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1 **Long-term increase in aboveground carbon stocks following exclusion**  
2 **of grazers and forest establishment in an alpine ecosystem**

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16 **Short title:** Grazing, treelines and carbon

17 **Author contributions:** JDMS, VM & GA carried out fieldwork and designed the study with input from AM,  
18 JM and ØH. GA and AM set up the exclosures. VM analysed soil and vegetation samples. JDMS analysed  
19 the data with input from VM. All authors contributed with interpretation of data and patterns. JDMS  
20 wrote the manuscript with input from all co-authors.

21

## 22 **Abstract**

23 Ecosystem stores of carbon are a key component in the global carbon cycle. Many studies have  
24 examined the impact of climate change on ecosystem carbon storage, but few have investigated the  
25 impact of land-use change and herbivory. However, land-use change is a major aspect of  
26 environmental change, and livestock grazing is the most extensive land-use globally. In this study we  
27 combine a grazing exclosure experiment and a natural experiment to test the impact of grazer  
28 exclusion on vegetation dynamics and ecosystem carbon stores in the short-term (12 years  
29 exclosures), and the long-term (islands inaccessible to livestock), in a heavily grazed mountain region  
30 in Norway. Following long-term absence of sheep, birch forest was present. The grazing resistant  
31 grass *Nardus stricta*, dominated under long-term grazing, whilst the selected grass *Deschampsia*  
32 *flexuosa* and herb species dominated the vegetation layer in the long-term absence of sheep. The  
33 established birch forest led to vegetation carbon stocks being higher on the islands (0.56 kg C m<sup>-2</sup> on  
34 the islands compared to 0.18 kg C m<sup>-2</sup> where grazed) and no difference in soil carbon stocks. In the  
35 short-term exclusion of sheep there were minor differences in carbon stocks reflecting the longer-  
36 term changes. These results show that aboveground carbon stocks are higher in the long-term  
37 absence of sheep than in the continual presence of high sheep densities, associated with a  
38 vegetation state change between tundra and forest. The reduction of herbivore populations can  
39 facilitate forest establishment and increase aboveground carbon stocks, however the sequestration  
40 rate is low.

41 **Keywords:** Biomass, Tundra, Herbivory, Land-use, Livestock, Treeline

## 42 **Introduction**

43 In response to recent global warming, the search for methods to mitigate climate change through the  
44 sequestration of carbon is one of major importance. However, knowledge of the extent to which land  
45 use and grazing affect the carbon cycle is relatively limited. Ecosystem carbon pools are a key  
46 component of the global carbon cycle (Cox and others 2000). Carbon lost from ecosystem stores to  
47 the atmosphere contributes to climatic warming, and warmer temperatures have been shown to  
48 change ecosystems carbon sinks into carbon sources (Oechel and others 1993; Melillo and others  
49 2002). Increases in atmospheric CO<sub>2</sub> concentration (Cao and Woodward 1998a) and nutrient  
50 enrichment (Hobbie and others 2002; Mack and others 2004) have also been implicated in changes in  
51 ecosystem carbon stocks. However, large herbivores can have important impacts on ecosystem state  
52 across biomes (McNaughton 1984; Augustine and McNaughton 2004; Van der Wal 2006; Speed and  
53 others 2010a; Hidding and others 2013), and are therefore expected to impact ecosystem carbon  
54 balance (Tanentzap and Coomes 2012; McSherry and Ritchie 2013). Despite this, the impact of large  
55 herbivores on ecosystem carbon stocks are less studied than climatic drivers, even though land-use  
56 change is a key component of global environmental change (Vitousek 1994), and livestock grazing, as  
57 the globally most extensive form of land use (Asner and others 2004), is in particular a key driver of  
58 ecosystem change.

59 Large herbivores may affect ecosystem carbon storage in the short term by changing vegetation  
60 biomass and productivity (Austrheim and others In Press), and by changing the quality and quantity  
61 of soil organic matter through impacting litter-fall, litter quality and decomposition rates (Harrison  
62 and Bardgett 2008; Piñeiro and others 2010; Tanentzap and Coomes 2012). However, in the longer  
63 term, herbivory can lead to changes in carbon storage through changes in plant community  
64 composition, with species differing in above and below-ground biomass, litter quality and quantity  
65 and subsequently quantity and quality of soil organic matter. For example, the presence of  
66 herbivores may constrain the distribution of woody trees and shrubs (Augustine and McNaughton  
67 2004; Olofsson and others 2009; Speed and others 2010a), and forest and shrub-land differ in terms

68 of carbon storage from savannah, grassland and tundra (Wilmking and others 2006; De Deyn and  
69 others 2008; Sjögersten and Wookey 2009; Hartley and others 2012). Furthermore, the  
70 establishment of forest on previously open landscapes can have further feedbacks to the global  
71 climate, and hence carbon cycles, by reducing albedo and facilitating warming (Chapin and others  
72 2005; de Wit and others In Press), highlighting the importance of the transition between arctic or  
73 alpine tundra and forest. Forest expansion following land-use change could amount to up to  
74 48 800 km<sup>2</sup> in Norway alone, and 10 992 km<sup>2</sup> in the mountains (elevation >800 m) (Bryn and others  
75 2013). Changes in land-use similar to those in Norway can be seen in many other alpine regions  
76 including the European Alps (e.g. Tasser and others 2007) and Eastern North America (e.g. Zald  
77 2009). Such land-use change has thus the potential to have a marked effect on carbon stores  
78 (Caspersen and others 2000).

79 Here we investigate the impact of grazers on ecosystem carbon in a mountain region of Southern  
80 Norway, with a long history of heavy sheep grazing. We investigate changes in vegetation and carbon  
81 stocks in aboveground pools and soils, in both the short term, using a 12-year enclosure experiment,  
82 and the long-term, using a natural experiment of islands in water bodies which are inaccessible to  
83 the dominant grazer, domestic sheep and thus represent the system state in the long-term absence  
84 of livestock grazing.

## 85 **Materials and methods**

### 86 **Study area and design**

87 This study was based in the region of Setesdal Vesthei, Southern Norway, spanning the counties  
88 Vest- and Aust-Agder (Figure 1). Setesdal is a heavily grazed low-alpine region with a long history of  
89 intensive summer-season sheep grazing involving some of the highest sheep densities in Norwegian  
90 mountain regions with densities in 2006 between 44 and 88 sheep km<sup>-2</sup> (densities estimated  
91 excluding ungrazeable land such as bare rock and boulder fields Rekdal and Angeloff 2007). There is  
92 also a small herd of wild reindeer (*Rangifer tarandus*) in the area (0.15 to 0.25 reindeer km<sup>-2</sup>). The

93 base rock is granitic and the mineral soil is acidic with low nutrient content; the climate is oceanic  
94 with high precipitation (Austrheim and others 2005). The soils are mostly wet consisting mainly of  
95 histosols and gleysols, however with podsols (IIUSS Working Group WRB 2006) in freely drained  
96 areas.

97 Palaeoecological data indicates that grazing has been practiced in Setesdal for around 5000 years,  
98 and a downward shift in the region's forest line occurred due to increased human impact around  
99 1500-2000 BP (Eide and others 2006). Sheep densities dramatically increased in the 1840s when  
100 sheep farmers in coastal areas started summer grazing in alpine pastures in Setesdal Vesthei (Drabløs  
101 1997). This transhumance system has kept continuous high densities of sheep for 160 years.  
102 Experimental sheep enclosures were established from year 2000 which caused a rapid increase in the  
103 highly selected *Deschampsia flexuosa* and decrease in the grazing resistant *Nardus stricta*, another  
104 clear indication of a high grazing pressure in the study area (Austrheim and others 2007).

105 In the early summer of the year 2000, 10 paired enclosure and unenclosed grazed plots were  
106 initiated. These were 20 x 50 m and located on S facing slopes, with approximately 30 m between the  
107 enclosure fences and the grazed plots to avoid edge effects. The plots were located within habitats  
108 selected by grazing sheep, in mostly humid grassy heathlands but avoiding bogs and wetlands.  
109 *Nardus stricta* dominated among vascular plants covering nearly one half of the field layer (total  
110 74%) while bryophyte cover was around 25%. The richness of vascular plants is low (50 species) of  
111 which graminoids (22 species) and dwarf-shrubs (14 species) dominated (Austrheim and others  
112 2007). The 10 pairs were spread over an area of approximately 15 x 8 km (Figure 1) spanning an  
113 elevational range of 866 to 1041 m (median 978 m). These plots are at least 5 km from the mountain  
114 birch (*Betula pubescens czerepanovi*) forest limit which is at an elevation of around 800 m, with only  
115 occasional birch individuals and groups of trees in the study region, tending to be in areas where  
116 sheep access is prevented such as steep cliffs. The enclosures are constructed out of wire mesh  
117 supported on wooden posts. Rodents and mountain hare could access the plots year round. The

118 fences were removed during winter (after the free-ranging sheep had been herded and removed)  
119 and reinstalled as soon as the snow melted. Thus the reindeer could access the exclosures between  
120 autumn and spring, but their impact is assumed to be minor due to the low population density and  
121 that they mainly use other areas of the mountain range (for more details see Austrheim and others  
122 2007).

123 Within the same region there are a number of lakes and within some of these water bodies islands  
124 exist supporting stunted birch forest. Three islands were selected on three separate water bodies,  
125 each with stunted birch forest. These islands were within the same region as the pairs of exclosures  
126 and grazed plots (Figure 1) and at similar elevations (842, 874 and 936 m). The islands are  
127 approximately 0.06, 0.16 and 0.15 km<sup>2</sup> in area (Figure 1) and showed similar levels of topographic  
128 heterogeneity to the mainland. The islands were generally not accessible for the region's sheep, and  
129 we assume that sheep grazing on these islands has been very rare. However, reindeer were able to  
130 access the islands during the winter when the lakes froze but we assume that they have low impact  
131 due to the low population density (demonstrated by the presence of one group of reindeer faecal  
132 pellets on one island; J. Speed, personal observation). The three islands are in lakes where the water  
133 level has been raised by human activities associated with hydropower generation. However, analysis  
134 of historic maps and data provided by the power companies demonstrates that the islands pre-date  
135 human manipulation of the water level (i.e. they were not formed when water levels were raised,  
136 Appendix A).

137 Islands may differ from mainland systems in ecological properties due to lower incidence of fires  
138 (Wardle and others 2012). However, in the subalpine and alpine regions of Setesdal, the charcoal  
139 record is very sparse throughout the Holocene period (Eide and others 2006; H. H. Birks unpublished  
140 data) suggesting that fires have been of very low frequency and importance in this highly oceanic  
141 region. Ecological systems on islands may also differ from those in land-locked situations due to the  
142 influence of water on local climatic conditions. Furthermore, the islands in this study were of

143 generally lower elevation than the enclosures/grazed pairs (see above). To check the sensitivity of  
144 our findings to the influence of lakes on local climate, and the minor difference in elevation, we  
145 repeated all analyses comparing the islands only to the lower-elevation and lakeside mainland plots  
146 (plots 1-5, Figure 1).

147 The enclosures were used to examine the impact of large herbivore exclusion on vegetation state and  
148 carbon pools in the short to medium term (12 years, hereon referred to as short-term), and the  
149 islands used to examine the vegetation state and carbon stocks in the system that would develop in  
150 the long-term absence of grazing livestock. During 25<sup>th</sup> to 29<sup>th</sup> June 2012 we sampled the field layer  
151 vegetation (all vegetation below the tree layer), mountain birch stands, and soils from the ten pairs  
152 of enclosure/grazed plots and the three islands.

### 153 **Field layer vegetation**

154 The field layer vegetation composition was sampled within 50 × 50 cm quadrats using a point  
155 intercept method. In each of the enclosure and grazed plots, three quadrats were located in  
156 representative vegetation, stratified by the upper, mid and lower part of the plot's slope. A total of  
157 16 regularly spaced pins were lowered into the plot, and every plant intercept recorded, including  
158 bryophytes, lichens and litter. For the determination of biomass, and measurement of carbon  
159 content, the total above ground vegetation biomass from the whole 0.25m<sup>2</sup> quadrat was  
160 destructively harvested using a pair of handheld clippers immediately after the point intercept  
161 assessment.

162 On the islands, three locations were selected in similar south facing slopes to the mainland plots,  
163 again avoiding bogs, wetlands and exposed rocks. At each of the three locations two quadrats were  
164 positioned within 5 m of each other, one immediately under the birch canopy and one not  
165 immediately under the birch canopy (thus six quadrats per island). The field layer vegetation  
166 composition and biomass harvests were carried out in the same way as in the grazed and enclosed  
167 quadrats. Based on species-accumulation curves, our sample number was not adequate for

168 estimating diversity. However, in terms of C dynamics, the dominant species are the most important,  
169 and these are well sampled with 6 quadrats per island. We also know from experience that the  
170 quadrat size is adequate (see Austrheim and others 2007). Furthermore, power-of-test analyses  
171 suggest that to detect a difference of 0.05 in relative abundance (5%) of a given species at the  $P < 0.05$   
172 level, a sample size of 3 is adequate (given the average standard deviation across species). For the  
173 more abundant (and hence higher standard deviation) *Nardus stricta* and *Deschampsia flexuosa*, a  
174 mean difference of 0.4 (the actual difference is 0.57) can be detected with a sample size of 6  
175 quadrats.

## 176 **Birch**

177 On the three islands, 10 m radius circles were established at each of the three locations, centred on  
178 the location of the field-layer vegetation quadrats. The density of birch individuals and stems was  
179 recorded within this circle (or a sector of the circle ensuring that a minimum of 50 stems were  
180 sampled per plot). The basal stem diameter of each birch stem was recorded. Density was expressed  
181 as tree individuals or stems per  $m^2$ . Three rowan *Sorbus aucuparia* individuals were recorded on  
182 island 2, but omitted from further analyses. At least three stems per circle were randomly selected  
183 for destructive harvesting. Stems were cut at ground level, or as close to ground level as possible. A  
184 basal disc was taken for age determination, and the rest of the biomass exported for biomass and  
185 carbon content analyses. A total of 33 stems were sampled for age determination and 28 for biomass  
186 determination. Age was determined by ring-counting after first smoothing the surface using  
187 sandpaper or cutting a thin slice. Zinc cream was applied to increase the ring contrast, and  
188 microscope used to view rings. Using the subsampled stems, relationships were developed between  
189 basal stem diameter and age (log-linear, Appendix B1), and basal stem diameter and stem biomass  
190 ( $2^{nd}$  order polynomial, since a quadratic term best reflected radial growth, Appendix B2). These  
191 relationships were used to estimate the age and stem biomass of the non-destructively harvested  
192 individuals.

193 **Soil**

194 Soils were sampled immediately adjacent to the field-layer vegetation quadrats in the grazed and  
195 exclosed plots and on the islands. Soil samples were collected using a 5.2 cm diameter auger. The soil  
196 was sampled by genetic horizon and the depth recorded. To obtain enough material for analysis, two  
197 to six soil samples from the horizons at each site were taken. These were bulked prior to analysis.  
198 The organic soil layer (as sub-horizons O<sub>i</sub>, O<sub>e</sub>, O<sub>a</sub> representing little, moderately and highly  
199 decomposed soil organic matter, respectively or the total organic layer O<sub>iea</sub>) was sampled from a  
200 location adjacent to each of the three field-layer quadrats within each grazed or exclosed plot (a total  
201 of 60 locations) or island (a total of 18 locations). Soil profiles (a total of 31 locations) were excavated  
202 on the mainland (10 of the grazed plots and 8 of the exclosures with 1 or 2 replicates per plot) and at  
203 all sites on the islands for soil characterization. On the mainland the mineral soil (E, B/C or A/C  
204 horizons) was sampled at 22 locations with Gleysols or Podzols (IIUSS Working Group WRB 2006).  
205 The profile at nine of these locations consisted of organic material only (Histosols). On the islands  
206 mineral soil (E, B/C or A/C horizons) was sampled at 10 locations with Gleysols or Podzols. Eight  
207 locations (including all locations at island 2) had Histosols. Data from the different soil types were  
208 analysed together, and soil type was used as a covariate in analyses of soil parameters. Soils were  
209 stored cold and dark prior to drying (40°C in a drying cabinet, Wascator, type NV-97-1).  
210 The dry matter mass (corrected for amount of roots and gravel) of the soils samples with a known  
211 volume was used to determine bulk density (BD, g cm<sup>-3</sup>). Roots with a diameter of over 2 mm are  
212 thus not included in estimates of C pools. Subsamples of the dried and sieved samples were dried at  
213 60 °C and milled prior to determination of total C and N concentration. Total C and N were  
214 determined by dry combustion (Leco CHN-1000; Leco Corporation, Sollentuna, Sweden) (Nelson and  
215 Sommers 1982) and the Dumas method (Bremmer and Mulvaney 1982), respectively. The carbon to  
216 nitrogen ratio (C:N) was calculated as total C (%) divided by total N (%). Due to the low pH (mean  
217 pH<sub>H<sub>2</sub>O</sub> at the grazed or exclosed plots = 4.7 and 4.6 in the O- and mineral horizon, respectively and  
218 mean pH<sub>H<sub>2</sub>O</sub> at island plots = 4.4 and 4.7 in the O- and mineral horizon, respectively), total C

219 represents organic C, because acid soils do not contain carbonates. Soil C and C:N ratio for the O  
220 horizon were estimated based on measured values for the bulked O horizons ( $O_{iea}$ ), whereas depth-  
221 weighted mean values were used for O horizons where  $O_i$ ,  $O_e$  and  $O_a$  were analysed separately.  
222 Carbon stocks were calculated by multiplying horizon depth, BD and C-concentration (Martinsen and  
223 others 2011) and expressed as  $kg\ C\ m^{-2}$ .

#### 224 **Biomass and carbon assessment**

225 Field layer vegetation and birch biomass harvests were dried at 40 °C in a drying cabinet (Wascator,  
226 type NV-97-1) for 7-8 days prior to determination of the dry biomass. C and N content were assessed  
227 on subsamples of the dominant plant species *Deschampsia flexuosa*, *Nardus stricta* and *Vaccinium*  
228 spp. *Vaccinium* species (*V. myrtillus*, *V. vitis-idaea* and *V. uliginosum*) were pooled for C and N  
229 analyses to increase the range of quadrats with viable samples. A random sample of these species  
230 was removed (in the case of *Vaccinium* both stem and leaf were sampled), ground and homogenized  
231 (1 mm sieve) in a plant mill (Culatti, type DFH48), and dried at 60°C prior to determination of total C  
232 and N. The total C and N concentrations were determined as described above for soil. For *Vaccinium*  
233 spp., C content and C:N were pooled across tissue types. The C content and C:N ratio of the field  
234 layer vegetation was estimated by multiplying the relative abundance (between 0 and 1) of each of  
235 the three species (out of the total number of intercepts for those three species) by the C or C:N value  
236 for that species. This was estimated at the quadrat level. The above-ground vegetation C stock was  
237 estimated as the C content for each species multiplied by the relative abundance of that species and  
238 the total vegetation biomass, then summed across the three species ( $g\ C\ m^{-2}$ ). These species  
239 accounted for a median of 91% of point interceptions across all quadrats (quartiles = 0.81, 0.95, see  
240 Figure 2) so basing estimates of carbon content on these species provides a very good estimate of  
241 the total vegetation carbon stock.

242 Birch carbon content and C:N were assessed on both the main stem and small twigs (<10 mm  
243 diameter). The birch biomass was ground and homogenized in a plant mill (Laboratory mill 3100,

244 Falling number) and dried at 60°C prior to determination of total C and N. Carbon content and C:N  
245 were pooled across tissue types. There was a strong quadratic relationship between birch stem  
246 biomass and stem diameter (Appendix B2). This relationship was used to estimate the biomass of all  
247 birch stems on the islands. The carbon content (%C) of birch did not vary with stem diameter of birch  
248 ( $F_{1,25} = 1.36$ ,  $P = 0.25$ ), nor per island ( $F_{1,25} = 2.81$ ,  $P = 0.11$ ), so birch C content was averaged across all  
249 trees, then multiplied by the biomass estimated at the individual stem level. This was summed and  
250 divided by the circle sector area to estimate the above-ground birch carbon pool ( $\text{g C m}^{-2}$ ).

## 251 **Statistical analyses**

252 In order to test whether carbon concentrations and stocks varied between grazed and ungrazed  
253 ecosystems we used Gaussian family mixed effect models to test whether the parameters varied  
254 between the three treatments (grazed, exclosures and islands). Variables and model residuals were  
255 visually checked for normality and homoscedasticity. Random intercepts were fitted to account for  
256 the nesting of quadrats and soil samples within plots and islands (further details in Appendix C).  
257 Islands ( $n = 3$ ) were equivalent to plots on the mainland ( $n = 10$ ), in the experimental design, with  
258 three vegetation quadrats and soil samples nested within each. Likelihood ratio tests (Wald F) were  
259 used to test whether parameters varied with treatment and contrasts are presented between each  
260 of short-term (exclosures) and long-term (islands) grazer exclusion and grazed plots. Analyses were  
261 carried out in the R statistical environment (R Development Core Team 2012) and the nlme package  
262 (Pinheiro and others 2009).

## 263 **Results**

### 264 **Field layer**

265 The three dominant species across treatments were *Nardus stricta* (relative abundance of  $0.47 \pm 0.04$   
266 of total intercepts, mean  $\pm$  standard error ), *Deschampsia flexuosa* ( $0.32 \pm 0.03$ ) and *Vaccinium*  
267 *myrtillus* ( $0.05 \pm 0.01$ ) (Figure 2). *Nardus stricta* was particularly abundant in the grazed quadrats  
268 ( $0.63 \pm 0.05$ ), and to a lesser extent in the exclosures ( $0.56 \pm 0.05$ ), but on the islands it was much

269 more sparse ( $0.06 \pm 0.04$ , Figure 2). On the islands, *Deschampsia flexuosa* was the dominant species  
270 ( $0.66 \pm 0.07$ ), whilst the same species was significantly less abundant in the exclosures ( $0.23 \pm 0.04$ )  
271 and where grazed ( $0.19 \pm 0.04$ , Figure 2), where it was the second most abundant species after  
272 *Nardus stricta*. The shrubs *Vaccinium myrtillus* and *Empetrum* sp. did not significantly differ in  
273 relative abundance between the treatments, but *Cornus suecica* was the third most abundant species  
274 on the islands, but absent from grazed plots and rarely encountered within the exclosures (Figure 2).

275 On the islands, there was no significant difference in vegetation composition between the island  
276 canopy and non-canopy plots (permutated ANOVA of RDA constrained on canopy/non-canopy  $F_{1,16} =$   
277  $0.23$ ,  $P = 0.87$ ). There was also no significant difference in vegetation biomass (ANOVA  $F_{1,16} = 1.21$ ,  $P$   
278  $= 0.29$ ), or the C content of *Deschampsia flexuosa* ( $F_{1,16} = 1.02$ ,  $P = 0.33$ ), or *Vaccinium* spp. leaves  
279 ( $F_{1,4} = 1.15$ ,  $P = 0.34$ ) or stems ( $F_{1,12} = 0.19$ ,  $P = 0.67$ ), between quadrats under the birch canopy and  
280 not directly under the canopy, so these were pooled (*Nardus stricta* was largely absent from the  
281 island quadrats so not tested).

282 Vegetation biomass and carbon pool of the field layer was significantly lower on the islands (biomass  
283  $= 140.7 \text{ g m}^{-2} \pm 19.6$ ; C  $65.2 \text{ g m}^{-2} \pm 8.9$ ) than where grazed (biomass  $= 385.6 \text{ g m}^{-2} \pm 31.2$ ; C  $= 178.5$   
284  $\text{g m}^{-2} \pm 15.0$ , Figure 3a), but vegetation biomass and carbon pool did not significantly differ between  
285 the exclosures and where grazed (Table 1). Carbon to nitrogen (C:N) ratio was significantly lower in  
286 the field layer vegetation on the islands ( $17.7 \pm 2.4$ ) than where grazed ( $29.5 \pm 1.5$ , Table 1), due to  
287 the higher relative abundance of *D. flexuosa* (species C:N of  $23.8 \pm 0.64$ ) and lower relative  
288 abundance of *N stricta* (C:N of  $34.7 \pm 0.88$ ). C:N ratio did not differ between the exclosures ( $32.45 \pm$   
289  $1.26$ ) and the grazed plots (Table 1). The analyses of vegetation composition, biomass and carbon  
290 concentration were not sensitive to the removal of mainland sites that were not on the lakeshore  
291 (Appendix D). However, after excluding the sites away from the lakeshore, the exclosed vegetation carbon  
292 stock was significantly lower in both exclosures ( $122.25 \pm 9.58$ ) and islands ( $65.19 \pm 8.88$ ) than where  
293 grazed ( $171.84 \pm 19.25$ ).

## 294 **Birch**

295 The mean density of birch individuals on the three islands ranged from 0.2 to 0.3 m<sup>-2</sup>, and the mean  
296 stem density (given that the majority of individuals were polycormic) ranged between 0.4 and 0.9 m<sup>-2</sup>. Birch was completely absent from the grazed plots, and a total of one individual sapling was  
297 present within the 10 exclosures (but not sampled). Thus the mean density within the exclosures is  
298 0.0001 m<sup>-2</sup> and for the purpose of this study is assumed equal to 0.

300 The median height of the birch on the islands was 151 cm (quartiles 106 and 196 cm). The estimated  
301 median age of the birch (based on relationship between stem diameter and age, Appendix B1) was  
302 between 33 and 35 years with the maximum being 69, 65 and 66 years on islands 1 to 3 respectively  
303 (Appendix B3). The age distributions of the birch on the three islands were uni-modal (Appendix B3).  
304 The above-ground birch carbon pool on the islands ranged between 309 to 666 g m<sup>-2</sup>, with an overall  
305 mean of 496 g m<sup>-2</sup> (SE = 104, n = 3, Table 1, Figure 3A). The total vegetation carbon stock (field layer  
306 vegetation plus birch) was significantly higher on the islands (561.3g m<sup>-2</sup> ± 7.7) than where grazed  
307 (178.5 g m<sup>-2</sup> ± 15.0, Figure 3A).

## 308 **Soil**

309 Organic-horizon depth was highly variable between plots but tended to be deeper on the islands  
310 (21.5 cm ± 8.0) than either the grazed (16.4 cm ± 3.3) or exclosed (14.0 cm ± 3.0) treatments (Table  
311 1). Similarly, the organic-horizon soil carbon pool tended to be higher on the islands (20.9 kg m<sup>-2</sup> ±  
312 8.4) than the grazed (13.1 kg m<sup>-2</sup> ± 2.6) or exclosed treatments (13.4 kg m<sup>-2</sup> ± 3.6), but also with high  
313 variability (Table 1, Figure 3B), and the difference was not significant. If island 2 was omitted (since  
314 the soils were Histosols), the total soil organic carbon pool on the islands was 13.53 ± 5 kg C m<sup>-2</sup>  
315 (depth 14.55 ± 4.7 cm) which is in the same range as for the grazed and exclosed plots (Table 1).  
316 Neither organic-horizon soil depth ( $F_{2,18}=0.61$ ,  $P=0.6$ ) nor organic-horizon soil carbon pool ( $F_{2,18}=0.78$ ,  
317  $P=0.5$ ) differed significantly between the grazing treatments after accounting for differences in soil  
318 type. Organic-horizon soil depth and carbon pools were more influenced by soil type than by sheep

319 exclusion (Table 1). However, the C:N ratio of the organic-horizon soil was significantly higher on the  
320 islands ( $20.1 \pm 0.9$ ) than where grazed ( $15.0 \pm 0.5$ , Table 1,  $F_{2,54} = 7.5$ ,  $P = 0.001$ ). Soil C:N was not  
321 associated with vegetation C:N (Pearson's product moment correlation:  $r = -0.16$ ,  $t_{67} = -1.28$   $P = 0.20$ ).  
322 When the analyses were repeated with inclusion of only the five lakeside and low-elevation mainland  
323 sites (sites 1-5, Figure 1), the same patterns were apparent. However, the higher C:N ratio on the  
324 islands than where grazed was not significant (although marginally so) when the non-lakeshore plots  
325 were excluded (Appendix D,  $F_{2,12} = 3.67$ ,  $P = 0.057$ ).

## 326 **Discussion**

327 Understanding the relationship between land-use and carbon stocks is of great importance during  
328 the current period of global warming. Globally, grazing by livestock is one of the most widespread  
329 forms of land-use, and recent changes in land-use have led to variations in densities of both wild and  
330 domestic herbivores in many regions (Tasser and others 2007; Apollonio and others 2010; Austrheim  
331 and others 2011). The impacts of grazing on ecosystem carbon stocks are of particular interest at  
332 northern latitudes, due to the extensive grazing of domestic, semi-domestic and wild large  
333 herbivores (Asner and others 2004; Forbes and Kumpula 2009; Austrheim and others 2011), and  
334 particularly high soil carbon stocks in these regions (Cao and Woodward 1998b). In our study we  
335 found that the aboveground carbon stock was around  $0.38 \text{ kg C m}^{-2}$  (S.E = 0.14) larger in the long-  
336 term absence of grazers than where continually grazed.

337 In order to assess the importance of our findings to the global carbon cycle, we extrapolated our  
338 findings across the whole of Norway. Land-use change could lead to forest expansion in Norway of a  
339 total land area of  $48\,800 \text{ km}^2$ , of which  $10\,992 \text{ km}^2$  is above 800 m in elevation (Bryn and others  
340 2013). The mean difference in aboveground carbon stock shown in our study between the long-term  
341 grazed and long-term ungrazed treatments is  $0.38 \text{ kg m}^{-2}$  (S.E: = 0.14) is in the above-ground pool  
342 (Figure 3). If Norwegian forest expansion was to meet its potential following cessation of sheep  
343 grazing, and our study is representative of the vegetation response across the region of potential

344 forest expansion in Norway (Bryn and others 2013), we roughly estimate that the carbon storage in  
345 Norwegian alpine ecosystems could increase by up to 4.2 million tonnes C in the above-ground  
346 vegetation pool. This would represent an increase of only 2% on the total aboveground C stocks in  
347 Norwegian forests (Kjønaas and others 2000). However, a cessation of sheep grazing is in conflict  
348 with the policy goal of increasing food production within Norway by 20% by 2020 (Norwegian  
349 Ministry of Agriculture and Food 2011).

350 The influence of livestock on carbon stocks was largely driven by birch forest establishment in the  
351 long-term absence of grazing livestock. If we assume that a birch forest with equivalent carbon pools  
352 as that on the islands could develop in 50 years following cessation of livestock grazing (although it is  
353 likely that the birch forest on these islands is older than this, the median age of stems recorded was  
354 36 years) then this equates to a sequestration rate of  $7.7 \text{ g C m}^{-2} \text{ yr}^{-1}$  (S.E = 2.8) into the aboveground  
355 vegetation C pool, driven by the vegetation change of birch forest establishment associated with  
356 cessation of livestock grazing (Speed and others 2010a). These rates are not high, compared to for  
357 example the  $50 \text{ g C m}^{-2} \text{ yr}^{-1}$  reported for the impact of the cessation of livestock grazing on *Molinia*  
358 *caerulea* swards in Scottish upland grasslands (Smith and others 2013). However, the size of the pool  
359 formed by transition from alpine vegetation to birch forest is large, but the rate is low due to the  
360 slow establishment and growth of mountain birch at high elevations. As the abandonment of  
361 extensive livestock grazing is occurring in many other alpine regions across the world (e.g. Tasser and  
362 others 2007; Zald 2009), the impact of changing land-use in mountains on global carbon budgets is  
363 likely to be noteworthy (Caspersen and others 2000), but requires further quantification.  
364 Furthermore, the influence of changing land-use on global climate is likely to be exacerbated by the  
365 low albedo of forest ecosystems (de Wit and others In Press).

366 Herbivores are known to play a role in ecosystem C dynamics (Frank and Groffman 1998; Olofsson  
367 and others 2004), and C storage (Martinsen and others 2011; Tanentzap and Coomes 2012). Indeed  
368 herbivory has been seen to reduce ecosystem carbon storage or uptake in a range of systems

369 (Tanentzap and Coomes 2012), including the tundra (Olofsson and others 2004; Speed and others  
370 2010b; Cahoon and others 2012). We found higher aboveground carbon stocks and no difference in  
371 organic-horizon soil carbon stocks under forest than the alternative vegetation state of alpine  
372 vegetation (under the long-term grazed system), although our study likely slightly underestimated  
373 belowground C pools on the islands as large-diameter birch roots were not sampled. Soil carbon  
374 pools are found to be higher above the treeline than below (Kammer and others 2009; Hartley and  
375 others 2012), but also increase with elevation as decomposition decreases at lower temperatures  
376 (Sjögersten and others 2011). Sjögersten and Wookey (2009) summarise that the colonisation of  
377 tundra heath by mountain birch forest increases the C flux from soil and reduces soil C sink strength,  
378 noting that the Scandinavian mountain birch forest is a only a weak C sink. However, Wilmking and  
379 others (2006) examined carbon storage under tundra and forest finding that while tussock tundra  
380 had higher ecosystem carbon content than forests and woodland, shrub tundra ecosystem carbon  
381 storage was comparable to that of forests and woodland. Thus assuming that there are no  
382 differences in soil moisture or temperature, the vegetation type on which trees are establishing has  
383 the greatest impact on carbon dynamics, and an increase in soil carbon stocks may not be ubiquitous.

384 It has been suggested that the lower carbon pool in forest than tundra is driven by high plant activity  
385 during the peak growing season within birch forests, priming the decomposition of older soil organic  
386 matter and hence reduction in forest soil carbon (Hartley and others 2012). However, a reduction in  
387 soil carbon stocks following an increase in grazing intensity (as well as an increase in soil carbon  
388 stocks following a decrease in grazing intensity) has also been observed in an alpine ecosystem  
389 independently of birch colonisation (Martinsen and others 2011); this was driven by grazers at high  
390 density increasing the breakdown of particulate organic matter, and reducing litter quantity  
391 (Martinsen and others 2011) indicating that grazing is a key driver of carbon storage in tundra  
392 ecosystems. We observed that soil C:N ratio was higher under a forest canopy than where grazing  
393 livestock prevented forest establishment, probably due to a greater fraction of woody material under  
394 forests. We did not find an association between the field layer vegetation C:N and the soil C:N across

395 samples, however, the birch C:N ratio was unsurprisingly far higher than the field vegetation. Thus  
396 birch litter quality and quantity may also play a role in regulating carbon dynamics in our system,  
397 potentially compensating for decomposition of old organic matter driven by birch colonisation.

398 We have assumed that the difference between the islands and the grazed mainland is due to the  
399 long-term differences in livestock grazing history. However, islands differ from mainland ecosystems  
400 due to a number of factors including differing ages, meso-climatic conditions and fire histories  
401 (Wardle and others 2012). In our system we believe that fire history has not played a role in shaping  
402 the islands and mainland, due to the high oceanicity of the climate. This is supported by the very  
403 sparse occurrence of charcoal in the region's palaeoecological record (Eide and others 2006; H. H.  
404 Birks, personal communication). Although our findings were not sensitive to the exclusion of the  
405 grazed sites that were not located at the lake shores, we cannot completely rule out an influence of  
406 the water-bodies in which the islands are located on the island ecosystems and hence the results  
407 presented here.

#### 408 **Forest development**

409 The birch (aboveground) carbon stocks found in our study forests are low in magnitude compared to  
410 those presented from northern Sweden by Hartley and others (2012). However, the forests in our  
411 study are small patches on islands and thus highly exposed, potentially reducing growth rates, and  
412 certainly limiting height. The age structure on the islands that we studied also suggests that these  
413 forests are old and degenerative, and recruitment may be limited. The island forests are of course  
414 limited in area, but forest development on the mainland if sheep grazing were abandoned would be  
415 more widespread, and may facilitate further recruitment and growth of birch (Smith and others  
416 2003; Batllori and others 2009), increasing the potential birch C pool. . Our study did not  
417 demonstrate a significant difference in soil carbon stocks between the treatments, in part due to  
418 differing soil types between the treatments, demonstrating the importance of controlling for soil  
419 types in comparative analyses of carbon stocks. Regardless, our study highlights the need to consider

420 historic land-use and grazing patterns in interpreting differences in carbon stocks between  
421 ecosystems.

422 Due to global warming, many treelines in alpine areas are no longer temperature limited, and in the  
423 absence of grazing, transformation of open alpine regions into birch forest is likely to occur (Cairns  
424 and Moen 2004; Speed and others 2010a), with a major influence on carbon stocks in these areas. In  
425 our study, following the long-term absence of grazing livestock, birch forest developed with  
426 increased aboveground vegetation biomass and carbon storage. This highlights how grazing livestock  
427 exert a strong influence on the carbon stocks in alpine ecosystems, and in particular how grazing  
428 prevents an increase in aboveground carbon storage otherwise brought about by a vegetation state  
429 shift to a birch forest. However, we found no evidence of tree recruitment in the exclosures after 12  
430 years of grazer removal. This contrasts with the rapid birch establishment (Speed and others 2010a)  
431 and growth (Speed and others 2011b; Speed and others 2011a) following sheep exclosure observed  
432 at another southern Norwegian mountain site. Recruitment of mountain birch is often site-limited  
433 due to the high dispersal of birch seeds (Molau and Larsson 2000; Hofgaard and others 2009),  
434 however, seed limitation may also play a role in our study region due to the remoteness of the birch  
435 forest which is estimated to be around 5 km from the nearest exclosure site. Mature birch are  
436 present closer than this on cliff faces, islands and other grazing-refugia suggesting that either  
437 conditions were more suitable for tree establishment in the past, or that recruitment is simply a slow  
438 process in this region.

### 439 **Short and long-term changes**

440 Although birch recruitment in the short-term did not reflect the longer-term forest development, the  
441 short-term change in the rest of the vegetation did reflect the longer-term change. Following 12  
442 years of grazer exclusion, the grazing resistant *Nardus stricta* was lower in abundance and the highly  
443 palatable *Deschampsia flexuosa* was higher in abundance than where grazed. Although the relative  
444 abundances were not significantly different at this point, the rates of change in these species did

445 significantly differ after just four years of livestock exclusion (Austrheim and others 2007). The short-  
446 term vegetation change was associated with a decrease in aboveground vegetation biomass and  
447 carbon content. Short-term change appears to be in the same direction as long-term change, with *D.*  
448 *flexuosa* being the dominant field-layer vascular plant on the islands, and a lower abundance of *N.*  
449 *stricta*. Herb species, notably *Cornus suecica* were also relatively abundant on the islands with  
450 similarities in vegetation composition to the dwarf cornel birch forest described by Wehberg and  
451 others (2005). The trend for short-term changes in vegetation to be indicative of long-term changes  
452 following herbivore removal, albeit with a lag time, has also been reported in the case of reindeer  
453 exclusion in sub-arctic tundra ecosystems (Olofsson 2006). However, it is important to note that the  
454 abandonment of livestock grazing may lead to the alpine tundra becoming a carbon source in the  
455 short-term as the field layer transitions from a *Nardus* dominated state to a *Deschampsia* dominated  
456 state with lower carbon content, before birch forest establishment occurs.

## 457 **Conclusions**

458 Our study shows that continuing land-use in the form of grazing high-densities of livestock prevents  
459 forest re-establishing in subalpine and alpine landscapes, and further, that following removal of  
460 livestock, forest re-establishment is a long-term process at sites distant from existing forest. The  
461 historic and current land-use of intensive livestock grazing in this region thus suppresses the  
462 aboveground carbon stock below its potential by around  $0.38 \text{ kg C m}^{-2}$ . This has clear implications for  
463 management for carbon storage: Reductions in livestock grazing in areas where the treeline has  
464 potential to advance will lead to increased carbon sequestration in aboveground pools, but at a low  
465 rate.

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614

615 **Electronic supplementary material**

616 Appendix A: Historical map showing the location of the three islands prior to construction of the  
617 dams.

618 Appendix B: Data summarising the birch sampled on islands. B1: Relationship between basal stem  
619 diameter and the age of the birch stem. B2: Relationship between birch stem diameter and biomass.  
620 B3: Histograms showing the proportional distribution of estimated birch ages for the three islands.

621 Appendix C: Full details of statistical modelling.

622 Appendix D: A table of the same structure as Table 1, comparing carbon stocks and concentrations  
623 across the islands and mainland plots, including only the five plots along the lake shores and at low  
624 elevation, and a figure showing the vegetation composition of the same lake shore plots and the  
625 inland plots.

626 **Tables**

627 Table 1: Carbon stocks of field vegetation (all above-ground vegetation other than trees), birch and  
 628 organic soil in quadrats with a long history of grazing, following 12 years of large-herbivore enclosure  
 629 and on large-herbivore free islands. The C content and C:N ratio of each fraction is presented along  
 630 with biomass of field vegetation and birch, and the depth of organic soil. Mean and standard errors  
 631 are shown estimated after pooling pseudo-replicates within each site or island (n = 10 for the grazed  
 632 and exclosures, and 3 for the islands, reduced to n = 8 for the exclosed sites for soil depth and soil C  
 633 stock). Likelihood ratio Wald-F tests are shown for treatment in a mixed effects model with site as a  
 634 random intercept. For the organic soil, soil type was included as a covariate in the models and  
 635 likelihood ratio Wald-F tests are shown for soil type in addition. Variables that significantly differ in  
 636 exclosures or islands from the grazed plots are denoted by bold text. Note that C stock units vary  
 637 between vegetation and soil pools.

Vegetation (n)	Biomass (g m <sup>-2</sup> )	C content (%)	C:N	C stock (g m <sup>-2</sup> )
Grazed (10)	385.63 ± 31.96	43.87 ± 1.55	29.49 ± 1.53	178.46 ± 15.02
Exclosed (10)	365.97 ± 29.59	45.18 ± 0.43	32.45 ± 1.26	167.94 ± 13.64
Islands (3)	<b>140.77 ± 19.63</b>	38.5 ± 4.40	<b>17.72 ± 2.37</b>	<b>65.19 ± 8.88</b>
	F <sub>2,53</sub> = 5.48, P=0.007	F <sub>2,53</sub> = 1.26, P = 0.293	F <sub>2,54</sub> = 9.30, P<0.001	F <sub>2,53</sub> = 5.54, P = 0.007
Birch (n)	Biomass (g m <sup>-2</sup> )	C content%	C:N	C stock (g m <sup>-2</sup> )
Grazed (10)	0 ± 0	NA	NA	0 ± 0
Exclosed (10)	0 ± 0	NA	NA	0 ± 0
Islands (3)	<b>1007.70 ± 140.99</b>	52.63 ± 0.22	91.62 ± 2.68	<b>496.16 ± 81.76</b>
Organic Soi (n)	Organic soil depth <sup>a</sup> (cm)	C content (%)	C:N	C stock (kg m <sup>-2</sup> )
Grazed (10)	16.36 ± 3.27	41.28 ± 1.95	15.02 ± 0.47	13.12 ± 2.60
Exclosed (8)	13.99 ± 3.00	<b>45.19 ± 1.53</b>	16.00 ± 0.50	13.43 ± 3.55
Islands (3)	21.53 ± 5.81	46.91 ± 1.81	<b>20.06 ± 0.93</b>	20.92 ± 6.01
	F <sub>2,23</sub> = 0.87, P = 0.432	F <sub>2,23</sub> = 5.12, P = 0.014	F <sub>2,23</sub> = 5.09, P = 0.015	F <sub>2,23</sub> = 1.68, P = 0.208
Soil Type	F <sub>2,23</sub> = 31.06, P < 0.001	F <sub>2,23</sub> = 2.25, P = 0.127	F <sub>2,23</sub> = 1.25, P = 0.304	F <sub>2,23</sub> = 21.75, P < 0.001

638 <sup>a</sup>Mean depth of the organic + mineral soil was 21.85 cm, 22.42 cm and 28.72 cm for the grazed,  
 639 exclosed and island plots, respectively.

640 **Figures**

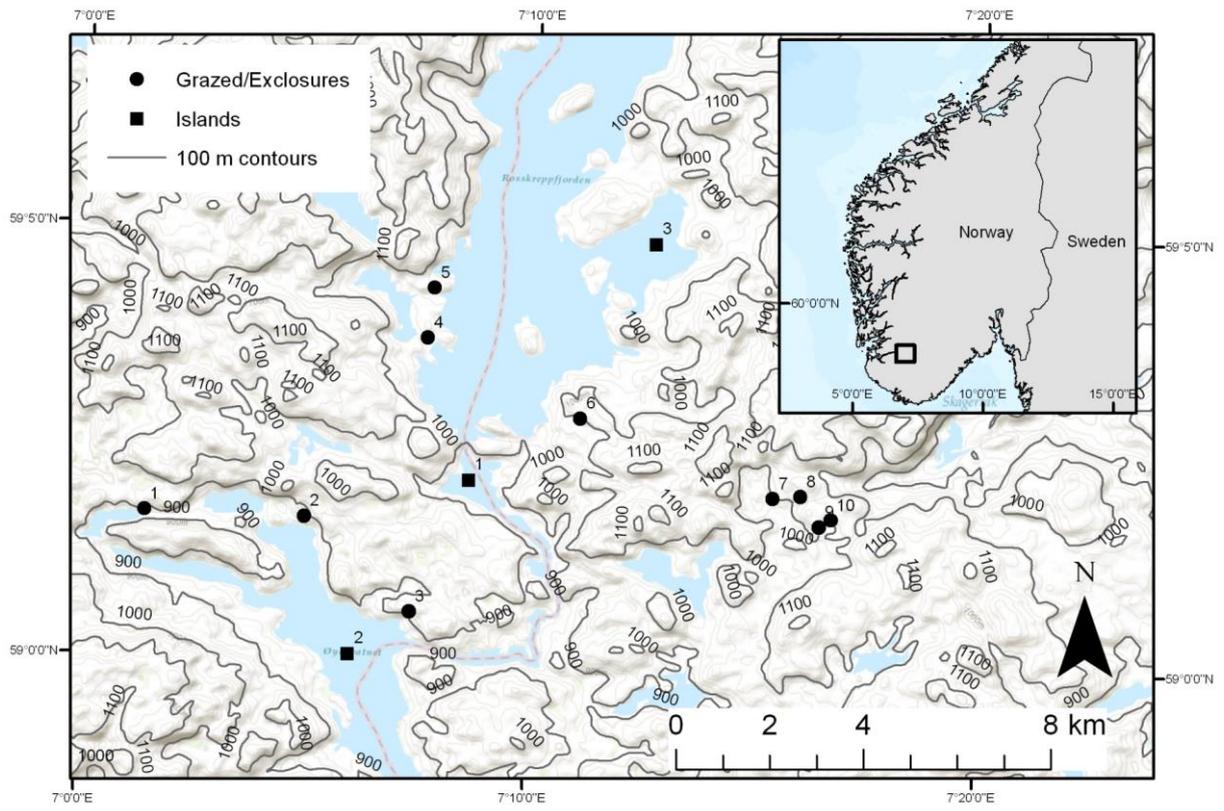
641 Figure 1. Map showing the locations of the ten paired enclosure and grazed sites and the three  
642 islands. The inset shows the location of the region of Setesdal in Southern Norway.

643 Figure 2: Relative abundance of vascular plant species across each treatment. Relative abundance is  
644 expressed as the number of point intercepts per species within each quadrat divided by the total  
645 number of point intercepts in that quadrat. Species are ordered according to their relative  
646 abundance across treatments. Mean and standard errors are shown. The inset shows a zoomed in  
647 view of the five most abundant species. Asterisks above the bars show where the relative abundance  
648 of a species in the enclosures or islands significantly differs from where grazed (\*\*\*)  $P < 0.001$ , five  
649 most abundant species only).

650 Figure 3 Carbon pools in different grazing treatments. (a) The field-layer vegetation and birch C pools  
651 and (b) soil C pools under grazing are presented. Mean values are shown, with shading indicating the  
652 contribution from different fractions. Standard errors around the overall carbon pool are also  
653 presented. Note the difference in scale of the y axes between the panels. Soil pools are estimated for  
654 the top 22 to 29 cm of the soil profiles, which were dominated by the O horizon (see Table 1).

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