

## The Quick and the Slow

Competitive ability of two silica-rich grasses influenced by large and small herbivores



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## 1 Summary

2 1. Silicate-rich grasses often dominate in heavily grazed areas, presumably because high  
3 amounts of silica deter herbivores. Activity of large herbivores and small rodent herbivores  
4 increase competitive ability of silicate-rich grasses, possibly through apparent competition.

5 Both types of herbivores often co-exist in grassland ecosystems. Their potential additive effect  
6 on competitive ability of silica-rich grasses has seldom been studied.

7 2. The impact of large and small rodent herbivores on silica-rich grasses, however, can differ.

8 The reason for this can be that small rodent herbivores extensively cut these grasses, for  
9 example for nest construction. This suggests that small rodent herbivores actually might have a  
10 negative impact on the biomass of the grasses, especially during population peaks. How the  
11 grasses respond to rodent activity (i. e. grazing and cutting) may differ depending on growth  
12 rate. The ability of a silica-rich grass to dominate the plant community is therefore possibly a  
13 result of tolerance through fast growth rate rather than resistance via silicates.

14 3. I compared the competitive ability (as measured by total and relative biomass) of two  
15 common and widespread grasses (*Deschampsia cespitosa* and *Nardus stricta*) with similar  
16 silica content and different growth rates to that of the surrounding vegetation. I used a three-  
17 year exclosure experiment in two sub-arctic riparian valleys, separating the effect of large  
18 (reindeer) and small rodent herbivores.

19 4. None of the grasses showed an exclusively positive biomass response to herbivory, as shown  
20 by decline of *Deschampsia* ( $-30.8 \pm 20.1 \text{ g/m}^2$ ) and *Nardus* ( $-57.3 \pm 12.3 \text{ g/m}^2$ ) biomass. Total  
21 biomass of *Deschampsia* decreased in response to the impact of only rodents, but recovered  
22 when rodent populations decreased. Relative biomass of *Deschampsia* was almost three times  
23 higher in both treatments allowing herbivores as compared to no herbivory, while *Nardus*



24 gained no biomass advantage from any type of herbivores. This suggests that growth rate is an  
25 important determinant of competitive ability under herbivory.

26 5. *Synthesis*: Competitive ability of one unpalatable grass with high growth rate, *Deschampsia*,  
27 increased with large and small herbivore activity, while that of another with low growth rate,  
28 *Nardus*, remained unaltered. Advantages gained by apparent competition is thus likely a result  
29 of high tolerance through high growth rates.

30

31 **Key words:** Competition, lemmings, Northern Norway, reindeer, tundra vegetation, Varanger  
32 National Park, voles

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## 44 Introduction

45 Apparent competition is an indirect interaction where one prey species exerts a negative effect  
46 on another prey species, where this effect is mediated by a shared predator (Morris, Lewis &  
47 Godfray 2004). This indirect interaction can have strong impacts on plant population dynamics  
48 and community structure (Morris, Lewis & Godfray 2004). Whether apparent competition  
49 affects a plant community may rely on what traits functional groups in the community possess  
50 and how these traits differ between the groups (Barbosa *et al.* 2009). Herbivore type and  
51 intensity may also be important factors (Barbosa *et al.* 2009). Thus, a plant less attractive in the  
52 eyes of its herbivore would benefit from apparent competition, possibly by rerouting the  
53 herbivore to neighboring vegetation (Atsatt & Dowd 1976). The lower attractiveness could  
54 stem from defensive measures such as spines, high C:N concentrations, or in the case of many  
55 grasses, a high content of silica. Here I will address the role of apparent competition in  
56 grasslands dominated by silica-rich grasses.

57 All grasses have innately high content of silica (Hodson *et al.* 2005). Even if silica  
58 content is an inherent trait, external factors, such as herbivory, can induce silica accumulation  
59 (Massey, Ennos & Hartley 2007b). Grasses from areas heavily grazed by large herbivores  
60 accumulate higher concentrations of silica than those from medium or lightly grazed areas  
61 (McNaughton & Tarrants 1983; McNaughton *et al.* 1985; Brizuela & Detling 1986) and silica  
62 has therefore been proposed to work as an anti-herbivory agent (McNaughton & Tarrants 1983;  
63 McNaughton *et al.* 1985). While having a large negative impact on preferred plants, herbivory  
64 has little effect on less preferred, abundant silica-rich grasses (Bråthen & Oksanen 2001),  
65 further indicating the role of silica as an herbivore deterrent. Moreover, positive effects have  
66 been found on silica-rich grass biomass under large herbivore grazing (Ravolainen *et al.* 2011).  
67 The positive effect of large herbivores therefore likely stems, at least partly, from removing  
68 competing plants while leaving silica-rich grasses alone. Findings supporting silica as an

69 herbivory defense compound come from several ecosystems. Apparent competition is therefore  
70 a possible way by which unpalatable plant communities establish, enabling these grasses to  
71 prosper in the presence of large herbivores.

72           The same impact on plant communities as large herbivores is often expected for smaller  
73 herbivores such as voles. Experimental studies (Massey & Hartley 2006; Massey, Ennos &  
74 Hartley 2007a; b; Massey *et al.* 2008) suggests that silica levels increase in grasses subjected to  
75 vole grazing, and that given a choice, voles will avoid eating grasses that have accumulated  
76 high levels of silica. Voles have also been shown to turn a palatable plant community into an  
77 unpalatable one over the course of a few years (Howe *et al.* 2006), but although silica-rich  
78 grasses were present their role was not addressed. Still, the results can be interpreted as an  
79 outcome of apparent competition that is similar to that of a situation with large herbivores. Even  
80 if studies of herbivory often focus on one herbivore type, both large and small herbivores co-  
81 exist in many ecosystems. Based on the common dislike of silica-rich grasses as food plants,  
82 and the assumption that apparent competition is an important mechanism, an additive effect of  
83 both herbivore-types on the biomass of silica-rich grasses might be expected. This could further  
84 promote an unpalatable plant community, as theorized for large herbivores.

85           However, small rodent herbivores can utilize grass for other purposes than food, such as  
86 for nests. Many silica-rich grasses form dense tussocks and have tough leaves. They could  
87 potentially serve as both protective habitat and nest material for small rodent herbivores. Voles  
88 frequently use stems of grasses for nest construction (Thomas & Birney 1979). This will result  
89 in cutting of grass even when it is not eaten. If the rodents cut dominant unpalatable grasses  
90 while large herbivores leave them alone, their effect on a plant community might be very  
91 different. Activities (cutting, burrowing, tunneling, nesting) by small rodents may have a more  
92 negative effect on the biomass of silica-rich grasses, counteracting the positive effect of large

93 herbivores. Benefits gained by silica-rich grasses from apparent competition could then  
94 potentially be lessened or completely removed.

95           If silica only acts as a defense mechanism against grazing, other traits will determine the  
96 impact of small rodent activities on grasses. One such trait is growth rate. Growth rate, while  
97 considered an important trait in competition, is also important to herbivory tolerance (Strauss &  
98 Agrawal 1999). When nesting activities by small rodents reaches high enough intensities, it is  
99 plausible that tolerance to herbivory through high relative growth rates becomes a more  
100 important protective measure than resistance through silicates. Grasses are generally attributed  
101 quick biomass increase in response to defoliation (Ferraro & Oesterheld 2002). Domination by  
102 silicate-rich grasses in areas with both large herbivore and small rodent herbivore activity is  
103 thus potentially mainly a result of swift compensatory growth.

104           Two silica-rich grasses, *Deschampsia cespitosa* and *Nardus Stricta* are both considered  
105 unpalatable (Grant *et al.* 1996; Ravolainen *et al.* 2011) and are common, and often dominant, in  
106 a wide range of ecosystems (Rodwell 1992; Fremstad 1997; Rosef, Langerud & Norderhaug  
107 2007). Both grasses are also frequently used as small rodent habitat. Where *Deschampsia* and  
108 *Nardus* differ greatly is growth rate. *Deschampsia* is a fast growing tussock grass (Davy 1980;  
109 Grime 1988), while *Nardus* is a relatively slow growing tussock grass (Chadwick 1960; Grime  
110 1988). Based on the assumption that herbivory tolerance increases with growth rate we could  
111 expect that these grasses would respond differently to grazing (if grazed at all) and small rodent  
112 activity. However, although tolerance to herbivore activity of *Deschampsia* is likely higher than  
113 that of *Nardus*, its importance in structuring plant communities where both of the grasses are  
114 present and common has not been investigated.

115           *Deschampsia* and *Nardus* are abundant in riparian meadows found on sub-arctic tundra,  
116 in areas where large herbivores (reindeer) and small rodent herbivores are active (Ravolainen *et*  
117 *al.* 2013). This makes the sub-arctic a good area to study the effects of large herbivore grazing

118 and small rodent grazing and cutting on the two different silicate-rich grasses. An enclosure  
119 experiment was therefore conducted in two riparian valleys on the Varanger Peninsula in  
120 northeastern Norway. Species pools were similar between the two riparian valleys, but within  
121 the valleys species abundances could vary substantially. The enclosure experiment consisted of  
122 open control plots, large-meshed enclosures excluding reindeer and small-meshed enclosures  
123 excluding both reindeer and small rodents. The focal small rodent species in this experiment  
124 were grey-sided voles, tundra voles and Norwegian lemmings, all of which display  
125 synchronized cyclic populations in these valleys (Killengreen *et al.* 2007; Henden *et al.* 2011).  
126 During the experiment the populations of rodents increased, reached peak-year and crashed,  
127 capturing large contrasts in rodent activity.

128 If apparent competition is the mechanism by which these grasses dominate in these meadows,  
129 then large herbivores and small rodent herbivores are expected to have a similar impact on the  
130 plant community. That is, unpalatable, silica-rich grasses will remain after the palatable portion  
131 of the vegetation is removed. The Prediction under that scenario is that both *Nardus* and  
132 *Deschampsia* will gain a competitive advantage in treatments allowing herbivore activity.

133         However, if large herbivores have a positive effect and small rodent herbivores have a  
134 negative effect on the biomass of silica-rich grasses, apparent competition might not be  
135 obvious. How the grasses respond to small rodent cutting depends on their growth rate, and my  
136 predictions therefore differ for *Deschampsia* and *Nardus*; the competitive ability of  
137 *Deschampsia* will be higher in plots grazed by both herbivore-types compared to plots grazed  
138 by none. Declining rodent populations and rapid regrowth of *Deschampsia* will further increase  
139 its competitive ability. In cages excluding only reindeer competitive ability of *Deschampsia*  
140 will decline compared to cages excluding both herbivores, as a result of no positive effect from  
141 reindeer and severe cutting by rodents. *Nardus* will react similarly in both herbivore treatments  
142 compared to treatments excluding all herbivores. *Nardus*, because of its slow growth rate, will

143 have lower competitive abilities in treatments allowing herbivores than in treatments excluding  
144 them.

145

## 146 **Material and method**

### 147 *Study area*

148 My study took place on the low-arctic tundra of the Varanger Peninsula (70 N, 31 E), where  
149 since 2006 both ecosystem monitoring and experiments have taken place (e.g Ravolainen *et al.*  
150 2011; Soininen *et al.* 2013) Mean temperature for July ranges from 9.5 to 10.4°C and drops  
151 about 0.5°C in August, while mean annual precipitation is 544 mm (Norwegian Institute of  
152 Meteorology). The area, which lies on top of sedimentary bedrock (Siedlecka 1990), consists of  
153 flat ridges dominated by *Empetrum* heathland and shallow riparian valleys where tall shrub-  
154 patches, sedges, grasses and forbs are common. *Deschampsia* can be especially dominant, with  
155 *Nardus* also frequently making up a substantial portion of the vegetation (Bråthen *et al.* 2007;  
156 Ravolainen *et al.* 2013). Two riparian valleys with grass-dominated vegetation are  
157 Sandfjorddalen (hereafter SA) and Hestdalen (hereafter HE). These valleys are often grazed in  
158 the summer by reindeer (*Rangifer tarandus*). The density of reindeer per km<sup>2</sup> was 2.93 in 2011  
159 and 3.42 in 2012 (Reindrifftsforvaltningen 2013) while the long-term average lies at 2.5 to 3  
160 animals per km<sup>2</sup> (Anonymous 2004). The valleys also harbor year-round resident populations of  
161 Norwegian lemming (*Lemmus lemmus*), grey-sided vole (*Myodes rufocanus*) and tundra vole  
162 (*Microtus oeconomus*), all of which fluctuate cyclically (Killengreen *et al.* 2007; Henden *et al.*  
163 2011). The study included at small rodent peak year in 2011 (table 1).

164

165 ***Experimental design***

166 In the meadows of SA and HE replicates of three different herbivore-treatments were  
167 established in two compositionally different vegetation types: *Deschampsia*-dominated meadow  
168 and *Nardus*-dominated meadow, where in both types, a wide range of other species also  
169 occurred (e.g. *Salix* spp, *Anthoxanthum nipponicum*, *Avenella flexuosa*, *Viola* spp, *Bistorta*  
170 *vivipara*, *Rumex* spp. Table 2). Herbivore-treatments were randomly assigned 50x50 cm plots  
171 with either *Deschampsia*-dominated meadow or *Nardus*-dominated meadow. The three  
172 herbivore-treatments were: No herbivore exclusion (open plots, henceforth Rod+Rein), large  
173 herbivore exclusion (50x50x60 cm cages covered by steel wire mesh with 3x3 cm openings,  
174 henceforth Rod) and exclusion of all vertebrate herbivores (50x50x60 cm cages covered by  
175 steel wire mesh with 1x1 cm openings, henceforth AllExclusion). Roots had to be cut when  
176 constructing the cages for the herbivore exclusion plots, so to make for equal conditions roots  
177 were cut to a depth of 20-30 cm for all treatments. Initially there were 17 (SA) and 7 (HE)  
178 replicates of each combination of herbivore-treatment and vegetation type, but one incident of  
179 sampling error, and loss of replicates mainly due to small rodent herbivores breaking in to the  
180 AllExclusion-cages (as evident by cut plants and tunnels), has led to fewer replicates (fig 1).  
181 This experiment overlapped with a *Salix* experiment, so present in each replicate was a *Salix*  
182 sapling. *Salix* may thus be overestimated in the experimental plots compared to the general  
183 vegetation.

184

185 ***Field measurements***

186 Apparent competition was in this study defined as the silicate-rich grasses competitive ability  
187 versus that of the collective surrounding vegetation in presence of herbivores. Competitive  
188 ability was measured by biomass increase, both total and relative. Relative biomass was

189 estimated per plot as the biomass of silicate-rich grass divided on the biomass of the other  
190 vascular plants present in the plot.

191 The experiment was established late August in 2010 (from 20<sup>th</sup> to 30<sup>th</sup>). Initial biomass  
192 composition of vascular plants was measured using the point frequency method (Bråthen &  
193 Hagberg 2004) A square frame with 3 x 3 pins attached at 10 cm intervals was placed in the  
194 plots and intercept between the pins and different species were counted. Only live vascular  
195 plants were registered. The point frequency data for the plants was then transformed to biomass  
196 estimates using calibrations provided by Ravalainen *et al.* (2010). Vegetation measurements  
197 were done at peak growing season (late July, from 20<sup>th</sup> to 30<sup>th</sup>) for 2011 and 2012. To estimate  
198 rodent activity each plot was divided into four quadrants, where signs of small rodent activity  
199 were noted as present or absent. There was rodent activity in most plots for both 2011 and  
200 2012. There are no clear sign of small rodent aggregation in Rod+plots (fig 2).

201

## 202 ***Statistical analysis***

203 Changes in total biomass of the silicate-rich grasses (*Deschampsia* or *Nardus*) per plot were  
204 fitted with a linear mixed model using the function `lme` from the `nmle`-package. The same was  
205 done for the biomass of the other plants per plot (changes in total vegetation biomass of other  
206 vascular plants), and changes in relative biomass of silica-rich grasses. The predictor for all  
207 models was an interaction term containing treatment and year as the yearly difference between  
208 the treatments were of interest. To deal with correlational errors within plots, plot identity was  
209 included as a random effect. Normal diagnostics were done to check for heteroscedasticity.  
210 Confidence intervals (CI) at a 95% level for the fixed effects were calculated with the function  
211 *intervals*, also from the `nmle`-package. The results are presented as the contrasts between the  
212 treatment levels of the factors used as fixed effects with confidence intervals. The information



213 used for the figures is extracted from the models, as well as the numbers presented in the results  
214 section. The full models can be found in supplementary information. All analyses were  
215 conducted using R (R Development Core Team 2013).

216

## 217 **Results**

218 Initially the *Deschampsia*-dominated vegetation consisted of 109.48 g/m<sup>2</sup> *Deschampsia* and  
219 84.9 g/m<sup>2</sup> other vascular plants. *Nardus*-dominated vegetation had a lower biomass of *Nardus*  
220 than other vascular plants (76.13 g/m<sup>2</sup> to 104.2 g/m<sup>2</sup>). These values are used as a reference level  
221 to the treatment effects.

222

223 There was no effect of Rod+Rein or Rod-treatments in terms of total biomass increase of either  
224 *Deschampsia* (fig 3a) or *Nardus* (fig 4a) compared to treatments excluding all herbivores.

225

226 *Competitive contrasts in plots with large and small rodent herbivore-activity vs. plots where*  
227 *herbivore activity was excluded*

228 While total biomass of *Deschampsia* in treatments allowing both herbivores never exceeded  
229 that of the all herbivore exclusion treatment, relative biomass increased.

230 Total biomass of *Deschampsia* was similar between Rod+Rein-plots and AllExclusion-plots in  
231 2011 (fig 3a). In 2012 (after peak year) total biomass of *Deschampsia* declined in the  
232 Rod+Rein-plots (-30.8±20.083 g/m<sup>2</sup>). Total biomass of the other vascular plants in the  
233 *Deschampsia*-dominated vegetation declined similarly (-33.46±21.3 g/m<sup>2</sup>). Relative to the other  
234 vascular plants, biomass of *Deschampsia* decreased less, which probably constitutes the relative  
235 increase of *Deschampsia* in Rod+Rein-plots compared to AllExclusion-plots (2.927±1.855).

236 Quite different to *Deschampsia*, *Nardus* had lower biomass in herbivore treatments both  
237 peak year and after peak compared to the reference level, and there was no change in relative  
238 biomass. *Nardus* in Rod+Rein-plots had lower biomass in the rodent peak year than  
239 AllExclusion-plots ( $33.947 \pm 12.237$  g/m<sup>2</sup>), and after the peak year biomass of *Nardus* in  
240 Rod+Rein-plots had decreased further ( $-57.271 \pm 12.258$  g/m<sup>2</sup>). This pattern was similar to that  
241 of the other vascular plants (fig 4b) and hence there were no changes in relative biomass of  
242 *Nardus* (fig 4c).

243

244 *Competitive contrasts in plots with only small rodent herbivores vs. plots where herbivore*  
245 *activity was excluded*

246 *Deschampsia* biomass decreased in the peak year, but recovered again the year after. The other  
247 vascular plants also decreased in peak year, and they didn't manage to recover, thus increasing  
248 relative biomass of *Deschampsia*. During the peak year biomass of *Deschampsia* in Rod-plots  
249 decreased to well under the biomass-levels in AllExclusion-plots ( $-42.622 \pm 20.083$  g/m<sup>2</sup>). The  
250 same happened with the other vascular plants in the Rod-plots ( $-42.05 \pm 21.31$  g/m<sup>2</sup>). The year  
251 after, *Deschampsia* in Rod-plots rose back to the levels found in AllExclusion-plots, while the  
252 other vascular plants remained low (fig 3b). This led to a relative increase in biomass of  
253 *Deschampsia* in Rod-plots after peak year ( $2.981 \pm 1.854$ ).

254 As in treatments allowing both herbivores, *Nardus* gained no advantage from rodent  
255 activity only. Biomass of *Nardus* in Rod-plots was lower than in AllExclusion-plots both in  
256 peak year ( $-53.804 \pm 12.258$ ) and after peak year ( $-61.43 \pm 12.258$ ). There were no changes in  
257 relative biomass of *Nardus* (Fig 4c).

258

259 *Contrasts between herbivore treatment plots in the small rodent peak year*

260 In the peak year treatments allowing both herbivore types had higher biomass of *Deschampsia*  
261 than treatments allowing only small rodents ( $34.28 \pm 20.083$  g/m<sup>2</sup>), as a result of decreasing  
262 biomass in Rod-plots. In the *Nardus*-dominated vegetation biomass of the other vascular plants  
263 were higher in Rod+Rein-plots compared to Rod-plots ( $40.97 \pm 25.1$ )

264

## 265 **Discussion**

266 The main result do draw from this study is that *Deschampsia* gains a competitive advantage  
267 where herbivores are present, while *Nardus* does not. Relative biomass of *Deschampsia* was  
268 higher the year after the rodent peak in treatments where reindeer and small rodent herbivores  
269 had access compared to where they were excluded. This was in accordance with the prediction  
270 that *Deschampsia* would gain an increase in competitive ability from herbivore activity. Still,  
271 the predicted increase in total biomass was not observed. As predicted on basis of its slow  
272 growth, total biomass of *Nardus* declined in both treatments with herbivores both in peak year  
273 and after peak year, and there was no change in relative biomass.

274

### 275 *The importance of growth rate*

276 As expected, relative biomass of *Deschampsia* increased, which indicates increased competitive  
277 ability for *Deschampsia*, promoted by either rodent or rodent and reindeer activity. This is  
278 partly in accordance with the findings of Howe *et al.* (2006), that small rodent herbivores can  
279 create unpalatable vegetation. Different to the assumptions of Howe *et al.* (2006) is that this  
280 competitive advantage of the unpalatable vegetation persists when large herbivores are present  
281 as well. However, in this case, as small rodents vigorously cut the silica-rich grasses, it was not  
282 the palatability of the plant that led towards an unpalatable community, but rather rapid relative  
283 growth rate. This could be an important determinant to why *Deschampsia* “wins” the

284 competition when both herbivore types are present. Growth rate is an important trait for  
285 tolerance and competition (Strauss & Agrawal 1999), and the relative growth rate of  
286 *Deschampsia* is high (Davy 1980; Suding *et al.* 2004). This might enable the grass to quickly  
287 utilize easily decomposable nutrition from fecal pellets, urine, more degradable plant matter  
288 (Frank & Evans 1997) and carcasses. In the year after rodent peak this could be especially  
289 useful and lead to an increase in biomass, as rodent ravaging has led to a release from  
290 competition of other plants, which might explain the rapid recovery of *Deschampsia* in  
291 treatments allowing only rodents. This aspect of nutrient dynamics remains to be studied.

292           According to my results, *Nardus* gained no benefit from having herbivores present.  
293 Total biomass declined and relative biomass remained the same. Opposed to the popular belief  
294 that *Nardus* is the incarnation of herbivory resistance (Grant *et al.* 1996), competitive ability  
295 seems to be hindered by activity of rodents and reindeer or rodents only. The reason might be  
296 that the relative growth rate of *Nardus* is significantly lower than that of *Deschampsia*  
297 (Chadwick 1960; Grime 1988). The unaltered relative biomass indicates that *Nardus* is not cut  
298 to a lesser degree than the surrounding vegetation is eaten, which might also be true for  
299 *Deschampsia*. However, *Deschampsia*, and its rapid relative growth rate, can quickly gain new  
300 biomass.

301           Based on the findings for the grasses, *Deschampsia* may become an even more common  
302 occupant in the sub-arctic riparian valleys as long as herbivores are present, while *Nardus*  
303 remains at a standstill. Growth rates undoubtedly play an important part in this, but it seems that  
304 disturbances by herbivores is necessary to utilize the growth rate advantage.

305

306 *The effect of small rodent herbivores*

307 As predicted, the activities of only small rodents during the peak year were negative for total  
308 biomass of *Deschampsia*, likely largely a result of cutting. When *Deschampsia* recovered the  
309 year after, it was probably because of cessation of rodent activity caused by the crash year.  
310 Although *Deschampsia* can potentially constitute a large portion of lemming and vole diet  
311 (Saetnan & Batzli 2009), diet data from the area (Soininen 2012) suggests that this probably  
312 isn't the case here. Rodents have a small gut volume and a limited gut flora, and should  
313 therefore be selective in their feeding (Ostfeld, Manson & Canham 1997). However, with a  
314 decline in total biomass for both years, and no change in relative biomass, this does not seem to  
315 be the case with *Nardus*. Small rodents can reduce biomass of dominating grass species  
316 significantly, even when more palatable species are present (Summerhayes 1941; Austrheim *et*  
317 *al.* 2007), possibly because searching for more palatable species is uneconomic (Wheeler  
318 2005). However, diet data from the region (Soininen 2012) reveals the same as it did for  
319 *Deschampsia*: *Nardus* is not a major constituent of small rodent diets. The reason small rodents  
320 cut the silica-rich grasses might therefore be because they have other applications than food.  
321 Indeed, the tussocks provide fine material and locations to establish nests (Summerhayes 1941;  
322 Thomas & Birney 1979; personal observation).

323 It is clear that small rodent herbivores can have a large negative impact on the biomass  
324 of silicate-rich grasses, but not necessarily by grazing. There does however seem to be a time-  
325 lagged benefit for the grasses when rodent populations decline, possibly through nutritious fecal  
326 pellets and a release from competition.

327

328 *The effect of large herbivores*

329 According to the prediction, biomass of *Deschampsia* in the peak year was higher where  
330 reindeer were allowed to graze compared to where only rodents were allowed and at the

331 reference level of all herbivore exclusion treatments. Biomass of *Nardus*, for both herbivore  
332 treatments, was under that of the reference level. Grasses with high silica content often  
333 dominate in areas heavily grazed by large herbivores (McNaughton & Tarrants 1983; Brizuela  
334 & Detling 1986), and large herbivores have been found to have a positive effect on biomass of  
335 silica-rich grasses (Ravolainen *et al.* 2011). This positive effect could stem from addition of  
336 nutrients through feces and urine, removal of competition by grazing neighbors (both grasses  
337 have been found to constitute little of large herbivore diet, Hill, Evans & Bell 1992; Eilertsen,  
338 Schjelderup & Mathiesen 2002), and light grazing, which could increase compensatory growth  
339 (McNaughton & Tarrants 1983). If increased tolerance through increase in compensatory  
340 growth plays an important role, then *Deschampsia* should benefit much more than *Nardus*  
341 under grazing by larger herbivores. This could be because of a higher growth rate of  
342 *Deschampsia* and it being used as fodder to a higher degree than *Nardus*, which could  
343 potentially stimulate compensatory growth more. Another way for the large herbivores to “aid”  
344 the grasses could be through keeping small rodents away. Rosef, Langerud & Norderhaug  
345 (2007) found that rodents were less active in vegetation where large herbivores also were  
346 present. However, the frequency of observed rodent activity in my study suggests that this is  
347 not the case.

348           It seems rodent cutting is not as severe when large herbivores are present, at least for  
349 *Deschampsia*. As relative biomass also remains higher than the reference level (all herbivore  
350 exclusion 2010), it is likely that *Deschampsia* gains facilitating effects of both large herbivores  
351 and small rodent herbivores.

352

353 ***Importance of cyclic rodent populations on the dominance of *Deschampsia* and consequence***  
354 ***of loss of cycles***

355 The quick recovery of *Deschampsia* biomass from peak year to the year after, and the increase  
356 in relative biomass, suggests that the cyclic behavior of small rodent populations may play a  
357 part in maintaining the *Deschampsia* dominated vegetation. The peak year may provide  
358 nutrients and a release from competition with other plants. After the peak year rodent densities  
359 will be low for a few years, thus keeping *Deschampsia* from getting cut. *Deschampsia* can then  
360 utilize its high growth rate to increase in biomass. However, within the plots where already  
361 established tussocks exist, potential for expansion is low (Davy 1980). Thus, the greatest  
362 potential for increase in biomass of *Deschampsia* would be in the formation of new tussocks,  
363 which is probably easier when rodents have laid the ground bare. Small rodent herbivore cycles  
364 are dampening (Ims, Henden & Killengreen 2008). This will possibly lessen or completely  
365 remove the positive effects provided by the small rodents. However, positive effects gained by  
366 reindeer will still remain, and so will maintenance of already dominant *Deschampsia* remain as  
367 well, although possibility of invading new turf will be lower.

368 **Conclusion**

369

370 When silica appears to be bypassed as an herbivory-avoidance mechanism in silica-rich grasses,  
371 tolerance by high relative growth rate seems to be the most important trait determining  
372 competitive ability in this system. *Deschampsia* is a rapid growing grass, and looked like it  
373 gained competitive advantages by having herbivores present. *Nardus* however, is a slow  
374 growing grass, and was affected negatively by reindeer and small rodent herbivore activity.  
375 Because rodents, probably for nesting purposes, cut the grasses to a large extent silica seems  
376 relatively unimportant as a defensive mechanism is. It looks like both large herbivores and

377 small rodent herbivores ultimately will affect *Deschampsia* positively, leading towards a more  
378 unpalatable plant community. However, this unpalatable community is not a product of  
379 defenses, but rather tolerance through high growth rates. Thus, it seems that apparent  
380 competition increases the competitive ability of *Deschampsia*, and could be the mechanism by  
381 which *Deschampsia* maintains dominance in the vegetation. For *Nardus* it looks like apparent  
382 competition provide no benefits or disadvantages compared to the other vascular plants.

383

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385 This study was done in cooperation with the "Ecosystem Finnmark" project. I want to extend  
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389 Anders Thingstad, Geir Vie, Johan Swärd, Vegard Nilsen and Emil Ruge for providing solid  
390 data.

391

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508 **Tables**

509 **Table 1. Abundances of the different small rodent herbivores in the Komag valley**  
 510 **(neighboring valley of SA and HE), measured by the number trapped per 100 trap nights.**  
 511 **S = spring, F = fall (Killengreen *et al.* 2013).**

	S 2010	F 2010	S 2011	F 2011	S 2012	F 2012
<i>Microtus. rufocanus</i>	0	4	3	10	3	3
<i>Myodes. oeconomus</i>	0	5	10	21	1	3
<i>Lemmus. lemmus</i>	0	1	2	5	0	0

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526 **Table 2. Vegetation composition in *Deschampsia* and *Nardus* dominated vegetation.**  
 527 **Composition is presented as mean dry biomass g/m<sup>2</sup> for the most abundant species and all**  
 528 **functional groups in 2010 across all plots in all treatments. For method of vegetation**  
 529 **measurement, see section “Field measurements”**

<i>Deschampsia cespitosa</i> -dominated plots			<i>Nardus stricta</i> -dominated plots		
Functional groups and species	Mean biomass g/m <sup>2</sup>	SD	Functional groups and species	Mean biomass g/m <sup>2</sup>	SD
Evergreen woody	1.541	13.170219	Evergreen woody	5.283	25.983591
<i>Empetrum hermafroditum</i>	0.5727	4.893532	<i>Empetrum hermafroditum</i>	7.655	21.563609
Deciduous woody	0	0	Deciduous woody	1.321	6.594648
<i>Betula nana</i>	0	0	<i>Betula nana</i>	1.096	9.234476
Grey-green <i>Salix</i>	15.46	30.920949	Grey-green <i>Salix</i>	27.95	49.292435
Green <i>Salix</i>	17.05	37.241487	Green <i>Salix</i>	13.7	38.960298
Prostrate <i>Salix</i>	0	0	Prostrate <i>Salix</i>	0	0
<i>Salix herbacea</i>	2.313	7.624613	<i>Salix herbacea</i>	3.70	12.928955
Evergreen non-woody	0.294	1.429900	Evergreen non-woody	0.3023	1.449307
Cyperacea	2.358	6.690524	Cyperacea	5.715	9.255953
Narrow grasses	11.626	14.401772	Narrow grasses	5.719	9.714155
<i>Nardus stricta</i>	4.012	12.139349	<i>Nardus stricta</i>	72.23	33.647044
Broad grasses	13.719	23.508646	Broad grasses	7.016	9.208419
<i>Deschampsia cespitosa</i>	112.70	55.616468	<i>Deschampsia cespitosa</i>	6.794	15.790145
<i>Calamagrostis phragmitoides</i>	2.299	7.567636	<i>Calamagrostis phragmitoides</i>	0.7385	3.577866
Tall herbaceous dicotyledons	0	0	Tall herbaceous dicotyledons	0	0

<i>Rumex acetosa</i>	3.626	9.912530	<i>Rumex acetosa</i>	0.2015	1.192024
Small herbaceous dicotyledons	17.149	14.926633	Small herbaceous dicotyledons	15.214	15.050701
Legumes and hemiparasites	0	0	Legumes and hemiparasites	0	0
Deciduous vascular cryptograms	0	0	Deciduous vascular cryptograms	0	0
<i>Equisetum</i>	2.314	5.028391	<i>Equisetum</i>	2.586	4.743051
<b>Total</b>	<b>207.03</b>	<b>83.45</b>	<b>Total</b>	<b>176.43</b>	<b>82.25</b>

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546 **Table 3. of the different treatment levels of interaction models related to *Deschampsia*-dominated**  
 547 **vegetation. The treatment levels are all herbivore exclusion (AllExclusion), only reindeer exclusion**  
 548 **(Rod) and no herbivore exclusion (Rod+Rein). The intercept level is the all herbivore exclusion-**  
 549 **treatment for 2010 (AllExclusion 2010). To calculate the estimate of for instance Rod:2011 you take**  
 550 **intercept+Rod:2010+AllExclusion:2011+Rod:2011. To get the contrasts used for the figures you**  
 551 **use the difference between the intercept and the estimate of Rod:2011.**

	Biomass of <i>Deschampsia</i>				Biomass of other vascular plants				Relative biomass of <i>Deschampsia</i>			
	Estimate	StE	DF	p-value	Estimate	StE	DF	p-value	Estimate	StE	DF	p-value
Fixed effects												
AllExclusion 2010 (intercept)	109.48	9.9787	121	0.000	84.90	10.544	121	0.000	1.689	0.8795	114	0.0573
Rod:2010	4.29	14.367	121	0.765	11.83	15.230	121	0.4387	1.429	1.2698	114	0.2627
Rod+Rein:2010	5.43	14.070	121	0.700	16.66	14.909	121	0.2660	0.516	1.2432	114	0.6788
AllExclusion:2011	-19.88	12.566	121	0.116	21.73	14.809	121	0.1449	0.150	1.2077	114	0.9009
AllExclusion:2012	-4.69	16.874	121	0.781	15.05	19.377	121	0.4399	0.421	1.5911	114	0.7917
Rod:2011	-27.03	17.862	121	0.132	-75.61	21.053	121	0.0005	-0.691	1.7501	114	0.6933
Rod+Rein:2011	6.11	17.676	121	0.730	-59.90	20.834	121	0.0048	0.509	1.7093	114	0.7660
Rod:2012	-6.18	21.116	121	0.770	-69.75	24.482	121	0.0052	1.130	2.0234	114	0.5776
Rod+Rein:2012	-31.58	20.960	121	0.134	-65.16	24.294	121	0.0083	2.029	1.9987	114	0.3120
Random effect												
Grid ID	24.84				12.59				1.392			
Residual	43.27				51.19				4.171			

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559 **Table 4. Estimates of the different treatment levels of interaction models related to *Nardus*-**  
 560 **dominated vegetation. The treatment levels are all herbivore exclusion (AllExclusion), only**  
 561 **reindeer exclusion (Rod) and no herbivore exclusion (Rod+Rein). The reference level is the all**  
 562 **herbivore exclusion-treatment for 2010 (AllExclusion 2010). To calculate the estimate of for instance**  
 563 **Rod:2011 you take intercept+Rod:2010+AllExclusion:2011+Rod:2011. To get the contrasts used**  
 564 **for the figures you use the difference between the intercept and the estimate of Rod:2011.**

	Biomass of <i>Nardus</i>				Biomass of other vascular plants				Relative biomass of <i>Nardus</i>			
	Estimate	StE	DF	p-value	Estimate	StE	DF	p-value	Estimate	StE	DF	p-value
Fixed effects												
AllExclusion 2010 (intercept)	76.130	6.079	97	0.000	103.00	12.679	121	0.000	1.085	0.2949	90	0.0004
Rod:2010	-7.350	8.597	68	0.3956	6.851	17.931	69	0.7035	-0.087	0.4171	68	0.8336
Rod+Rein:2010	-4.360	8.690	68	0.6176	9.140	18.307	69	0.6192	0.146	0.4307	68	0.7356
AllExclusion:2011	-12.037	7.007	97	0.0890	21.100	16.707	121	0.2091	-0.150	0.3878	90	0.6994
AllExclusion:2012	-11.157	7.288	97	0.1291	3.347	17.541	121	0.8490	0.158	0.4025	90	0.6942
Rod:2011	-29.287	10.113	97	0.0047	-77.40	23.449	121	0.0013	0.076	0.5723	90	0.8942
Rod+Rein:2011	-15.745	9.609	97	0.1045	-39.190	23.449	121	0.0973	-0.195	0.5414	90	0.7190
Rod:2012	-36.954	10.870	97	0.0010	-44.301	24.212	121	0.0698	0.188	0.6203	90	0.7619
Rod+Rein:2012	-29.375	10.700	97	0.0072	-40.884	24.190	121	0.0936	-0.684	0.6081	90	0.2636
Random effect												
Grid ID	19.744				27.804				0.732			
Residual	22.297				55.544				1.245			

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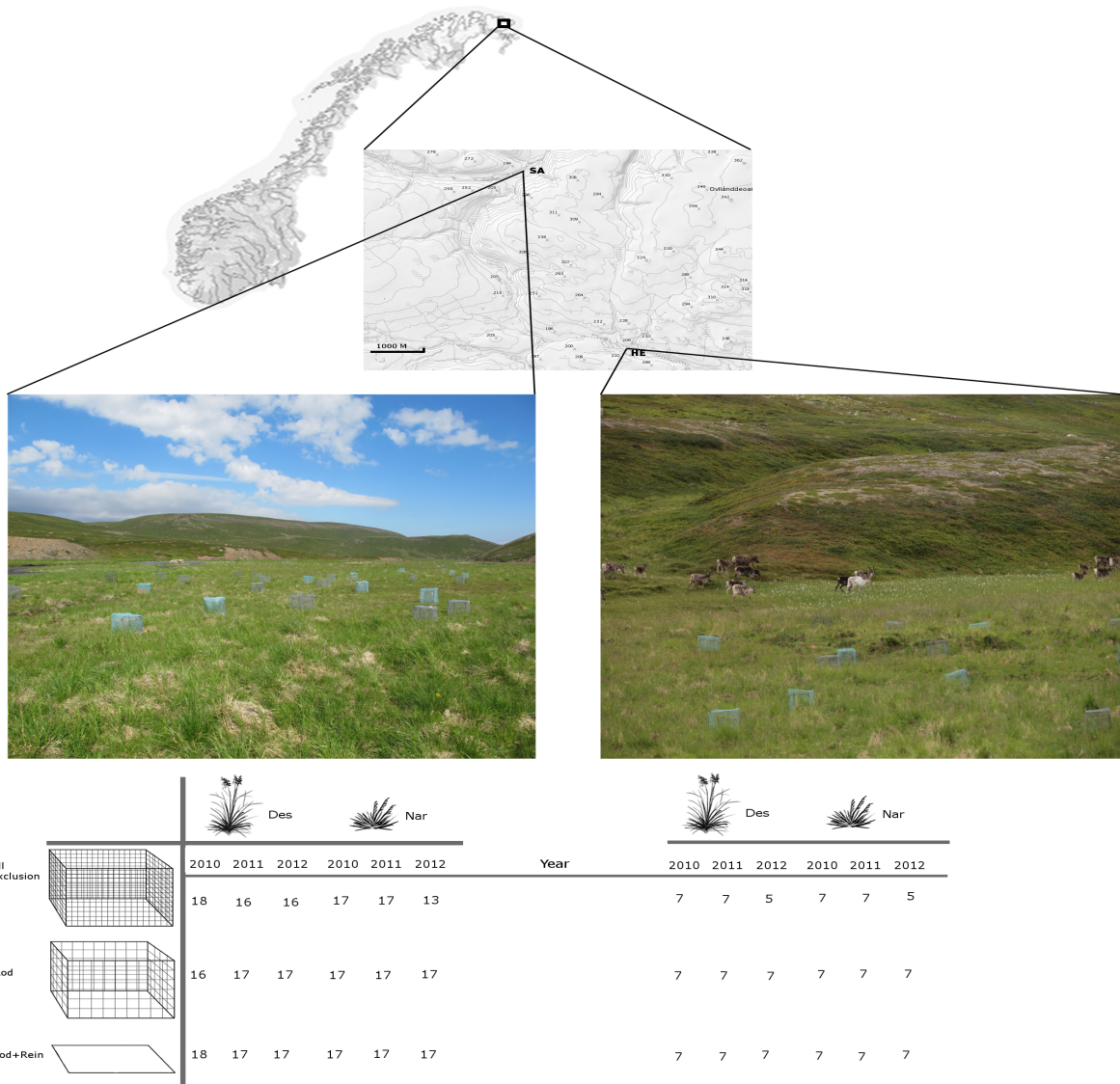
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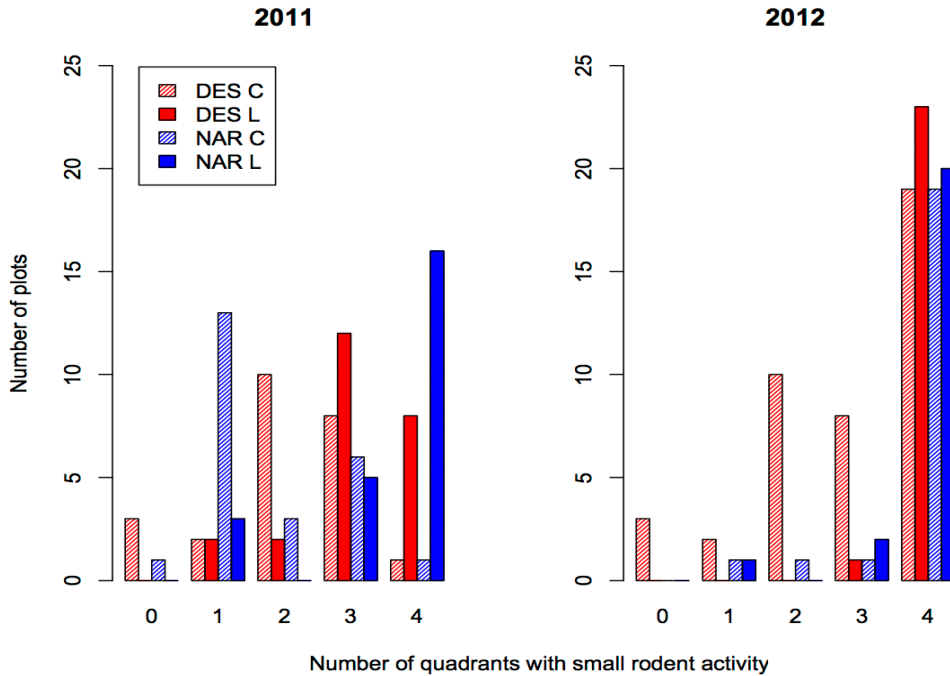


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576 **Figure 1. The two riparian meadows the study was conducted in, photos showing part of**  
 577 **each valley. To the left is Sandfjorddalen (SA) and to the right is Hestdalen (HE), and**  
 578 **below the photos of each respective valley is a table summarizing the number of replicates**  
 579 **for each treatment in each of the different vegetation types throughout the three years of**  
 580 **the study. The different herbivore treatments are, from bottom up: Reindeer and rodent-**  
 581 **plots (Rod+Rein), rodent only-plots (Rod) and all vertebrate herbivore exclusion (All**  
 582 **exclusion-plots). The different vegetation types are, from left to right: *Deschampsia-***  
 583 **dominated (Des) and *Nardus*-dominated (Nar).**

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587 **Figure 2. Signs of small rodent activity in Rod+Rein-plots and Rod-plots in in 2011 (peak**  
 588 **year) and 2012 (after peak year). This is measured as number of quadrants with signs of**  
 589 **activity. DES C = *Deschampsia*-dominated Rod+Rein-plots, DES L = *Deschampsia*-**  
 590 **dominated Rod-plots, NAR C = *Nardus*-dominated Rod+Rein-plots, NAR L = *Nardus*-**  
 591 **dominated Rod-plots.**

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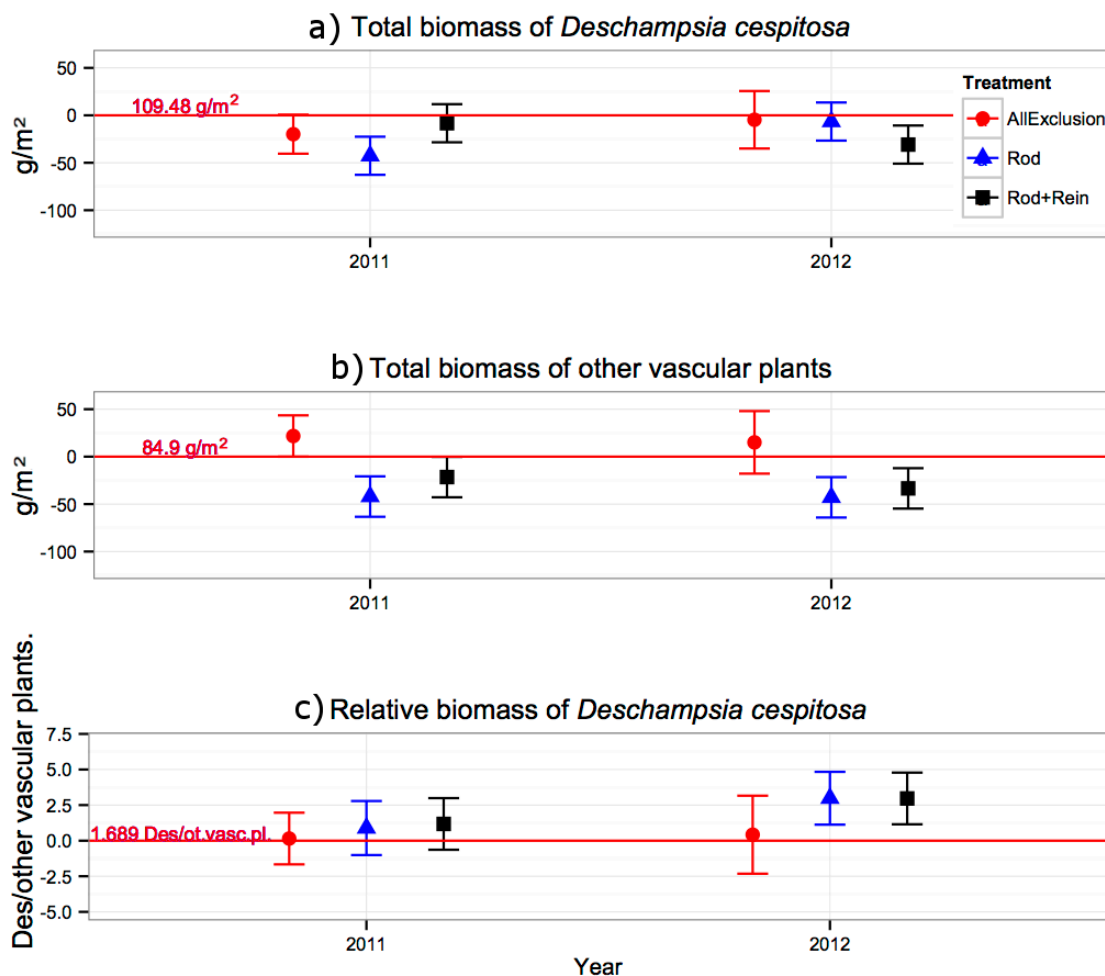
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600 **Figure 3. Responses to the treatments in *Deschampsia*-dominated vegetation in 2011**  
 601 **(rodent peak year) and 2012 (after rodent peak year). Effect sizes are given with 95 %**  
 602 **confidence intervals, and compared against a reference level (number in red) that includes**  
 603 **the estimates from AllExclusion-plots in 2010, indicated by a red line. a) Changes in total**  
 604 **biomass of *Deschampsia*, b) changes in total biomass of the other vascular plants, and c)**  
 605 **relative changes in biomass of *Deschampsia*.**

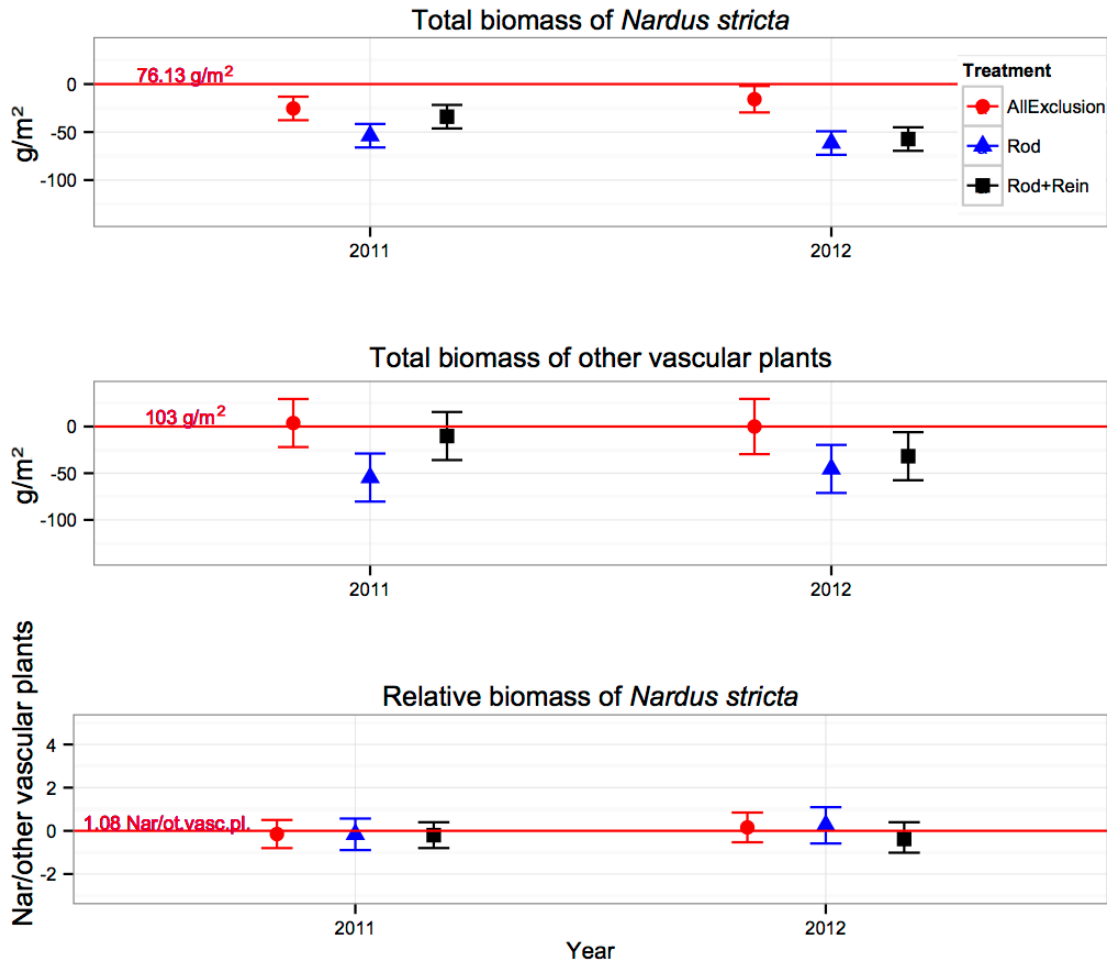
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612 **Figure 4. Responses to the treatments in *Nardus*-dominated vegetation in 2011 (rodent**  
 613 **peak year) and 2012 (after rodent peak year). Effect sizes are given with 95 % confidence**  
 614 **intervals, and compared against a reference level (number in red) that includes the**  
 615 **estimates from AllExclusion-plots in 2010, indicated by a red line. a) Changes in total**  
 616 **biomass of *Nardus*, b) changes in total biomass of the other vascular plants, and c) relative**  
 617 **changes in biomass of *Nardus*.**

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