

186 almost all plots all years (Table 1). *Viola riviniana*, *Maianthemum bifolium* and *Veronica*

187 *serpyllifolia* were among the eight species only occurring in open plots. *Corylus avellana* and

188 *Populus tremula* were among the ten species unique to the exclosure plots. Occurences of

189 species unique to one treatment were rare, however.

190 Ten years of excluding red deer significantly decreased alpha diversity (Shannon index 2011

191 ± SE: open plots, 2.21 ± 0.02; exclosure plots, 2.14 ± 0.03, T = -2.046, df = 332, P = 0.042,

192 Table S2). However, herbivory intensity and alpha diversity were uncorrelated (P = 0.918,

193 Table S2). Evenness did not differ between open and exclosure plots (evenness 2011± SE:

194 open plots, 0.57 ± 0.01; exclosure plots, 0.57 ± 0.01, P = 0.568), but there was a negative

195 effect of herbivory intensity on evenness within the open plots (β = -0.132 ± 0.043, T = -

196 3.052, df = 25.7, P = 0.005, Table S2). Excluding red deer did not affect the alpha diversity

197 within the bottom, field or understory tree layer (all, P > 0.05, Table S3), but herbivory

198 intensity reduced the field layer alpha diversity (β = -0.747 ± 0.239, T = -3.121, P = 0.002,

199 Table S3). Evenness was negatively related to herbivory intensity in the field (β = -0.201 ±

200 0.060, T = -3.331, P = 0.002) and understory tree layers (β = -0.464 ± 0.1655, T = -2.807, P =

201 0.010, Table S3).

202 **Effect of red deer herbivory on temporal heterogeneity**

203   Temporal species turnover (Bray-Curtis dissimilarity, BC, within plot, between years)

204 was significantly higher in exclosure plots than in open ones for the first five-year period (P =

205 0.005). In the last five-year period, however, temporal species turnover in the exclosures was

206 reduced (P = 0.023), reaching the same level as in the open plots (Fig. 2, Table 2). Temporal

207 species turnover increased significantly with increasing intensity of herbivory (P < 0.001, Fig.

208 3, Table 2), but became non-significant, although still positive, when the plots in the red deer

209 farm were omitted (P = 0.136, Table S4, Fig. S1).

210

211 **Effect of red deer herbivory on spatial heterogeneity**

212   Spatial species turnover (BC between plots in same macroplot) was higher in

213 exclosures than in open plots 10 years after the experiment started (P < 0.001), whereas five

214   years of exclusion was not enough to reveal the effect of red deer (P = 0.270). On the open

215   plots, BC remained stable throughout (Fig. 4, Table 2). Similar results were obtained when

216   plots in the red deer farm were omitted (Table S4). Spatial species turnover tended to be

217   positively correlated with the intensity of herbivory overall (P = 0.089, Table 2), but the effect

218   disappeared when the plots in the red deer farm were omitted from the model (P = 0.488,

219   Table S4).

220

221   **DISCUSSION**

222   The two dimensions of vegetation heterogeneity have contrasting characteristics. Temporal

223   heterogeneity can destabilize the ecosystem, whereas spatial heterogeneity can stabilize the

224   ecosystem (May 1974). A temporally heterogeneous forest will favour early succession

225   species and will be more susceptible to invading species, stochastic events such as small-scale

226   fires or wind throws, and state shifts. A spatially heterogeneous forest, on the other hand, will

227   have higher resilience, and will thus be more robust to stochastic events.

228   In this study, we investigated the role of the red deer in forming the heterogeneity of

229   the boreal forest understory vegetation over 10 years, and found two key effects. Firstly,

230   excluding red deer caused a distinct shift in species composition, reflected in both spatial and

231   temporal species turnover (Predictions 1a and 2a). Secondly, we found that the intensity of

232   herbivory had a strong positive impact on temporal species turnover (Prediction 1b), and a

233   weak positive impact on spatial species turnover (Prediction 2b).

234   Higher temporal species turnover in sites with high intensities of herbivory (Prediction

235   1b) implies that the species composition in such sites was less stable than in sites with lower

236   herbivory intensity. High levels of herbivory benefit pioneer and unpalatable species, and

237   inhibit the growth and reproduction of slow growing species such as trees or shrubs (Hegland

238   & Rydgren 2016), and this pattern is reflected in the reduction in evenness among the plant

239   species (Table S2). By contrast, unpalatable species declined under high densities of white-

240   tailed deer in Pennsylvania, USA, perhaps because trampling by the deer caused soil

241   compression, limiting the growth potential of all plants (Heckel et al. 2010). In an old-growth,

242   temperate forest in Poland, Kuijper et al. (2010) found that herbivory limited trees from

243   growing larger than 50 cm. Likewise, we have previously shown that in our study area young

244   deciduous trees germinated better in sites experiencing high levels of herbivory, but when

245   seedlings became taller than the field layer vegetation, tree species richness decreased

246   (Hegland et al. 2013). Red deer also strongly limit the abundance (number of individuals) in

247   this size class (Hegland & Rydgren 2016). Thus, increased herbivory intensity reduces the

248   number of trees reaching reproductive age, and therefore is a crucial factor in forest

249   regeneration (Tremblay et al. 2006).

250   Temporal species turnover increased significantly in the exclosures during the first

251   five years of the study. This implies that removing red deer herbivory from the system created

252   a distinct and rapid shift in the species composition. Changes in vegetation inside exclosures

253   after removing a cause of disturbance can reveal the plants' recovery abilities (Beschta &

254   Ripple 2009). The marked increase in temporal species turnover demonstrated in our

255   exclusion plots is an important finding because it shows the high capacity of boreal forest

256   plant species to recover, even after experiencing high levels of herbivory. Nevertheless, the

257   effect of herbivory will likely persist for some decades after the reduction or removal of red

258   deer (Nuttle et al. 2014), probably depending on the original density of herbivores (Schütz et

259   al. 2003).

260   Temporal species turnover did not differ significantly between exclosures and open

261   plots (Prediction 1a) during the last five years of the study, which suggests rapid stabilization

262   of species composition in our study system. When we omitted data from the red deer farm

263   (those sites with extremely high red deer densities) from our analyses, however, temporal

264   species turnover remained higher in the exclosure plots than in the open plots ten years after

265   excluding red deer (Table S4). This indicates that rapid changes in temporal species turnover

266   can be expected after dramatic changes in an ecosystem (e.g., removing large herbivores). The

267   continued difference in temporal species turnover between the exclosures and open plots

268   outside the farm shows that red deer can increase temporal species turnover, also at low to

269   medium densities, but that the effect is stronger at high densities.

270   Spatial species turnover did not decrease as red deer density increased (Prediction 2b);

271   instead it increased weakly. However, in line with Prediction 2a, we found that excluding red

272   deer from forest patches stimulated spatial species turnover. This suggests that red deer

273   herbivory can have a homogenizing effect on the forest understory although in our study, this

274   effect took 10 years to become apparent. The potential for herbivores to alter vegetation

275   heterogeneity depends on the intrinsic spatial pattern of the vegetation and its interaction with

276   that of herbivory (Adler et al. 2001). Our study examined the effects of herbivory in a boreal

277   forest, with relatively homogenous vegetation. Although red deer use a range of different

278   habitat types, productive boreal forest is the habitat where Scandinavian red deer spend most

279   of their time during daylight, as it is more important for foraging than earlier believed

280   (Godvik et al. 2009). Red deer feeding in the forest understory is not spatially homogeneous,

281   based purely on the availability of forage plants, but depends also on factors such as the

282   distance to human infrastructure or predators, and the availability of resting spots and high

283   quality forage (e.g. pastures and meadows, Adrados et al. 2008; Godvik et al. 2009).

284   Exclusion of red deer resulted in 7 % reduction of the plant species diversity

285   (transforming Shannon index to effective numbers, $\exp(H')$, Jost (2006)). If all species were

286   evenly common (which they are not), this diversity would translate to a species loss of 1.2

287   species. Such loss may not seem substantial, but if there are no other functionally similar

288   species, it may affect long-term ecosystem functioning (e.g. Mori et al. 2013; Sitters et al.

289   2016).

290   Our study was conducted over a relatively small area, within an island of 11 km^2. By

291   locating our sites along a gradient of herbivory intensity within this island, and focusing on

292   the fine-grained plant-species responses within these sites and all within the pine-bilberry

293   forest ecotype, we eliminated as many sources of variation as possible. We are thus able to

294   isolate the effect of herbivory intensity on plant species heterogeneity. A study across a larger

295   spatial extent and with several vegetation types, could potentially reveal greater effects of

296   excluding red deer, but may not detect the fine scaled effect of herbivory intensity seen here.

297   Selectivity and aggregation are two important processes governing the effects of

298   herbivory on vegetation heterogeneity and diversity (Augustine & McNaughton 1998). Patch-

299   grazing herbivores are more likely to increase spatial heterogeneity than species that feed

300   homogenously or highly selectively (Adler et al. 2001). Studies on other large herbivores have

301   shown that herbivory can either reduce (white-tailed deer, Rooney 2009) or increase (sheep,

302   (DeGabriel et al. 2011); black-tailed deer, *Odocoileus hemionus,*(Gaston et al. 2006)) spatial

303   heterogeneity. For example, in a study on the previously ungulate-free islands in British

304   Columbia, Canada, Gaston et al. (2006) found that uninvaded islands were more similar in

305   plant species composition than islands with introduced black-tailed deer. Islands without deer

306   were smaller than those with deer, and therefore theoretically should be more homogeneous

307   (MacArthur & Wilson 1963), suggesting that deer drove biotic differentiation rather than

308   homogenization. Red deer, being intermediate feeders, may have less of an effect on spatial

309   heterogeneity. They feed on a broader range of species than black-tailed deer (Hofmann 1989)

310   and aggregate in smaller groups (Adler et al. 2001). Our results indicate that red deer

311   herbivory spatially homogenize even relatively uniform vegetation, whereas the opposite

312   would be expected (Adler et al. 2001).

313   Preferred species in heavily browsed areas may depend on ephemeral recruitment

314   opportunities; that is, periods when herbivore populations are low (Fornara & du Toit 2007).

315   Fluctuations in the density of large herbivore populations, spatially and in time, is therefore

316   likely to be important for plant recruitment (Kuijper et al. 2010). Such ephemeral windows

317   are not always sufficient for vegetation regeneration, especially if the ecosystem is not

318   adapted to herbivory by the particular species. For example, in New Zealand, introduced red

319   deer populations were reduced by about 92% and were kept at low densities for four decades

320   (Tanentzap et al. 2009). Despite this, tree recruitment remained low; recovery in heavily

321   herbivore-disturbed systems, particularly those that have evolved in absence of large

322   herbivores, can take decades (Tanentzap et al. 2009). To permit natural regeneration,

323   managers in areas with high red-deer densities need to provide for periodic ephemeral

324   windows for recruitment, either in time or spatially, in their management plans (Sage et al.

325   2003).

326

327   **Conclusions**

328   Understanding both the spatial and the temporal components of vegetation heterogeneity is

329   crucial to advancing our knowledge of ecosystem functioning and the associated role of large

330   herbivores (Soininen 2010). Our results show that a combined focus on the effects of

331   exclusion and the intensity of herbivory provides new insights into the ecological role of red

332   deer in boreal forests. Interestingly, temporal heterogeneity of the forest understory increased

333   with increasing red deer herbivory intensity, as well as when red deer were excluded.

334   Increased temporal heterogeneity after excluding red deer either suggests that low densities of

335   deer stabilize the species turnover, or that the recovery after long-term herbivory takes more

336   than a decade. Further monitoring of the vegetation will illuminate this uncertainty. However,

337   the spatial heterogeneity was indeed highest where red deer were excluded. Thus, our results

338   suggest that removing red deer would effectively result in the most stable ecosystem over a

339   prolonged period of time. However, the lowest species diversity of plants appeared where red

340   deer were excluded. If both stable but also species rich ecosystems are the management goal,

341   managers should sustain naturally fluctuating, but moderate red deer densities.

REFERENCES

351

352 Adler PB, Raff DA, Lauenroth WK (2001) The effect of grazing on the spatial heterogeneity

353 of vegetation. Oecologia 128: 465-479.

354 Adrados C, Baltzinger C, Janeau G, Pepin D (2008) Red deer *Cervus elaphus* resting place

355 characteristics obtained from differential GPS data in a forest habitat. Eur J Wildl Res 54:

356 487-494. DOI: 10.1007/s10344-008-0174-y

357 Augustine DJ, McNaughton SJ (1998) Ungulate effects on the functional species composition

358 of plant communities: herbivore selectivity and plant tolerance. J Wildl Manage 62: 1165-

359 1183. DOI: 10.2307/3801981

360 Austrheim G, Solberg EJ, Mysterud A (2011) Spatio-temporal variation in large herbivore

361 pressure in Norway during 1949-1999: has decreased grazing by livestock been countered by

362 increased browsing by cervids? Wildl Biol 17: 286-298. DOI: 10.2981/10-038

363 Bakker C, Blair JM, Knapp AK (2003) Does resource availability, resource heterogeneity or

364 species turnover mediate changes in plant species richness in grazed grasslands? Oecologia

365 137: 385-391. DOI: 10.1007/s00442-003-1360-y

366 Bates D, Maechler M, Bolker B, Walker S (2014) lme4: Linear mixed-effects models using

367 Eigen and S4. R package version 1.1-7. https://CRAN.R-project.org/package=lme4, pp.

368 Beschta RL, Ripple WJ (2009) Large predators and trophic cascades in terrestrial ecosystems

369 of the western United States. Biol Cons 142: 2401-2414. DOI:

370 http://dx.doi.org/10.1016/j.biocon.2009.06.015

371 Côté SD, Rooney TP, Tremblay J-P, Dussault C, Waller DM (2004) Ecological impacts of

372 deer overabundance. Annu Rev Ecol Evol Syst 35: 113-147. DOI:

373 10.1146/annurev.ecolsys.35.021103.105725

374 Crawley MJ (2007) The R book. Wiley, Chichester

375   DeGabriel JL, Albon SD, Fielding DA, Riach DJ, Westaway S, Irvine RJ (2011) The presence

376   of sheep leads to increases in plant diversity and reductions in the impact of deer on heather. J

377   Appl Ecol 48: 1269-1277. DOI: 10.1111/j.1365-2664.2011.02032.x

378   Elmqvist T, Folke C, Nystrom M, Peterson G, Bengtsson J, Walker B, Norberg J (2003)

379   Response diversity, ecosystem change, and resilience. Front Ecol Envir 1: 488-494. DOI:

380   10.2307/3868116

381   Fornara DA, du Toit JT (2007) Browsing lawns? Responses of *Acacia nigrescens* to ungulate

382   browsing in an African savanna. Ecology 88: 200-209. DOI: 10.1890/0012-

383   9658(2007)88[200:blroan]2.0.co;2

384   Frelich LE, Lorimer CG (1985) Current and predicted long-term effects of deer browsing in

385   hemlock forests in Michigan, USA. Biol Cons 34: 99-120. DOI: 10.1016/0006-

386   3207(85)90103-x

387   Fuller RJ, Gill RMA (2001) Ecological impacts of increasing numbers of deer in British

388   woodland. Forestry 74: 193-199. DOI: 10.1093/forestry/74.3.193

389   Gaston AJ, Stockton SA, Smith JL (2006) Species-area relationships and the impact of deer-

390   browse in the complex phytogeography of the Haida Gwaii archipelago (Queen Charlotte

391   Islands), British Columbia. Ecoscience 13: 511-522. DOI: 10.2980/1195-

392   6860(2006)13[511:sratio]2.0.co;2

393   Godvik IMR, Loe LE, Vik JO, Veiberg V, Langvatn R, Mysterud A (2009) Temporal scales,

394   trade-offs, and functional responses in red deer habitat selection. Ecology 90: 699-710. DOI:

395   10.1890/08-0576.1

396   Heckel CD, Bourg NA, McShea WJ, Kalisz S (2010) Nonconsumptive effects of a generalist

397   ungulate herbivore drive decline of unpalatable forest herbs. Ecology 91: 319-326. DOI:

398   10.1890/09-0628.1

399   Hegland SJ, Lilleeng MS, Moe SR (2013) Old-growth forest floor richness increases with red

400   deer herbivory intensity. Forest Ecology and Management 310: 267-274. DOI:

401   http://dx.doi.org/10.1016/j.foreco.2013.08.031

402   Hegland SJ, Rydgren K (2016) Eaten but not always beaten: winners and losers along a red

403   deer herbivory gradient in boreal forest. Journal of Vegetation Science 27: 111-122. DOI:

404   10.1111/jvs.12339

405   Hester AJ, Edenius L, Buttenschon RM, Kuiters AT (2000) Interactions between forests and

406   herbivores: the role of controlled grazing experiments. Forestry 73: 381-391. DOI:

407   10.1093/forestry/73.4.381

408   Hofmann RR (1989) Evolutionanry steps of ecophysiological adaptation and diversification

409   of ruminants: A comparative view of their digestive-system. Oecologia 78: 443-457. DOI:

410   10.1007/bf00378733

411   Hovick TJ, Elmore RD, Fuhlendorf SD, Engle DM, Hamilton RG (2015) Spatial

412   heterogeneity increases diversity and stability in grassland bird communities. Ecol Appl 25:

413   662-672. DOI: 10.1890/14-1067.1.sm

414   Jones CG, Lawton JH, Shachak M (1994) Organisms as ecosystem engineers. Oikos 69: 373-

415   386. DOI: 10.2307/3545850

416   Jost L (2006) Entropy and diversity. Oikos 113: 363-375. DOI: 10.1111/j.2006.0030-

417   1299.14714.x

418   Kindt R, Coe R (2005) Tree diversity analysis: a manual and software for common statistical

419   methods for ecological and biodiversity studies. World Agroforestry Centre (ICRAF),

420   Nairobi, Kenya

421   Koleff P, Gaston KJ, Lennon JJ (2003) Measuring beta diversity for presence-absence data. J

422   Anim Ecol 72: 367-382. DOI: 10.1046/j.1365-2656.2003.00710.x

423 Kuijper DPJ, Jędrzejewska B, Brzeziecki B, Churski M, Jędrzejewski W, Żybura H (2010)

424 Fluctuating ungulate density shapes tree recruitment in natural stands of the Białowieża

425 Primeval Forest, Poland. J Veg Sci 21: 1082-1098. DOI: 10.1111/j.1654-1103.2010.01217.x

426 Kuznetsova A, Brockhoff PB, Christensen RHB (2015) lmerTest: Tests in Linear Mixed

427 Effects Models. R package version 2.0-25., pp.

428 Legendre P, Legendre L (1998) Numerical ecology. Elsevier, Amsterdam

429 MacArthur RH, Wilson EO (1963) An Equilibrium Theory of Insular Zoogeography.

430 Evolution 17: 373-387. DOI: 10.2307/2407089

431 Mackey RL, Currie DJ (2001) The diversity-disturbance relationship: Is it generally strong

432 and peaked? Ecology 82: 3479-3492. DOI: 10.1890/0012-

433 9658(2001)082[3479:tddrii]2.0.co;2

434 May R (1974) Ecosystem patterns in randomly fluctuating environments. In: R Rosen, F Snell

435 (eds) Progress in Theoretical Biology. Academic Press, New York, pp. 1-50

436 Mori AS, Furukawa T, Sasaki T (2013) Response diversity determines the resilience of

437 ecosystems to environmental change. Biol Rev 88: 349-364. DOI: 10.1111/brv.12004

438 Mysterud A, Askilsrud H, Loe LE, Veiberg V (2010) Spatial patterns of accumulated

439 browsing and its relevance for management of red deer *Cervus elaphus*. Wildlife Biology 16:

440 162-172. DOI: 10.2981/09-043

441 Nuttle T, Ristau TE, Royo AA (2014) Long-term biological legacies of herbivore density in a

442 landscape-scale experiment: forest understoreys reflect past deer density treatments for at

443 least 20 years. J Ecol 102: 221-228. DOI: 10.1111/1365-2745.12175

444 Proulx M, Mazumder A (1998) Reversal of grazing impact on plant species richness in

445 nutrient-poor vs. nutrient-rich ecosystems. Ecology 79: 2581-2592. DOI: 10.1890/0012-

446 9658(1998)079[2581:rogiop]2.0.co;2

447 R Core Team (2014) R: A language and environment for statistical computing. The R

448 Foundation for Statistical Computing, Vienna, Austria, pp.

449 Rooney TP (2009) High white-tailed deer densities benefit graminoids and contribute to biotic

450 homogenization of forest ground-layer vegetation. Plant Ecol 202: 103-111. DOI:

451 10.1007/s11258-008-9489-8

452 Rydgren K (1993) Herb-rich spruce forests in W Nordland, N Norway: an ecological and

453 methodological study. Nordic Journal of Botany 13: 667-690. DOI: 10.1111/j.1756-

454 1051.1993.tb00112.x

455 Rydgren K, Økland RH, Hestmark G (2004) Disturbance severity and community resilience

456 in a boreal forest. Ecology 85: 1906-1915. DOI: 10.1890/03-0276

457 Sage JRW, Porter WF, Underwood HB (2003) Windows of opportunity: white-tailed deer and

458 the dynamics of northern hardwood forests of the northeastern US. Journal for Nature

459 Conservation 10: 213-220.

460 Schütz M, Risch AC, Leuzinger E, Krusi BO, Achermann G (2003) Impact of herbivory by

461 red deer (*Cervus elaphus* L.) on patterns and processes in subalpine grasslands in the Swiss

462 National Park. For Ecol Manage 181: 177-188. DOI: 10.1016/s0378-1127(03)00131-2

463 Sitters H, Di Stefano J, Christie F, Swan M, York A (2016) Bird functional diversity

464 decreases with time since disturbance: Does patchy prescribed fire enhance ecosystem

465 function? Ecol Appl 26: 115-127. DOI: 10.1890/14-1562

466 Skogen A, Lunde BN (1997) Flora og vegetasjon på Svanøy i Sunnfjord, med

467 vegetasjonskart, Botanical Institute, University of Bergen. Norway, pp.

468 Soininen J (2010) Species turnover along abiotic and biotic gradients: Patterns in space equal

469 patterns in time? BioScience 60: 433-439. DOI: 10.1525/bio.2010.60.6.7

470   Steyaert S, Bokdam J, Braakhekke W, Findo S (2009) Endozoochorical plant seed dispersal

471   by red deer (*Cervus elaphus*) in the Poľana Biosphere Reserve, Slovakia. Ekológia 28: 191-

472   205.

473   Tanentzap AJ, Burrows LE, Lee WG, Nugent G, Maxwell JM, Coomes DA (2009)

474   Landscape-level vegetation recovery from herbivory: progress after four decades of invasive

475   red deer control. J Appl Ecol 46: 1064-1072. DOI: 10.1111/j.1365-2664.2009.01683.x

476   Tremblay JP, Huot J, Potvin F (2006) Divergent nonlinear responses of the boreal forest field

477   layer along an experimental gradient of deer densities. Oecologia 150: 78-88. DOI:

478   10.1007/s00442-006-0504-2

479   van der Maarel E (1979) Transformation of cover-abundance values in phytosociology and its

480   effects on community similarity. Vegetatio 39: 97-114. DOI: 10.1007/BF00052021

481   Økland R (1990) Vegetation ecology: theory, methods and applications with reference to

482   Fennoscandia. Sommerfeltia Suppl 1: 1-233.

483

484   FIGURES

485   **Fig. 1** Our study included 12 sites. The design shows the placement of seven plots in one open

486   and one exclosure macroplot at each site. Due to topography, the distance between exclosure

487   and open macroplots varied between 10 and 50 m.

488   **Fig. 2** Mean (±SE) five-year temporal species turnover, measured by the Bray-Curtis

489   dissimilarity index within plot: exclosure (black circles) and open (white circles) plots during

490   10 years of experiment.

491   **Fig. 3** Fitted relationship (black line, $P < 0.001$) and 95 % CI ($\beta \pm 1.96 * SE$, grey shade)

492   between temporal species turnover, measured with Bray-Curtis dissimilarity index within plot

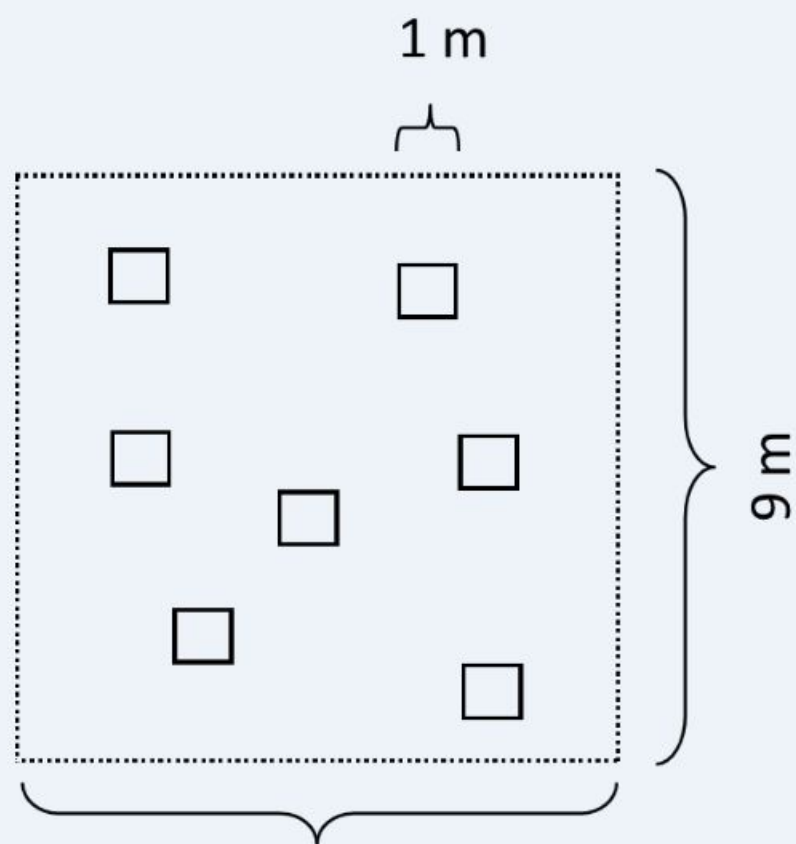493   between years, in relation to the gradient of herbivory intensity.

494   **Fig. 4** Mean (±SE) spatial species turnover, measured with Bray-Curtis dissimilarity index

495   between plots within the same macroplots: exclosure (black circles) and open (white circles)
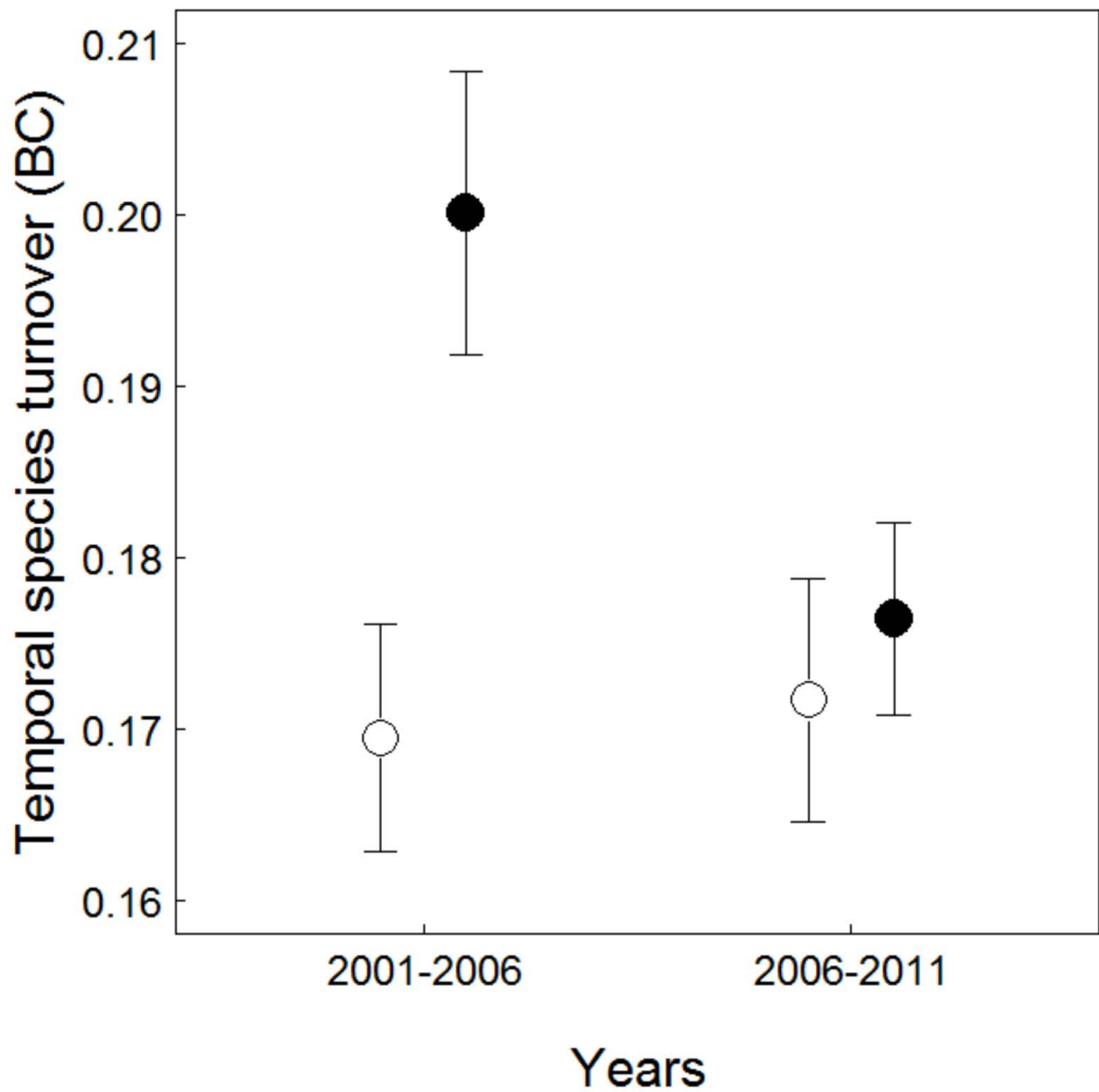
496   plots during the 10-year experiment.
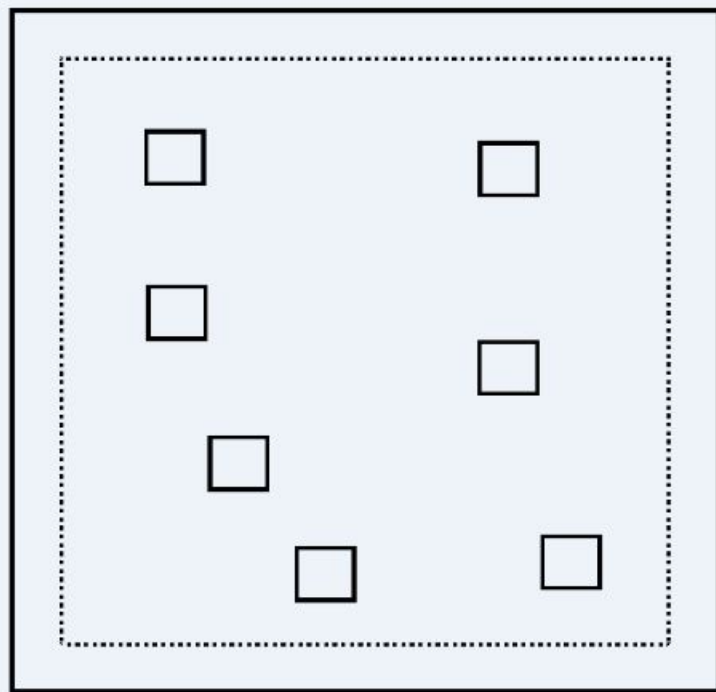
Exclosure
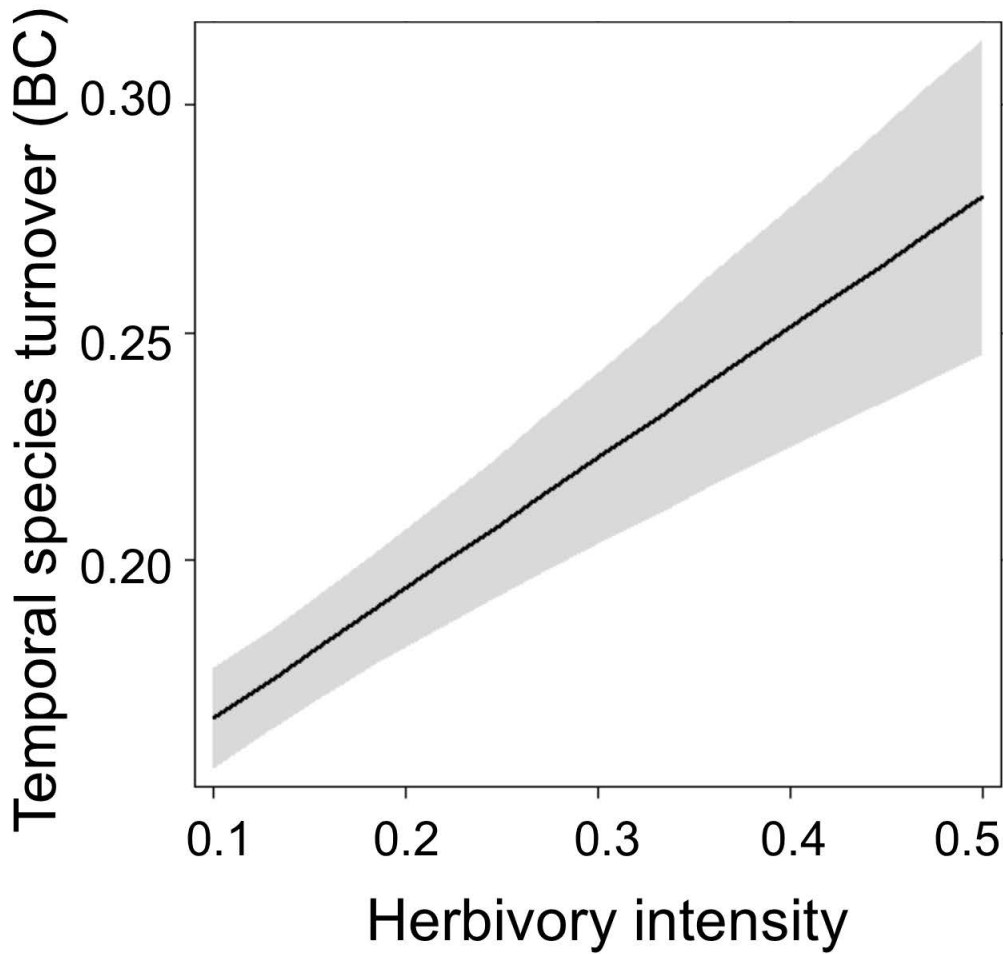
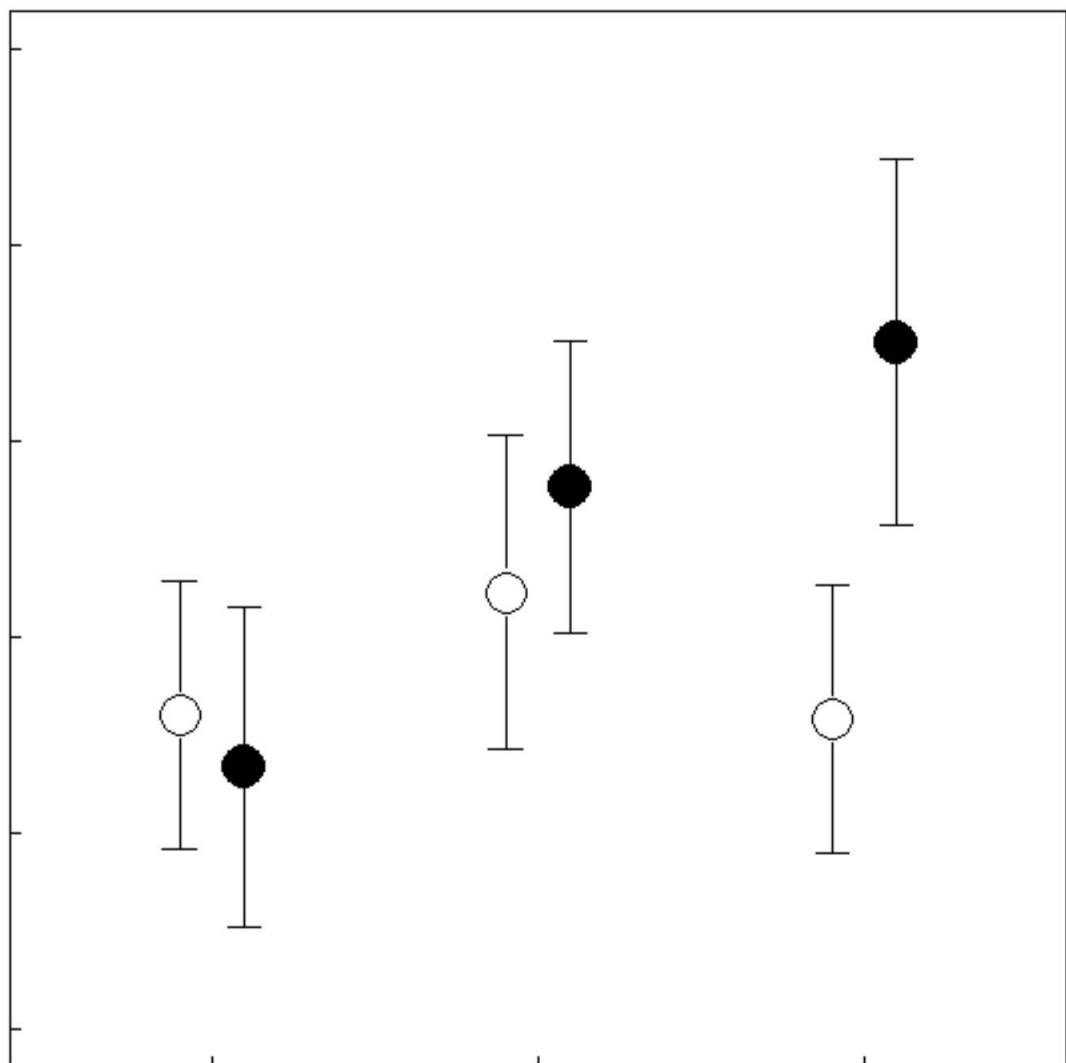Open

Fence

Plot

Macroplot

1 m

9 m

Table 1 Frequency, F (percent of all plots where the species occurred; n = 84 for each treatment), and mean subplot frequency, MSF (arithmetic mean of the subplot frequencies for a species, calculated from the plots where the species occurred), for species occurring in ≥25 % of the plots in one year and treatment

Species	Grazed						Ungrazed					
	2001		2006		2011		2001		2006		2011	
	F	MSF	F	MSF	F	MSF	F	MSF	F	MSF	F	MSF
Calluna vulgaris	33	16	25	25	21	24	42	24	45	55	39	62
Empetrum nigrum	54	38	46	54	43	56	58	34	48	47	48	32
Pinus sylvestris	0	0	6	1	44	3	0	0	5	1	30	2
Sorbus aucuparia	74	6	70	6	64	7	69	4	58	6	64	6
Vaccinium myrtillus	100	74	100	82	99	81	100	68	99	80	99	80
Vaccinium vitis-idaea	98	47	93	35	88	27	96	47	93	43	94	36
Agrostis capillaris	5	32	24	35	25	41	5	29	14	18	11	15
Anemone nemorosa	29	10	31	10	26	8	17	8	12	9	12	12
Avenella flexuosa	100	85	100	95	100	92	100	85	100	96	100	96
Linnaea borealis	77	31	80	33	76	19	74	29	85	28	73	17
Luzula sylvatica	60	35	57	35	61	43	58	40	56	44	58	48
Melampyrum pratense	32	9	33	8	44	6	57	8	62	12	51	7
Oxalis acetosella	56	20	58	28	54	31	51	26	52	23	60	21
Potentilla erecta	58	22	63	25	60	29	57	19	54	22	54	25
Pteridium aquilinum	10	6	19	15	21	14	12	4	26	8	18	14
Trientalis europaea	68	12	75	11	65	10	70	9	63	10	49	7
Dicranum spp.	69	22	68	25	70	26	65	20	64	14	63	19
Hylocomium splendens	100	73	100	79	100	88	100	70	99	63	100	82
Plagiothecium undulatum	21	11	18	9	31	8	25	16	14	7	27	11
Pleurozium schreberi	52	9	38	7	31	3	46	9	27	4	36	5
Polytrichum spp.	33	17	31	23	40	16	30	20	27	19	32	14
Pseudoscleropodium purum	58	19	69	20	71	17	60	18	73	20	81	18
Ptilium crista-castrensis	71	22	68	26	77	26	63	16	58	18	67	26
Rhytidiadelphus loreus	85	29	83	20	83	29	82	27	71	17	76	15
Sphagnum spp.	26	22	32	22	32	28	29	26	29	26	31	27

Table 2 Effect of (a) exclosure treatment, and (b) herbivory intensity on temporal and spatial species turnover (BC); parameter estimates for the most parsimonous model of the effects of year, treatment or herbivory intensity, and interactions

(a) Exclosure vs open plots						(b) Herbivory intensity					
Fixed effects	Estimate	SE	df	t	P	Fixed effects	Estimate	SE	df	t	P
Temporal species turnover											
(1a)						(1b)					
Intercept	0.173	0.011	17.5	15.652	<0.001	Intercept	0.136	0.008	8.2	17.690	<0.001
Exclosure (vs open)	0.027	0.009	25.1	3.069	**0.005**	Herbivory intensity	0.287	0.044	13.0	6.507	**<0.001**
Year 2006–2011 (vs 2001–2006)	0.002	0.008	161.0	0.271	0.787						
Exclosure × year 2006–2011	−0.026	0.011	161.0	−2.298	**0.023**						
Spatial species turnover											
(2a)						(2b)					
Intercept	0.281	0.019	18.3	15.157	<0.001	Intercept	0.276	0.017	12.3	16.374	<0.001
Exclosure (vs open)	−0.007	0.019	11.6	−0.369	0.719	Herbivory intensity	0.055	0.032	168.3	1.712	0.089
Year 2006	0.007	0.005	314.2	1.591	0.113						
Year 2011	0.001	0.005	314.2	0.162	0.872						
Exclosure × year 2006	0.007	0.006	312.0	1.106	0.270						
Exclosure × year 2011	0.021	0.006	312.0	3.268	**0.001**						

The models are linear mixed models fit with REML Satterthwaite approximations to calculate degrees of freedom, with spatial random factor plot in macroplot by site for model 1a and 2a, and plot by site for model 1b, and plot by site plus temporal random factor year for 2b. Reference factors are Open 2001–2006 and Open 2001 for 1a and 2a, respectively, and represented by the intercept. A significant interaction term means that the turnover is different in exclosure than in open plots the last five years (1a) and after 10 years (2a)

Bold values indicate significant p-values ($p \leq 0.05$)

SE standard error, *df* degrees of freedom