

1 **Consequences of grazer-induced vegetation transitions on ecosystem carbon**
2 **storage in the tundra**

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14 Running headline: Grazing shapes tundra carbon storage

15 **Summary**

- 16 1. Large herbivores can control plant community composition and, under certain conditions,
17 even induce vegetation shifts to alternative ecosystem states. As different plant assemblages
18 maintain contrasting carbon (C) cycling patterns, herbivores have the potential to alter C
19 sequestration for regional scales. Their influence is of particular interest in the tundra,
20 where a large share of the world's soil C reservoir is stored.
- 21 2. We analysed how grazer-induced vegetation shifts affect tundra C stocks by resampling
22 two sites located along 50-year-old reindeer pasture rotation fences in northern Norway. At
23 both sites, heavy grazing intensity had promoted the establishment of graminoid-dominated
24 vegetation several decades ago next to the fences. In comparison, the lightly grazed areas
25 on the other side of the fences and the moderately grazed areas further away from the fences
26 were dominated by shrubs. After the previous investigation, both reindeer densities and
27 temperatures have increased and more time has passed for transient dynamics to proceed.
- 28 3. At the site, where relative reindeer numbers and trampling intensity had increased the most,
29 we found that graminoid-dominated vegetation had expanded to the moderately grazed
30 area. On the other site, no grazing-dependent changes in vegetation were found.
- 31 4. We found that the graminoid-dominated areas generally stored less C aboveground
32 compared to the shrub-dominated areas indicating a grazing-induced decrease in
33 aboveground C. Yet, the consequences of grazing belowground varied between the sites:
34 grazing did not alter organic soil C stocks at one of the sites, whereas at the other site, heavy
35 grazing intensity increased organic soil C stocks.
- 36 5. We suggest that the site-specific responses of organic soil C stocks to grazing are explained
37 by the dominant plant functional types, and that the grazing-induced replacement of

38 deciduous shrubs by graminoids could increase soil C sequestration. Ultimately, better
39 understanding on the impact of grazers could serve carbon neutral land-use planning in the
40 tundra.

41

42 Keywords: Ecosystem C storage, CO₂ flux, Grazing, Reindeer, *Rangifer tarandus*, Plant functional
43 traits, Plant–soil (below-ground) interactions

44 **Introduction**

45 Current evidence suggests that ongoing climate warming increases the abundance of shrubs
46 throughout the circumpolar Arctic (Myers-Smith *et al.* 2011, 2015a; Elmendorf *et al.* 2012b).
47 Although this shrubification of tundra increases carbon (C) storage within plant biomass, it may
48 under some conditions be accompanied by warmer soil temperatures (Sturm *et al.* 2005), higher
49 rates of nutrient cycling (Buckeridge *et al.* 2010) and increased ecosystem respiration (Cahoon *et*
50 *al.* 2012). If soil microbial activity in terms of C decomposition is enhanced more than plant
51 production, this could lead to substantial C losses from the soil and turn arctic ecosystems into a
52 net C source (Mack *et al.* 2004; Nobrega & Grogan 2008; Grogan 2012). The magnitude of the
53 potential C release could be of global significance because a large share of world's soil C is
54 currently stored in tundra soils (Tarnocai *et al.* 2009).

55
56 Herbivores such as reindeer (*Rangifer tarandus*) and small rodents are known to exert a major
57 influence on tundra plant communities and to partially counteract the warming-induced increase in
58 shrub abundance (Post & Pedersen 2008; Olofsson *et al.* 2009; Zamin & Grogan 2013a). **High**
59 **abundance of large herbivores can induce a vegetation transition from bryophyte and shrub -**
60 **dominated tundra towards dominance by graminoids (Thing 1984; Olofsson *et al.* 2001; Olofsson,**
61 **Stark & Oksanen 2004; van der Wal 2006). At the same, grazing also increases soil nutrient**
62 **availability, enhances the rates of C and nutrient cycling and alters soil physical properties (Stark,**
63 **Strommer & Tuomi 2002; Olofsson *et al.* 2004; Stark & Väisänen 2014). These transitions**
64 **constitute unique model systems to address how grazing-induced shifts in the dominant vegetation**
65 **influence an ecosystem's capacity to store C.** Although it is assumed that herbivores generally
66 decrease ecosystem C storage by reducing plant biomass (Tanentzap & Coomes 2012), the long-

67 term-effects of grazing on tundra C stocks are more complicated, as most of the ecosystem C is
68 stored in the soil (Hartley *et al.* 2012) and plant species, in turn, have largely varying effects on
69 soil C sequestration (Cornwell *et al.* 2008; De Deyn, Cornelissen & Bardgett 2008; Bardgett,
70 Mommer & De Vries 2014). Shrubs that dominate under light grazing store considerable quantities
71 of C in their biomass (Mack *et al.* 2004; Myers-Smith *et al.* 2011) and produce coarse, woody
72 debris that is recalcitrant to microbial decomposition (De Deyn *et al.* 2008). However, the influence
73 of shrubs on soil C sequestration varies among species. Deciduous shrubs produce litter that is of
74 less recalcitrance compared with the litter produced by evergreen shrubs (De Deyn *et al.* 2008) and
75 certain deciduous shrubs are associated with particularly high rates of soil C turnover due to their
76 symbiosis with ectomycorrhizal fungi (Clemmensen *et al.* 2013, 2015; Parker, Subke & Wookey
77 2015). On the other hand, graminoids that may be promoted by intensive grazing have a high
78 potential for soil C sequestration through the allocation of resources to root biomass, which is also
79 recalcitrant to decomposition (De Deyn *et al.* 2008; Freschet *et al.* 2013). To the best of our
80 knowledge, it has not been assessed whether more C is presently sequestered in shrub- or
81 graminoid-dominated tundra when the distribution of these vegetation types is controlled by
82 grazers. This could be achieved through the comparison of different grazing intensities. However,
83 the factors constantly influencing ecosystem processes, such as the climate, changing reindeer
84 numbers (Uboni *et al.* 2016) and transient dynamics (Olofsson *et al.* 2004), need to be considered.
85

86 In the present study, we revisited two tundra sites where fences built for reindeer management have
87 separated a lightly grazed area from a heavily and a moderately grazed area for the past 50 years.
88 The data collected 14 years earlier demonstrated that the heavy grazing intensity in the close
89 vicinity of the fence had induced a vegetation shift from a shrubs to graminoids and increased soil
90 temperatures and nutrient availability (Olofsson *et al.* 2004). Weaker effects were detected in the

91 moderately grazed area located further away from the fence. Since then, the tundra climate has
92 become warmer (IPCC 2014), there has been more time for the transient dynamics of vegetation
93 to proceed and reindeer numbers have increased (Uboni *et al.* 2016), with the latter factor being
94 particularly important under heavy and moderate grazing. We quantified how combined climate
95 warming and increased reindeer numbers affect ecosystem C stocks under contrasting grazing
96 intensities, and acquired an improved estimate of the total ecosystem C. We hypothesized that the
97 warming-induced increase in the abundance of shrubs would have occurred only under light
98 grazing (Post & Pedersen 2008; Olofsson *et al.* 2009), possibly resulting in higher aboveground C
99 stocks (Mack *et al.* 2004). On the heavily grazed area, we predicted that concurrent changes in
100 reindeer numbers and climate would have increased the abundance of graminoids and the
101 availability of soil nutrients. As graminoids store less C in aboveground biomass but have high
102 capacity to produce large quantities of root litter that is recalcitrant to microbial decomposition (De
103 Deyn *et al.* 2008), we predicted that the increase in graminoids would have decreased aboveground
104 C and increased root and soil C stocks. The grazing effects were expected to be limited only to the
105 highest grazing intensity in the vicinity of the fences.

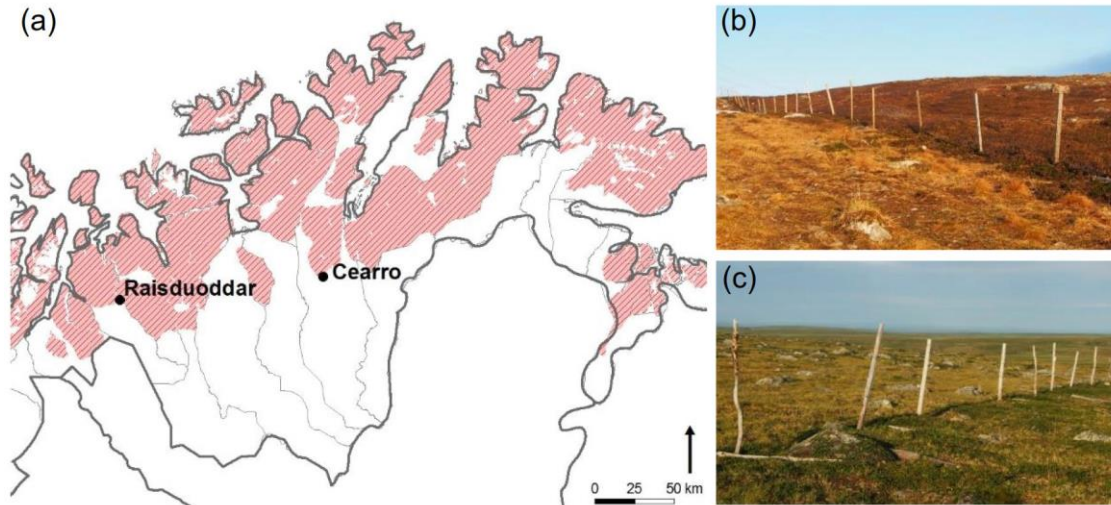
106 **Materials and methods**

107 Study area and setting

108 This study was conducted at two tundra sites approximately 100–200 m above the timberline in
109 northern Norway: Raisduoddar (69°31'29 N, 21°19'16 E; altitude 430–570 m asl; Fig. 1) and
110 Čearro (69°43'23 N, 21°37'45 E; altitude 540–570 m asl). Raisduoddar belongs to the suboceanic
111 region of northernmost Fennoscandia, where the dominant vegetation is of the *Empetrum*–
112 *Dicranum*–Lichens type and Čearro is located in the continental area dominated by *Betula nana*–
113 *Cladina*-type lichen heaths (Oksanen & Virtanen 1995). At both sites, a pasture rotation fence built
114 in the 1960s separates the coastal summer ranges from the autumn and winter ranges further inland.
115 Reindeer start to migrate from their summer ranges during late summer and stay within the vicinity
116 of the fences for approximately 2–3 weeks before being released to the autumn and spring range.
117 As a consequence, the summer range at the study sites is heavily grazed and trampled – especially
118 within close vicinity of the fence (Oksanen 1978; Olofsson *et al.* 2001). **In Raisduoddar, the**
119 **autumn–spring range near the fence is only sporadically used during the autumn migration, because**
120 **reindeer pass quickly eastward along a fixed transit route. In Čearro, reindeer stay near the fence**
121 **in October–November and feed on lichens by digging through the snow. However, reindeer induce**
122 **less damage through trampling and eating during winters (Kumpula, Stark & Holand 2011) and,**
123 **therefore, we define local grazing pressure based on the intensity of summer grazing.**

124
125 Study plots within three different grazing intensities were selected based on the distance to the
126 pasture rotation fences. At both sites, eight **geologically and topographically homogenous** transects
127 were established **perpendicular to the reindeer fences** 100 m apart from each other in the year 2000
128 (Olofsson *et al.* 2004). **Within each transect, plots were placed** approximately 10 m from the fence

129 on the autumn-spring range to a lightly grazed zone (LG) and, on the summer range, 10 m from
130 the fence to a heavily grazed zone (HG) and 100 m from the fence on a moderately grazed zone
131 (MG) (Oksanen 1978; Olofsson *et al.* 2004). One plot was set to each grazing zone along the eight
132 transects yielding a total of 24 study plots at both study sites. In Raisduoddar, vascular vegetation
133 composed of *Betula nana*, *Empetrum nigrum* ssp. *hermaphroditum*, *Phyllodoce caerulea*,
134 *Vaccinium vitis-idaea*, *V. myrtillus* and *V. uliginosum* under light grazing, *Deschampsia cespitosa*,
135 *D. flexuosa*, *Poa alpina*, *Phleum alpinum*, *Juncus trifidus*, *Carex* spp. (including *C. lachenalii*, *C.*
136 *canescens*, *C. bigelowii* and *C. nigra*), *Bistorta vivipara*, *Rumex acetosa* and *Cerastium fontanum*
137 under heavy grazing, and *Carex bigelowii*, *Festuca ovina*, *F. vivipara* and *E. hermaphroditum*
138 under moderate grazing. Under light grazing, the dominant bryophytes were *Pleurozium schreberi*,
139 *Hylocomium splendens* and *Dicranum* sp., and under heavy and moderate grazing were mostly
140 bryophytes *Dicranum* and *Polytrichum* species. In Čearro, vegetation under both heavy and
141 moderate grazing was dominated by the deciduous shrub *B. nana*. The ground layer composed of
142 the lichens *Cladonia mitis*, *C. gracilis*, *C. rangifera*, *C. arbuscula*, *C. stellaris*, *Cetraria islandica*
143 and *Flavocetraria nivalis* under light grazing and of the bryophytes from the genera *Dicranum* and
144 *Polytrichum* under moderate grazing. Graminoids *Carex bigelowii*, *Festuca ovina*, *F. vivipara*, *B.*
145 *nana* and bryophytes from the genera *Polytrichum* and *Pohlia* dominated under heavy grazing.



146 **Fig. 1** a) The study sites are located in northern Norway between the coastal summer grazing ranges
 147 (red) and the inland autumn–spring and winter ranges of reindeer. Both b) Raisduoddar (69°31'29
 148 N, 21°19'16 E; altitude 430–570 m asl) and c) Čearro (69°43'23 N, 21°37'45 E; altitude 540–570
 149 m asl) are bisected by pasture rotation fences built in 1960s. These separate the graminoid-
 150 dominated, heavily grazed summer range (on the left) and the shrub-dominated, lightly grazed
 151 winter range (on the right). As reindeer graze in particular next to the fence, moderate grazing
 152 intensity was defined 100 m away from the fence on the summer range.

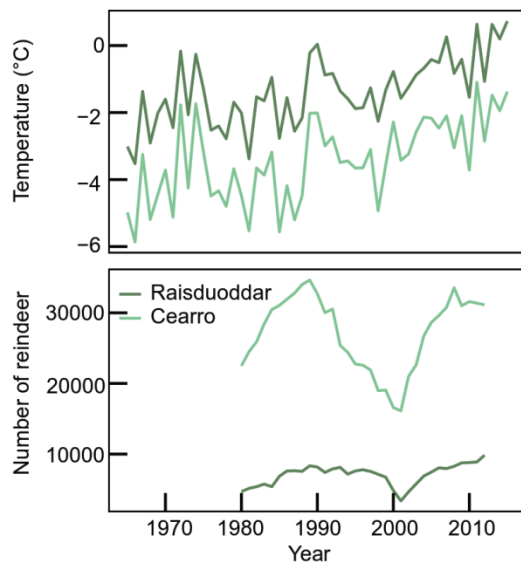
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154 Recent trends in temperature and reindeer numbers

155 At the study sites, the mean annual temperatures have increased quite dramatically over the last 50
 156 years, at a rate of almost 1 degree per decade (Fig. 2a). In Čearro, the temperature was
 157 approximately 1 °C warmer in 2014 than in 2000, whereas in Raisduoddar, the temperature
 158 difference between the sampling occasions was more than 1.5 °C. Concurrent with the overall
 159 increasing trend in Norwegian reindeer densities over the last century, the reindeer densities on the
 160 studied herding districts had increased between the years 2000 and 2014 (Fig. 2b). Reindeer
 161 population densities showed a peak in the 1980s followed by a population collapse around the year

162 2000 due to changed governmental subsidies and harsh overwintering conditions (Næss & Bårdsen
163 2013). Since then, reindeer numbers have again increased and the relative increase has been higher
164 in Raisduoddar compared to Čearro.

165



166 **Fig. 2.** Trends in a) mean annual air temperature and b) winter reindeer numbers in the reindeer
167 herding district of Čohkolat (Raisduoddar) and in the herding zone of Karasjok vest (Čearro). At
168 both sites, temperatures have increased during recent decades and there has been an increase in
169 reindeer numbers between 2000 and 2014. The reindeer data and the gridded temperature data for
170 the locations are provided by the Norwegian Agriculture Agency (Landbruksdirektoratet) and the
171 Norwegian Meteorological Institute.

172

173 Quantification of reindeer activity

174 Reindeer activity within each grazing intensity was monitored with trampling indicators (Bayfield
175 1971; Olofsson *et al.* 2004). We attached a 5-cm-long iron wire to a nail and pushed the nail down
176 into the soil with the iron wire standing straight up. If trampled, the iron wire would bend. At the

177 beginning of August 2014, we placed twenty-five trampling indicators under each grazing zone
178 along five transects at both sites and recorded the number of trampled indicators in July 2015.

179

180 Ecosystem C stocks

181 We analysed ecosystem C stocks in 2014 on the three different grazing zones and compared these
182 results with measurements conducted 14 years earlier. The exact locations of the study plots and
183 transects used in 2000 could no longer be found; therefore, new plots of same size were established
184 on the basis of field notes and site maps and we estimate their locations to be within 10–20 m of
185 the original study plots. We selected 50 × 50 cm study plots representative of the surrounding
186 vegetation and harvested the aboveground vascular plant biomass during the peak growing season
187 (July 18th – 22nd, 2014) and immediately sorted it into growth forms. Bryophyte, lichen and litter
188 biomass was collected with two intact vegetation-soil cores (Ø 11.95 cm) from which all biomass
189 above 2 mm was harvested in the laboratory. We collected soil C stocks with 5–10 soil cores (Ø
190 2.9 cm) beneath the litter layer until the corer hit large stones and sorted the sample into mineral
191 and organic soil layers in the field. This procedure will not give a thorough estimation of mineral
192 soil C stocks. However, large stones are likely to be found at similar depth within transects and,
193 therefore, this procedure can be assumed to give an estimate of grazer-induced changes in mineral
194 soil. Samples from the organic and mineral soil layers were combined to form composite samples
195 per plot that were sieved (2 mm mesh) in the laboratory. We obtained a composite sample of
196 vascular belowground biomass from the material that did not pass through the sieve and washed
197 this from soil particles above a thinner sieve. All soil and biomass samples were oven-dried (60
198 °C, 72 h) and subsequently weighed, milled (25 revs s⁻¹ for 20 s, Retsch MM301 mill) and analysed
199 for C and N concentrations using a CHNS–O Elemental analyser (EA1110, CE Instruments).

200
201 There were some differences in the procedure used to collect samples between the years 2000 and
202 2014 (Olofsson *et al.* 2004). In 2000, only the top 5 cm of the organic soil layer was included in
203 the analyses, thus underestimating organic soil C stocks and vascular belowground biomass in
204 approximately 17% of the soil cores in Raisduoddar and 1% of the soil cores in Čearro (estimation
205 based from the percentage of soil cores deeper than 5 cm in 2014). This method also excluded the
206 soil and vascular belowground C stocks in the mineral soil layer that were now analysed for the
207 first time. Moreover, in 2000, only the visible litter from the surface was collected, whereas in
208 2014, also bryophyte necromass (i.e., dead bases of bryophytes) was included. Due to these
209 differences in sampling, we compare changes between the years 2000 and 2014 only for
210 aboveground vegetation and organic soil and present a new estimate of total ecosystem C based on
211 the data from 2014. In this paper, we present two different values for organic soil C stocks: the
212 uncorrected organic soil C stocks and a standardized organic soil C stock in which the soil dry
213 weight is recalculated to represent only top 5 cm (if soil layer depth above 5 cm: standardized dw
214 = measured dw / measured soil layer thickness × 5 cm). We consider that this correction improves
215 our estimation of the temporal change in organic soil C.

216
217 Soil parameters
218 As grazing intensity is known to influence the soil physical properties, microclimate and nutrient
219 availability (Olofsson *et al.* 2004), we assessed soil moisture, organic matter content, C:N ratio,
220 bulk density, soil temperature and nutrient availability under the grazing intensities in 2014. Soil
221 temperature and nutrient availability measurements were conducted only in Raisduoddar, because
222 logistic reasons prevented the continuous measurements in Čearro. We collected soil samples on

223 three sampling dates at Raisduoddar (June 11th, June 25th and July 19th) and once at Čearro (July
224 23rd; see protocol in the previous paragraph) and analysed these for soil moisture (dried at 105 °C,
225 12 h) and organic matter content (loss on ignition at 475 °C, 4 h). The bulk density was counted by
226 dividing the dry weight of the sieved sample by the volume of corers. Soil ammonium (NH₄⁺-N)
227 was extracted with 0.5 M K₂SO₄ from the sieved organic soil samples and consequently, the NH₄⁺-
228 N concentrations were analyzed colorimetrically (SFS 3032, Shimadzu UV-1700
229 spectrophotometer). Soil temperature (at a depth of approximately 5 cm) was recorded with
230 temperature data loggers (n = 4, EasyLog EL-USB-1, Lascar Electronics) with one-hour intervals
231 during the growing season of 2014 in Raisduoddar.

232

233 Statistical analyses

234 To test for differences in the ecosystem C stocks and **organic** soil parameters between the years
235 2000 and 2014, we used a mixed-effects model separately for each site (Pinheiro *et al.* 2014). Year
236 and grazing intensity were set as fixed factors and plots within transects were treated as repeated
237 factors. The analysis was followed by **Bonferronis** post hoc test for pairwise comparisons of
238 grazing intensities. The **trampling intensity, mineral soil parameters and the more detailed C stock**
239 **data from 2014 were tested with a one-way ANOVA separately for each side with grazing intensity**
240 **as a fixed factor and transect as a random factor. Also this test was followed by a Bonferronis post**
241 **hoc test.** If the assumption of a normal distribution was not met, we used logarithmic or square root
242 transformations on the variables. All analyses were conducted with R software for statistical
243 computing (**version 3.0.1, R Core Team 2012**).

244 **Results**

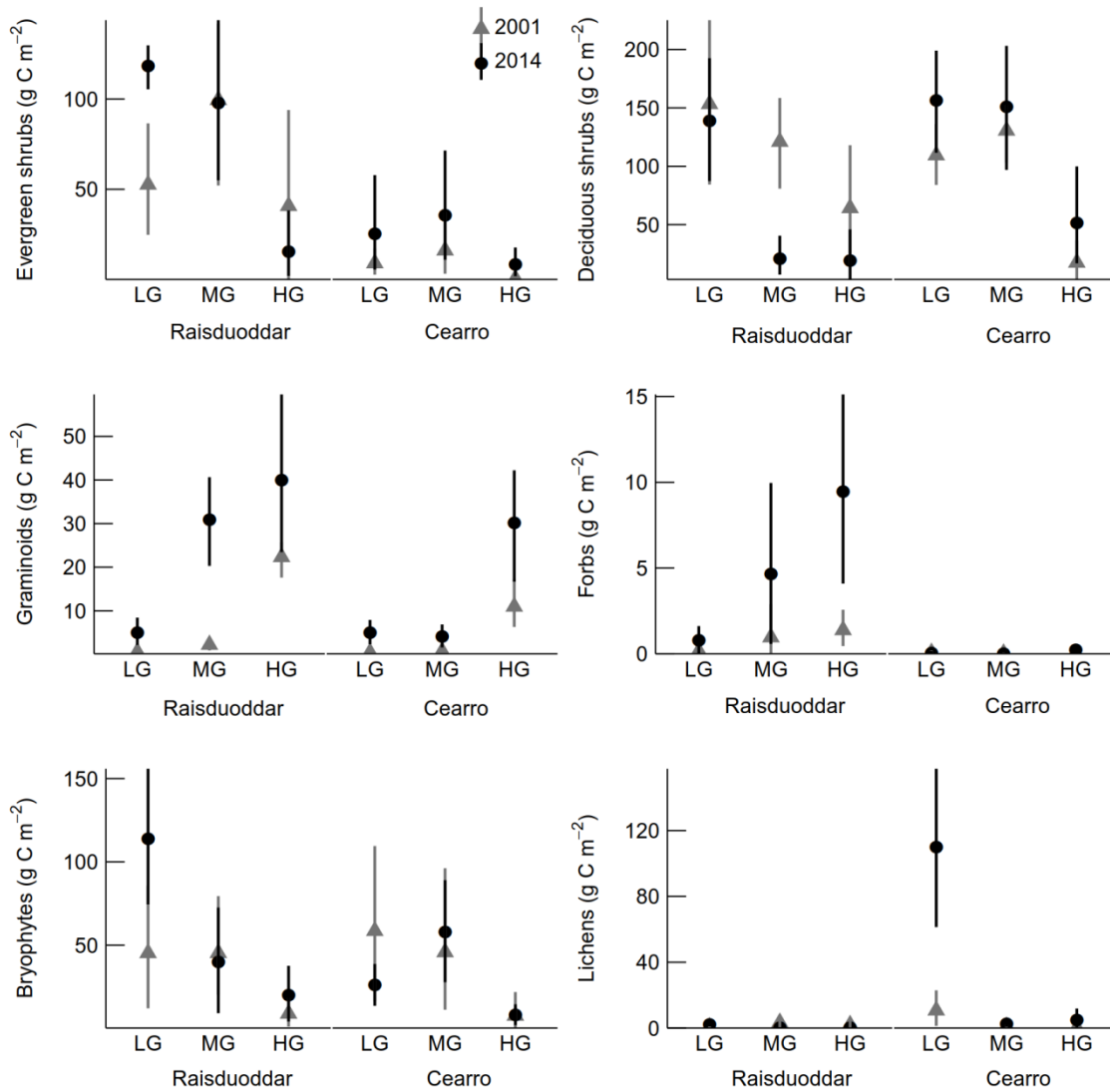
245 Reindeer activity in 2014

246 In both Raisduoddar and Čearro, the trampling intensity was 10 times lower under light than heavy
247 grazing in 2014 (Fig. S3; $F_2 = 256$, $P < 0.001$; $F_2 = 16.9$, $P = 0.002$, respectively). Almost all
248 trampling indicators were trampled on in the heavily grazed areas at both sites and in the
249 moderately grazed area in Raisduoddar. This resulted in no difference in the measured reindeer
250 activity between the moderately and heavily grazed area in Raisduoddar, and thus indicates
251 increased the trampling intensity particularly under moderate grazing. However, true differences
252 between the grazing intensities may be stronger than recorded due to the saturation of trampling
253 indicators.

254

255 Changes in C stocks between 2000 and 2014

256 Overall, the main patterns in vegetation C stocks did not change from the year 2000 to 2014: At
257 both sites, heavy grazing had decreased the C stocks in deciduous and evergreen shrubs, bryophytes
258 and lichens and increased the C stocks in graminoids compared to light grazing (Fig. 3; Table 2; as
259 in Olofsson *et al.* 2004). During the 14 years, the C stocks in evergreen shrubs, graminoids and
260 lichen had increased in Čearro independent on grazing intensity. In Raisduoddar, the C stocks in
261 graminoids, forbs and bryophytes had increased and the C stocks in deciduous shrubs had
262 decreased. The only grazing-dependent changes took place in Raisduoddar, where both lichen and
263 bryophyte C increased under light grazing and graminoid C increased the most under moderate
264 grazing. The abundance of plant growth forms and an ordination diagram of the impact of grazing
265 on plant species composition can be found in Figures S1 and S2 in the Supplementary Information
266 files.



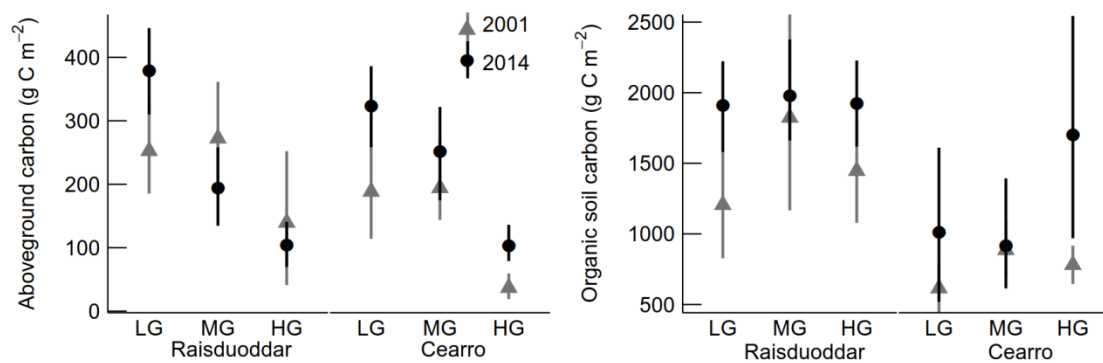
267 **Fig. 3.** Aboveground plant C stocks under three grazing intensities in Raisduoddar and Čearro (LG
 268 = light grazing, MG = moderate grazing, HG = heavy grazing) in 2000 and 2014 ($n = 8$). The results
 269 from 2000 are published in Olofsson *et al.* 2004. Values are the mean \pm 95% confidence interval
 270 based on a bootstrap.

271

272 The changes in growth forms resulted in a general increase in aboveground vegetative C stocks in
 273 Čearro, whereas in Raisduoddar there was no temporal trend in aboveground vegetative C between
 274 the years (Fig. 4; Table 2). Common to both sites was, however, that the change in time did not
 275 vary among the grazing intensities. The C stocks in the organic soil layer show an increasing trend
 276 over the past 14 years, but there was no grazing \times year interaction at either of the sites (Fig. 4;
 277 Table 2). The sum of aboveground vegetative and organic soil C stocks indicated a general increase
 278 in ecosystem C at both sites independent of the grazing intensity.

279

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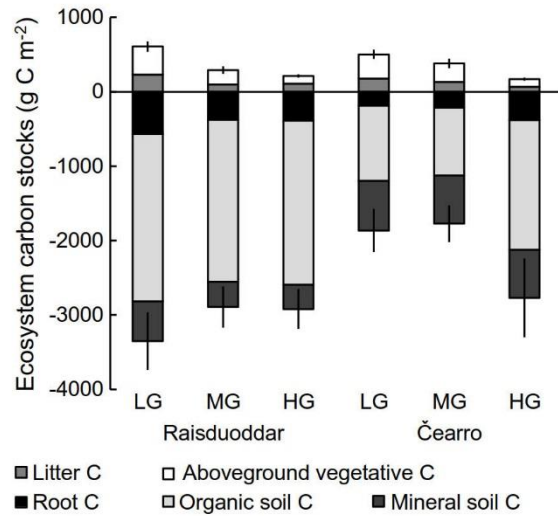


281 **Fig. 4. Aboveground and organic soil C stocks in 2000 and 2014 under three grazing intensities in**
 282 **Raisduoddar and Čearro (LG = light grazing, MG = moderate grazing, HG = heavy grazing; n =**
 283 **8). Values are means \pm 95% confidence interval based on a bootstrap. The aboveground C stocks**
 284 **represent the sum of vascular aboveground C and cryptogam C. The organic soil C stocks in 2014**
 285 **are standardized to represent only the top 5 cm of the soil to improve comparison with the data**
 286 **from 2000.**

287

288 Ecosystem C stocks in 2014

289 The new estimate of ecosystem C storage that comprised C stocks in the entire organic soil layer
290 and the uppermost mineral soil horizon, indicated that the majority of ecosystem C is stored in soils
291 (representing about 64–85% of total ecosystem C; Fig. 5). There was no difference among the
292 grazing intensities in the total ecosystem C at either of the sites. Yet, the distribution of C varied
293 with grazing. Litter C stocks were higher under light grazing at both sites (Fig. 5; Table 4), where
294 also aboveground vegetative C stocks were the highest. At both sites, heavy grazing had increased
295 the proportion of root biomass in relation to shoot biomass and decreased the above:belowground
296 C ratio (Table 4). In Čearro, organic soil and vascular belowground C stocks were higher under
297 heavy grazing than under light and moderate grazing. In Raisduoddar, grazing did not alter the C
298 stocks in organic soil or vascular belowground biomass. At both sites, the C stocks in mineral soil,
299 analysed now for the first time, did not differ among grazing intensities.



300 **Fig. 5.** Total ecosystem C (mean g C m⁻²) under light grazing (LG), moderate grazing (MG) and
 301 heavy grazing (HG) in Raisduoddar and Čearro in 2014. Positive values indicate aboveground C
 302 stocks and negative values indicate belowground C stocks. Error bars denote standard error of
 303 aboveground and belowground stocks. n = 8.

304

305 Soil parameters

306 The organic soil layer thickness was higher under heavy grazing than under light grazing in Čearro
 307 (F = 9.79, P = 0.002; Table S1; Fig. S3). Soil moisture, organic matter content, C concentration
 308 and C:N ratio in the soil organic layer were lower under heavy than moderate and light grazing in
 309 Čearro. In Raisduoddar, there was no difference in organic soil layer thickness between the grazing
 310 intensities. Yet, the soil C:N ratio was decreased by heavy grazing compared to light grazing in
 311 Raisduoddar, and did not differ between heavy and moderate grazing. At both sites, moisture and
 312 organic matter content in the mineral soil layer increased with grazing intensity being the highest
 313 under the graminoid-dominated areas (e.g. heavy and moderate grazing in Raisduoddar and heavy
 314 grazing in Čearro; Fig. S4, Table S2). **Average soil temperature and soil ammonium (NH₄⁺-N)**
 315 **concentrations per kg SOM increased with grazing intensity in Raisduoddar (F = 12.59, P = 0.002**

316 and $F = 13.26$, $P = 0.001$, respectively; Table S1; Fig. S3). On area basis, NH_4^+ -N concentration
317 was higher in the heavily and moderately grazed areas than in the lightly grazed area only in 2014
318 (Grazing \times Year: $F = 5.51$, $P = 0.012$).

319 **Discussion**

320 1) Main findings

321 In this study, we assessed recent changes in vegetative and organic soil C stocks and obtained an
322 estimate of grazer control on total ecosystem C. In contrast to our hypothesis, the vegetative
323 aboveground C stocks had changed similarly during the last 14 years under both heavy and light
324 grazing. The most evident changes were found under moderate grazing intensity in Raisduoddar,
325 where trampling intensity and soil nutrient concentrations were increased and graminoids had
326 become the most dominant plant functional type. The reindeer-induced “*grassification*”, whether
327 established in recent years or decades earlier, decreased aboveground C stock at both sites, which
328 was in line with our hypothesis. Still, the consequences of grazing to belowground only partially
329 supported our hypothesis as grazing did not alter the organic soil C stocks in Raisduoddar. Yet in
330 Čearro the soil C stocks were higher under the graminoid-dominated heavily grazed area compared
331 to the shrub dominated lightly and moderately grazed areas. These results demonstrate that despite
332 the negative effect of grazers on aboveground C (Tanentzap & Coomes 2012), grazing-induced
333 grassification in the tundra can increase or have no effects on soil C sequestration, possibly through
334 higher vegetative investment to belowground resources. These belowground consequences indicate
335 that grazing has the potential to alter C storage in arctic ecosystems, and therefore, the abundance
336 of grazers could also affect the climate change induced changes in the carbon cycle.

337

338 2) Grazing x Year –interactions 1): graminoid abundance

339 Our results strongly suggest that a regularly occurring pulse of heavy grazing may alter vegetation
340 composition, soil abiotic environment and potentially even the capacity of the ecosystem to
341 sequester C. We found that in Raisduoddar, the “*grassification*” of the vegetation had advanced to

342 the moderately grazed area, which was still dominated by shrubs 14 years earlier (Olofsson *et al.*
343 2004). Now, the vegetation composition, the soil nutrient concentrations and soil temperatures
344 under moderate grazing closely resembled those under heavy grazing. In addition, bryophyte and
345 lichen C stocks were lower under both moderate and heavy grazing compared to light grazing in
346 2014. These grazing-induced changes occurred parallel to higher reindeer numbers and an increase
347 in trampling intensity – and thus, could reflect the capacity of tundra ecosystem to adjust to new
348 grazing pressures – yet the fast pace could also have been accelerated by the warmer temperatures.
349 Noteworthy, in Čearro, where reindeer numbers increased less and the change in trampling
350 intensity was similar among grazing intensities, no advancement of graminoids was evidenced.
351 These results support the idea that grazer-driven vegetation transitions are tightly linked to the
352 grazing intensity – although, the transition could take several years to take place (Olofsson *et al.*
353 2004).

354

355 3) Summary and the constraints of the yearly comparison

356 Despite the changes in reindeer numbers and the warming trend, it is remarkable that we found
357 very few evidence of grazing-dependent changes in vegetation. This could be linked to the changes
358 in the sampling techniques between the years and a potential shift in the exact locations of the study
359 plots within the landscape. In Čearro, the aboveground C stocks increased between the years
360 regardless of grazing, concurrent with other observations of recent changes in tundra. In contrast,
361 in Raisduoddar, aboveground C stocks were lower in 2014 than in 2000, which could be linked to
362 the expanded range of graminoids that generally store less carbon than shrubs. At both sites, the
363 organic soil C stocks were higher in 2014 than in 2000 irrespective of grazing, indicating an
364 accumulation of C into the system. Although the increase in soil C is within the magnitude of
365 previous estimates from dry tundra sites (Klaminder, Yoo & Giesler 2009), we warrant that the

366 method should rather be used to address whether the change in time varied in response to grazing
367 intensity.

368

369 4) Explanation 1: Soil C responses to grazing due to Plant Functional Types

370 We propose that the divergent responses of organic soil C stocks to grazing at the different sites
371 derive from differing dominant plant functional types under light grazing. Noteworthy, the organic
372 soil C stocks under heavy grazing were of similar magnitude in the two sites, whereas these differed
373 between the sites under light grazing: The organic soil C stocks were lower in the *B. nana*-
374 dominated Čearro compared to the C stocks in Raisduoddar with mixed vegetation of *E.*
375 *hermaphroditum* and *B. nana*. This difference is consistent with the observations from subarctic
376 Sweden, where soil respiration was higher and organic soil C stocks lower under *B. nana* shrub
377 tundra (C stock $\sim 3 \text{ kg m}^{-2}$) than under a heath with a mixed abundance of *B. nana* and *E.*
378 *hermaphroditum* (4.5 kg m^{-2} ; Parker *et al.* 2015). The difference was proposed to result from the
379 type of mycorrhizal symbiosis associated with the dominant shrub; the ectomycorrhizal *B. nana*
380 may enhance microbial activity and promote high rates of soil C turnover (Clemmensen *et al.* 2013,
381 2015; Parker *et al.* 2015), whereas the ericoid mycorrhizal *E. hermaphroditum* may promote soil
382 C sequestration through allelopathic effects on microbial activity and through the recalcitrance of
383 mycorrhizal hyphae to microbial decomposition (Nilsson & Wardle 2005; Clemmensen *et al.* 2013,
384 2015). Although differences in climatic and topographic factors also affect plant productivity and
385 microbial activity on our study sites, it is possible that the dominant shrub species under light
386 grazing could explain the differences in organic soil C stocks between the sites. Soil C sequestration
387 could be higher under graminoid-dominated heavily grazed compared to *B. nana* -dominated
388 lightly grazed tundra, whereas graminoid-dominated tundra may lie, based on its ability to
389 accumulate soil C, at the same level as the mixed *Empetrum* and *B. nana* heath. The difference

390 found in Čearro could also be linked to higher allocation of graminoid biomass to belowground,
391 which could have been stimulated by grazing (Gao *et al.* 2007; Hafner *et al.* 2012). As root litter
392 is relatively recalcitrant to microbial decomposition, this could enhance soil C sequestration
393 (Rasse, Rumpel & Dignac 2005; De Deyn *et al.* 2008; Freschet *et al.* 2013).

394

395 5) Explanation 2: Direct effect of grazing / soil-mediated feedbacks...

396 The grazing-induced change in aboveground vegetation was coupled with considerable changes in
397 the soil environment that contribute to process rates in soils – and potentially, to the magnitude of
398 soil C stocks. At both sites, heavy grazing increased soil nutrient availability, soil temperature and
399 led to more compacted soils, as documented earlier at the sites (Olofsson *et al.* 2001, 2004; Stark
400 & Väisänen 2014), in other tundra areas (e.g. Stark *et al.* 2002; Stark, Julkunen-Tiitto & Kumpula
401 2007) and in other biomes worldwide (Milchunas & Lauenroth 1993; McNaughton 1997). Also in
402 line with previous observations from other sites (e.g. Stark, Männistö & Smolander 2010), heavy
403 grazing decreased organic soil moisture in Čearro. Lower moisture, warmer temperature and
404 increased nutrient availability are often found to induce higher microbial activity for the
405 decomposition of soil C (Kim *et al.* 2014); xxx). However, previous evidence from Raisduoddar
406 indicates that this may not be straight-forwardly the case: Soil microbial communities were found
407 to be more cold-adapted under low than high grazing intensity (Stark *et al.* 2015) and soil microbial
408 activities insensitive to variations in nitrogen availability connected to reindeer migration (Stark &
409 Väisänen 2014). In the present paper, we assessed the effect of grazing also on the mineral soil
410 layer, which, to our knowledge, has not been reported before. In direct contrast to the organic soil
411 layer, mineral soil moisture and OM % were higher under heavy than light grazing. Yet, the
412 different grazing intensities stored similar amounts of C in the mineral soil layer, which is in
413 contrast to observations of higher mineral soil C storage under graminoid- compared to shrub-

414 dominated tundra (Johnson *et al.* 2011; Petrenko *et al.* 2016). As we found similar responses in the
415 mineral and organic soil properties to grazing at both sites whereas the responses of soil C we
416 contrasting, we suggest that other mechanisms, such as vegetation-driven differences could be
417 more likely.

418

419 6) Summarising results, part 1: Differences among grazing intensities

420 The results of this study strongly suggest that although grazers reduce plant carbon stocks
421 (Tanentzap & Coomes 2012), this reduction is not reflected as lower accumulation of C to soils. In
422 contrast, heavy grazing induced a relocation of vegetative biomass to belowground and in the
423 longer run, had either a neutral or positive effect on soil C storage. The consequences belowground
424 are of particular interest, since large parts of tundra C are stored in soils and these are projected to
425 be sensitive to climate change. In Raisduoddar, where soil C stocks were of equal magnitude among
426 the grazing intensities, individual mechanisms behind ecosystem C cycling could still be different
427 as indicated by previous studies: the growing seasonal CO₂ uptake has been documented to be
428 smaller and soil respiration higher under heavy compared to light grazing (Väisänen *et al.* 2014,
429 2015). The results from Čearro, on the other hand, provide support for the theory that vegetation
430 transition from dwarf shrubs to graminoid promotes tundra carbon storage (also referred to as the
431 steppe-tundra transition by Zimov *et al.* 2009). This study, however, adds that this is not always
432 the case, and suggests that the different responses between the study sites could be explained by
433 the attributes of shrubs under light grazing. We suggest that the transition from a deciduous shrub
434 tundra to a graminoid tundra due to increasing grazing intensity would increase ecosystem C,
435 whereas the transition from an ericoid shrub heath to graminoid-dominated vegetation would have
436 no effect on the ecosystem C. Still, we warrant that these conclusions are limited to certain

437 ecosystem types and cannot be extrapolated to permafrost systems or wetlands where methane also
438 plays a role.

439
440 7) Summarising results, part 2: Expected changes in C stocks (This discussion was asked for by
441 the associate editor)

442 The question remains to which extent changes in ecosystem C stocks in response to climate
443 warming could depend on grazing intensity. Variety of evidence has suggested that deciduous
444 shrubs will increase their range and biomass in high latitude ecosystems (Myers-Smith *et al.* 2011,
445 2015b; Elmendorf *et al.* 2012a) and that grazing could negate this expansion of shrubs (Post &
446 Pedersen 2008; Olofsson *et al.* 2009; Kaarlejärvi, Hoset & Olofsson 2015). In this study we
447 however, found almost no differences between the heavy and lightly grazed areas in the recent
448 changes in vegetation and the sole grazing-dependent changes occurred in graminoids, bryophytes
449 and lichen – and only on the more fertile site, Raisduoddar. The negative effect of grazers on lichen
450 is the sole generalizable effect documented from grazing (Bernes *et al.* 2015), and also elsewhere
451 the increase in graminoids has been linked to negative effects on the ground layer (xx). Yet, grazing
452 by large herbivores does not always promote the establishment of graminoids and, recently,
453 evidence of grazing-induced replacement of deciduous by evergreen shrubs has been brought up
454 (Zamin & Grogan 2013b; Vowles *et al.* 2017a; b). In general, there still remains a lack of
455 understanding, what to expect with warmer temperatures on the grazed areas. As grazers are found
456 throughout the circumpolar tundra, this knowledge would be needed.

457 **Author's Contributions**

458 SS, JO and LO designed the experiment and conducted the analyses in 2000. HY and SS carried
459 out sampling and data-analysis in 2014. HY and SS led the writing of the manuscript to which all
460 authors gave significant contributions and approved the final version.

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646 **SUPPORTING INFORMATION**

647 Additional supporting information may be found in the online version of this article:

648 [Figure S1 Abundance of plant growth forms in 2014.](#)

649 [Figure S2 Plant species composition in 2014.](#)

650 [Figure S3 Grazing effects on organic soil parameters in 2000 and 2014](#)

651 [Table S1 ANOVA results from the changes in organic soil parameters 2000–2014.](#)

652 [Figure S4 Grazing effect on mineral soil in 2014](#)

653 [Table S2 ANOVA results from the effect of grazing intensity on mineral soil in 2014](#)

654 **Tables**

655 **Table 1.** The effects of year, grazing and their interaction ($G \times Y$) on C stocks in Raisduoddar and Čearro. Values are derived from
 656 repeated measures ANOVA, and those differences that were statistically significant ($P < 0.05$) in the Bonferroni pair-wise comparison
 657 are indicated in bold. The direction of the change between the years 2000 and 2014 is indicated by an arrow. In this comparison, the
 658 organic soil C stocks were standardized to represent only the top 5 cm of soil.

	Grazing		Raisduoddar				Grazing		Čearro			
	F	P	F	P	F	P	F	P	F	P	F	P
Vegetative aboveground C	12.90	0.001b	0.09	0.769	2.31	0.124	27.27	<0.001b	15.19	0.001 ↑	0.91	0.418
Evergreen C	6.57	0.010b	0.72	0.40	3.29	0.057	10.29	0.002b	10.85	0.004 ↑	0.86	0.436
Deciduous C	10.05	0.002c	7.89	0.010 ↓	2.82	0.082	16.70	<0.001b	4.10	0.056	0.21	0.811
Graminoid C	41.31	<0.001e	41.27	<0.001 ↑	6.08	0.008 *	28.47	<0.001b	21.96	<0.001 ↑	1.63	0.219
Forb C	8.226	0.004b	11.03	0.003 ↑	0.59	0.57	0.79	0.47	2.86	0.106	3.08	0.067
Bryophyte C	7.43	0.006c	4.67	0.042 ↑	3.48	0.049 ^	4.99	0.023d	0.33	0.574	0.372	0.694
Lichen C	2.21	0.146	0.47	0.502	4.21	0.029 `	11.06	0.001a	32.52	<0.001 ↑	0.185	0.833
Organic soil C	1.05	0.374	7.19	0.014 ↑	0.72	0.499	2.38	0.129	5.21	0.033 ↑	1.88	0.177
Aboveground vegetation + organic soil C	0.84	0.451	7.06	0.015 ↑	1.23	0.313	0.45	0.646	8.21	0.009 ↑	1.86	0.181

a) HG and MG differ from LG; b) HG differs from LG and MG; c) HG differs from LG; d) HG differs from MG; e) all differ from each other

* HG differs from both LG and MG in 2001, HG and MG differ from LG in 2014; ^ HG and MG differ from LG in 2014; ` HG differs from LG in 2014

659 **Table 2.** The ANOVA results of grazing effects on ecosystem C stocks in Raisduoddar and Čearro
 660 in 2014. Significant differences ($P < 0.05$) in the Bonferroni pair-wise comparison among grazing
 661 intensities are indicated in bold. Herein, the total ecosystem C stock includes C in above and
 662 belowground vegetation, organic and mineral soil layers and litter.

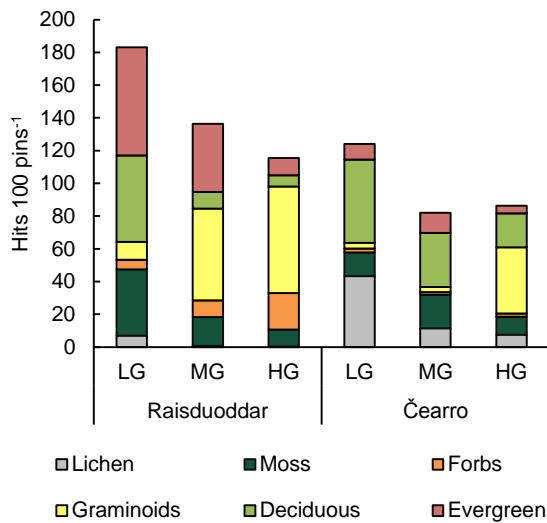
	Raisduoddar		Čearro	
	F	P	F	P
Litter C	4.08	0.040*	5.46	0.018"
Vascular belowground C	0.05	0.956	3.73	0.050"
Organic soil C	0.01	0.987	5.21	0.020^
Mineral soil C	2.61	0.109	0.12	0.884
Total ecosystem C	0.78	0.48	2.47	0.12
Root:shoot C ratio	7.76	0.005"	7.46	0.006^
Above:belowground C ratio	7.16	0.007*	10.94	0.001"

* HG and MG differ from LG; ^ HG differs from MG and LG; " HG differs from LG

664 Supporting information, Yläne *et al.* “Consequences of grazer-induced vegetation
 665 transitions on ecosystem carbon storage in the tundra”

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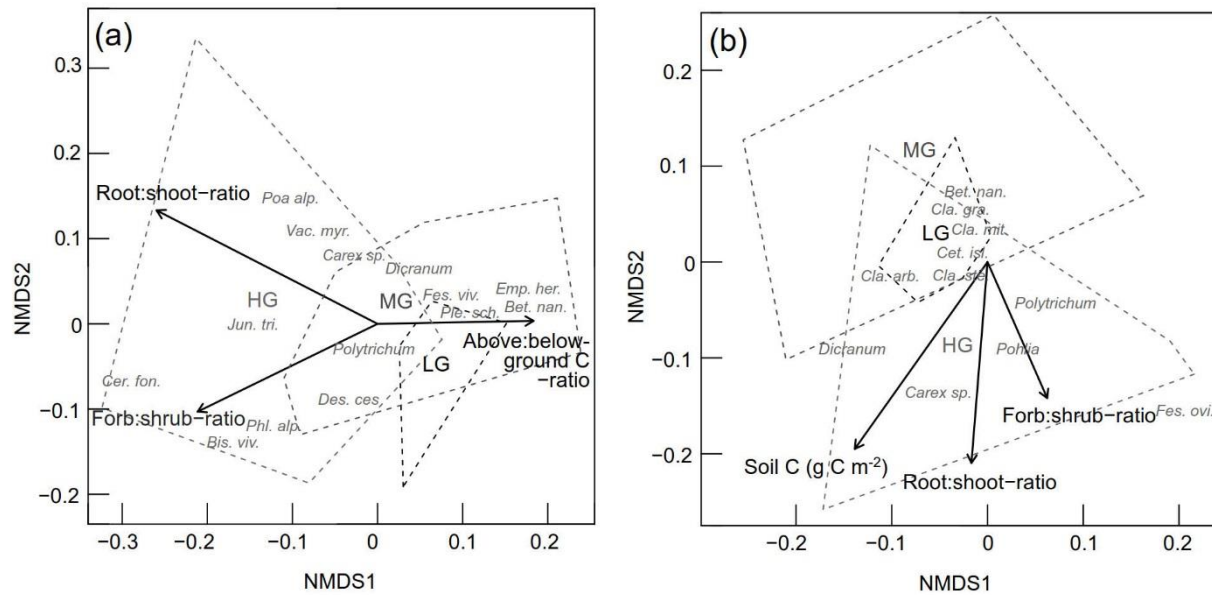
667 **Figure S1. Abundance of plant growth forms in 2014**



668 **Fig. S1.** The abundance of plant growth forms under the three grazing intensities in Raisduoddar
 669 and Čearro in 2014. In Raisduoddar, under light grazing (LG), the vascular vegetation was
 670 dominated by evergreen and deciduous shrubs. Beneath these, bryophytes formed a uniform layer
 671 with an average thickness of 3 cm. Under heavy grazing (HG), the vascular vegetation was
 672 dominated by graminoids with forbs being also abundant. Under moderate grazing (MG),
 673 graminoids were the dominant plant functional group, accompanied by patches of evergreen
 674 shrubs. Under both heavy and moderate grazing, the ground layer was patchy with bryophytes
 675 (thickness < 0.5 cm). In Čearro, the non-resinous deciduous shrub *B. nana* dominated under light
 676 and moderate grazing and accounted for 50–95% of the hits on vascular vegetation. Under light
 677 grazing, the ground layer was rich in lichens, whereas the ground layer under moderate grazing
 678 was dominated by mosses. Graminoids were the dominant functional group under heavy grazing,

679 where also *B. nana* and bryophytes occurred in patches. The abundance data presented in this figure
680 was measured as hits 40 pins⁻¹ during the peak growing season (July 18th – 22nd, 2014). All hits of
681 vascular vegetation were recorded at the species level, whereas only the first hit from the ground
682 layer (i.e., bryophytes and lichens) was recorded.

683 **Figure S2. Plant species composition in 2014**



684 **Fig. S2.** Two-dimensional NMDS ordination diagram of plant species composition in 2014 in a)
 685 Raisduoddar (N = 24; stress = 0.172) and b) Čearro (N = 24, stress = 0.170). For both sites, the
 686 point-intercept data of vegetation abundance (see methods in Fig. S1) were fitted to an ordination
 687 diagram by non-metric multidimensional scaling (NMDS) with the vegan package (Oksanen *et*
 688 *al.* 2015). We used Euclidean distance between study plots and incorporated the results from the
 689 C stocks into the figures. In the figure, gray polygons envelop plots within grazing intensities
 690 (HG = heavy grazing, MG = moderate grazing and LG = light grazing). The figure shows
 691 abbreviations for the following vascular species: *Betula nana*, *Empetrum nigrum* ssp.
 692 *hermaphroditum*, *Phyllodoce caerulea*, *Vaccinium myrtillus*, *Deschampsia cespitosa*, *Poa alpina*,
 693 *Phleum alpinum*, *Juncus trifidus*, *Festuca ovina*, *Festuca vivipara*, *Bistorta vivipara* and
 694 *Cerastium fontanum*. The abbreviated cryptogram species are: *Pleurozium schreberi*, *Cladonia*
 695 *mitis*, *Cladonia gracilis*, *Cladonia arbuscula*, *Cladonia stellaris* and *Cetraria islandica*. Fit of the
 696 parameters in Raisduoddar: Above:belowground C ratio $r^2 = 0.247$, $P = 0.05$; Root:shoot ratio: r^2
 697 $= 0.672$, $P < 0.001$; Forb:shrub ratio: $r^2 = 0.434$, $P = 0.007$ and in Čearro: Organic soil C stock:

698 $r^2 = 0.313, P = 0.022$; Root:shoot ratio: $r^2 = 0.426, P = 0.001$, Forb:shrub ratio: $r^2 = 0.236, P =$
699 0.061 .

700 **Table S1. ANOVA results from the changes in organic soil parameters**

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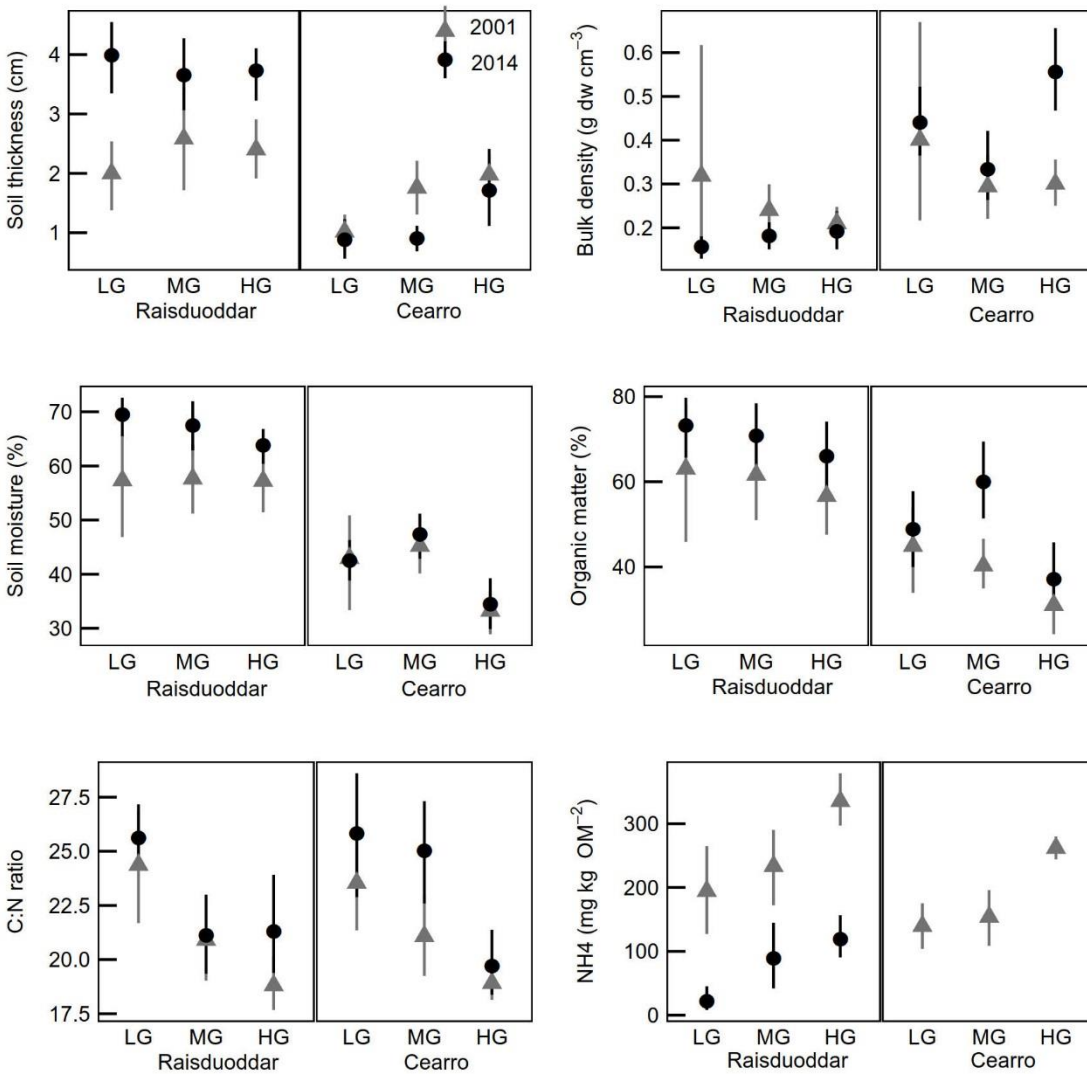
702 **Table S1.** The effects of grazing, year and their interaction ($G \times Y$) on the organic soil layer in Raisduoddar and Čearro. Values are
 703 derived from repeated measures ANOVA ($n = 8$). P values that remained significant ($P < 0.05$) with the Bonferroni correction are
 704 indicated in bold and the small letters denote the pairwise differences. Herein, we used the uncorrected values for soil parameters in 2014
 705 and, therefore, differences in sampling depth between the years may account for some of the variation between the years. Soil temperature
 706 and soil ammonium ($\text{NH}_4^+\text{-N}$) concentrations were recorded in 2014 only in Raisduoddar.

	Grazing		Raisduoddar Year		G × Y		Grazing		Čearro Year		G × Y	
	F	P	F	P	F	P	F	P	F	P	F	P
Thickness of organic soil layer (cm)	0.069	0.933	28.34	<0.001	1.00	0.385	9.79	0.002a	6.33	0.020	1.77	0.195
Bulk density of organic soil (g dw cm ⁻³)	0.21	0.810	3.50	0.075	0.34	0.716	2.11	0.158	8.80	0.007	2.07	0.151
Organic soil moisture (%)	0.42	0.662	13.11	0.002	0.38	0.691	12.70	0.001b	0.23	0.639	0.13	0.879
Soil organic matter content	0.73	0.500	3.99	0.059	0.00	0.996	13.29	0.001b	13.54	0.001	3.38	0.054
Organic soil C %	0.58	0.571	4.57	0.044	0.03	0.971	13.25	<0.001b	18.30	<0.001	2.99	0.072
Organic soil C:N ratio	13.31	<0.001c	2.50	0.129	0.65	0.53	14.09	<0.001b	7.63	0.012	1.15	0.335
$\text{NH}_4^+\text{-N}$ (mg kg OM ⁻¹)	13.26	0.001a	77.49	<0.001	1.06	0.366						
$\text{NH}_4^+\text{-N}$ (mg m ⁻²)	10.99	0.001	27.63	<0.001	5.51	0.012*						
Soil average temperature												

a) HG differs from LG; b) HG differs from LG and MG; c) HG and MG differ from LG; * in 2014, HG and MG differ from LG

707

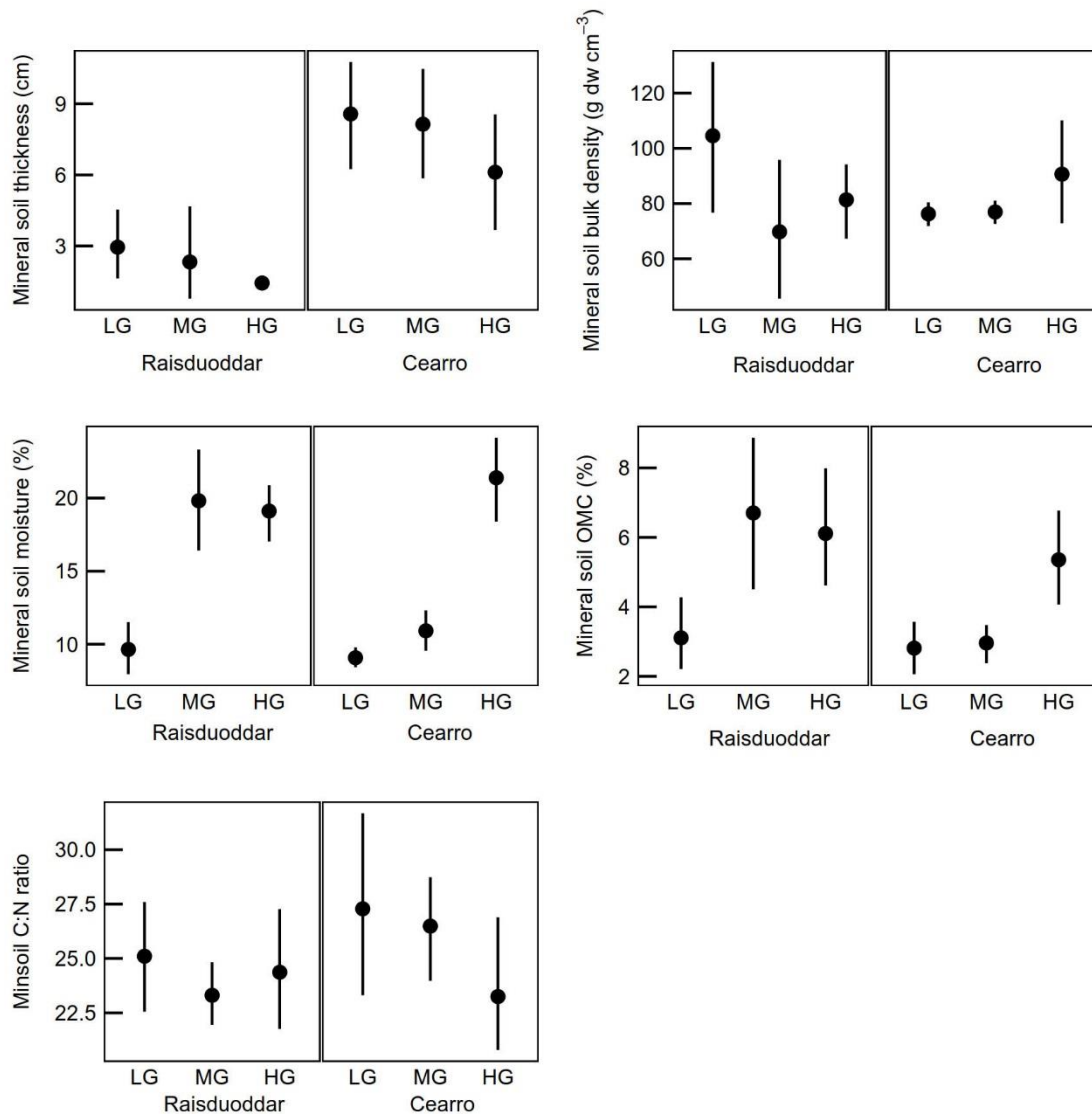
708 **Figure S3. Organic soil parameters under the different grazing intensities in 2000 and 2014**



709
 710 **Fig. S3. Organic soil parameters and the trampling intensity under the three grazing intensities in**
 711 **Raisduoddar and Čearro (LG = light grazing, MG = moderate grazing, HG = heavy grazing) in**
 712 **2000 and 2014 (n = 8). Values are the mean ± 95% confidence interval based on a bootstrap. In**
 713 **Raisduoddar, the depth of the organic layer, bulk density, soil moisture, organic matter content,**
 714 **and soil ammonium (NH₄⁺-N) concentrations represent averages of three sampling dates in 2014,**
 715 **whereas in Čearro, these were measured only once in 2014. Soil ammonium (NH₄⁺-N)**

716 concentrations and soil temperature over the growing season (average of hourly recordings during
717 June 24th – August 31st, 2014) were recorded in 2014 only in Raisduoddar. Trampling intensity is
718 presented as % of trampled indicators during August 2014 – July 2015 and August 2000 – August
719 2001. The data from 2000 is already published by Olofsson, Stark and Oksanen (2004).

720 **Figure S4. Grazing effects on mineral soil in Raisduoddar and Čearro in 2014**



721 **Fig. S4. Mineral soil parameters under the three grazing intensities in Raisduoddar and Čearro (LG**
 722 **= light grazing, MG = moderate grazing, HG = heavy grazing) in 2014 (n = 8). Values are the mean**
 723 **± 95% confidence interval based on a bootstrap.**

724 **Table S2. ANOVA results of grazing effect on mineral soil layer in Raisduoddar and Čearro.**

725

726 **Table S2.** The effects of grazing on mineral soil parameters in Raisduoddar and Čearro. Values are

727 derived from repeated measures ANOVA (n = 8). P values that remained significant ($P < 0.05$)

728 with the Bonferroni correction are indicated in bold and the small letters denote the pairwise

729 differences.

	Raisduoddar		Čearro	
	F	P	F	P
Thickness (cm)	0.92	0.421	1.51	0.256
Bulk density (g dw cm ⁻³)	2.98	0.083	1.74	0.212
Moisture (%)	14.20	<0.001a	36.2	<0.001b
OMC (%)	4.05	0.041c	5.50	0.017b
C:N ratio	0.40	0.675	2.14	0.155

a) HG and MG differ from LG; b) HG differs from LG and MG c) MG differs from LG