

# Long-Term Increase in Aboveground Carbon Stocks Following Exclusion of Grazers and Forest Establishment in an Alpine Ecosystem

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## ABSTRACT

Ecosystem stores of carbon are a key component in the global carbon cycle. Many studies have examined the impact of climate change on ecosystem carbon storage, but few have investigated the impact of land-use change and herbivory. However, land-use change is a major aspect of environmental change, and livestock grazing is the most extensive land use globally. In this study, we combine a grazing exclusion experiment and a natural experiment to test the impact of grazer exclusion on vegetation dynamics and ecosystem carbon stores in the short term (12-year exclusions), and the long term (islands inaccessible to livestock), in a heavily grazed mountain region in Norway. Following long-term absence of sheep, birch forest was present. The grazing-resistant grass *Nardus stricta*, dominated under long-term grazing, whilst the selected grass *Deschampsia flexuosa* and herb species dominated the

vegetation layer in the long-term absence of sheep. The established birch forest led to vegetation carbon stocks being higher on the islands (0.56 kg C m<sup>-2</sup> on the islands compared to 0.18 kg C m<sup>-2</sup> where grazed) and no difference in soil carbon stocks. In the short-term exclusion of sheep, there were minor differences in carbon stocks reflecting the longer term changes. These results show that aboveground carbon stocks are higher in the long-term absence of sheep than in the continual presence of high sheep densities, associated with a vegetation state change between tundra and forest. The reduction of herbivore populations can facilitate forest establishment and increase aboveground carbon stocks, however, the sequestration rate is low.

**Key words:** biomass; tundra; herbivory; land-use; livestock; treeline.

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**Author contributions** JDMS, VM GA carried out fieldwork and designed the study with input from AM, JM and ØH. GA and AM set up the exclusions. VM analyzed soil and vegetation samples. JDMS analyzed the data with input from VM. All authors contributed with interpretation of data and patterns. JDMS wrote the manuscript with input from all co-authors.

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## INTRODUCTION

In response to recent global warming, the search for methods to mitigate climate change through the sequestration of carbon is one of major importance. However, knowledge of the extent to which land use and grazing affect the carbon cycle is relatively limited. Ecosystem carbon pools are a key compo-

ment of the global carbon cycle (Cox and others 2000). Carbon lost from ecosystem stores to the atmosphere contributes to climatic warming, and warmer temperatures have been shown to change ecosystem carbon sinks into carbon sources (Oechel and others 1993; Melillo and others 2002). Increases in atmospheric CO<sub>2</sub> concentration (Cao and Woodward 1998a) and nutrient enrichment (Hobbie and others 2002; Mack and others 2004) have also been implicated in changes in ecosystem carbon stocks. However, large herbivores can have important impacts on ecosystem state across biomes (McNaughton 1984; Augustine and McNaughton 2004; Van der Wal 2006; Speed and others 2010a; Hidding and others 2013), and are therefore expected to impact ecosystem carbon balance (Tanentzap and Coomes 2012; McSherry and Ritchie 2013). Despite this, the impact of large herbivores on ecosystem carbon stocks are less studied than climatic drivers, even though land-use change is a key component of global environmental change (Vitousek 1994), and livestock grazing, as the globally most extensive form of land use (Asner and others 2004), is in particular a key driver of ecosystem change.

Large herbivores may affect ecosystem carbon storage in the short term by changing vegetation biomass and productivity (Austrheim and others in press), and by changing the quality and quantity of soil organic matter through impacting litter-fall, litter-quality and decomposition rates (Harrison and Bardgett 2008; Piñeiro and others 2010; Tanentzap and Coomes 2012). However, in the longer term, herbivory can lead to changes in carbon storage through changes in plant community composition, with species differing in above and below-ground biomass, litter quality and quantity and subsequently quantity and quality of soil organic matter. For example, the presence of herbivores may constrain the distribution of woody trees and shrubs (Augustine and McNaughton 2004; Olofsson and others 2009; Speed and others 2010a), and forest and shrub-land differ in terms of carbon storage from savannah, grassland and tundra (Wilmking and others 2006; De Deyn and others 2008; Sjögersten and Wookey 2009; Hartley and others 2012). Furthermore, the establishment of forest on previously open landscapes can have further feedbacks to the global climate, and hence carbon cycles, by reducing albedo and facilitating warming (Chapin and others 2005; de Wit and others 2013), highlighting the importance of the transition between arctic or alpine tundra and forest. Forest expansion following land-use change could amount to up to 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 2013). Changes in land use similar to those in Norway can be seen in many other alpine regions including the European Alps (for example, Tasser and others 2007) and Eastern North America (for example, Zald 2009). Such land-use change has thus the potential to have a marked effect on carbon stores (Caspersen and others 2000).

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

## MATERIALS AND METHODS

### Study Area and Design

This study was based in the region of Setesdal Vesthei, Southern Norway, spanning the counties Vest- and Aust-Agder (Figure 1). Setesdal is a heavily grazed low-alpine region with a long history of intensive summer-season sheep grazing involving some of the highest sheep densities in Norwegian mountain regions with densities in 2006 between 44 and 88 sheep km<sup>-2</sup> (densities estimated excluding ungrazeable land such as bare rock and boulder fields Rekdal and Angeloff 2007). There is also a small herd of wild reindeer (*Rangifer tarandus*) in the area (0.15–0.25 reindeer km<sup>-2</sup>). The base rock is granitic and the mineral soil is acidic with low nutrient content; the climate is oceanic with high precipitation (Austrheim and others 2005). The soils are mostly wet consisting mainly of histosols and gleysols, however, with podsols (IIUSS Working Group 2006) in freely drained areas.

Palaeoecological data indicates that grazing has been practised in Setesdal for around 5,000 years, and a downward shift in the region's forest line occurred due to increased human impact around 1500–2000 BP (Eide and others 2006). Sheep densities dramatically increased in the 1840s when sheep farmers in coastal areas started summer grazing in alpine pastures in Setesdal Vesthei (Drabløs 1997). This transhumance system has kept continuous high densities of sheep for 160 years. Experimental sheep enclosures were established

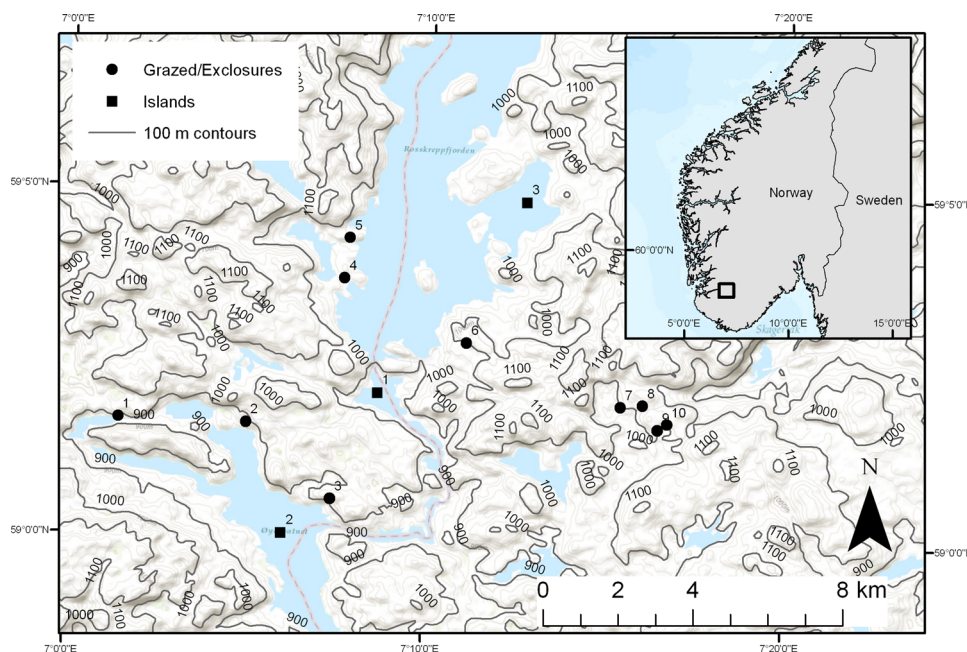


Figure 1. Map showing the locations of the ten paired exclosure and grazed sites and the three islands. The inset shows the location of the region of Setesdal in Southern Norway.

from year 2000 which caused a rapid increase in the highly selected *Deschampsia flexuosa* and decrease in the grazing-resistant *Nardus stricta*, another clear indication of a high grazing pressure in the study area (Austrheim and others 2007).

In the early summer of the year 2000, ten paired exclosure and unexclosed grazed plots were initiated. These were 20 × 50 m and located on S facing slopes, with approximately 30 m between the exclosure fences and the grazed plots to avoid edge effects. The plots were located within habitats selected by grazing sheep, in mostly humid grassy heathlands but avoiding bogs and wetlands. *N. stricta* dominated among vascular plants covering nearly one half of the field layer (total 74%) whereas bryophyte cover was around 25%. The richness of vascular plants is low (50 species) of which graminoids (22 species) and dwarf-shrubs (14 species) dominated (Austrheim and others 2007). The ten pairs were spread over an area of approximately 15 × 8 km (Figure 1) spanning an elevational range of 866–1,041 m (median 978 m). These plots are at least 5 km from the mountain birch (*Betula pubescens czerepanovi*) forest limit which is at an elevation of around 800 m, with only occasional birch individuals and groups of trees in the study region, tending to be in areas where sheep access is prevented such as steep cliffs. The exclosures are constructed out of wire mesh supported on wooden posts. Rodents and mountain hare could access the plots year round. The fences were removed during winter (after the free-ranging sheep had been herded and removed) and rein-

stalled as soon as the snow melted. Thus, the reindeer could access the exclosures between autumn and spring, but their impact is assumed to be minor due to the low population density and that they mainly use other areas of the mountain range (for more details see Austrheim and others 2007).

Within the same region, there are a number of lakes and within some of these water bodies islands exist supporting stunted birch forest. Three islands were selected on three separate water bodies, each with stunted birch forest. These islands were within the same region as the pairs of exclosures and grazed plots (Figure 1) and at similar elevations (842, 874 and 936 m). The islands are approximately 0.06, 0.16 and 0.15 km<sup>2</sup> in area (Figure 1) and showed similar levels of topographic heterogeneity to the mainland. The islands were generally not accessible for the region's sheep, and we assume that sheep grazing on these islands has been very rare. However, reindeer were able to access the islands during the winter when the lakes froze but we assume that they have low impact due to the low population density (demonstrated by the presence of one group of reindeer faecal pellets on one island; J. Speed, personal observation). The three islands are in lakes where the water level has been raised by human activities associated with hydropower generation. However, analysis of historic maps and data provided by the power companies demonstrates that the islands pre-date human manipulation of the water level (that is, they were not formed when water levels were raised, Appendix "A", Supplementary material1).

Islands may differ from mainland systems in ecological properties due to lower incidence of fires (Wardle and others 2012). However, in the subalpine and alpine regions of Setesdal, the charcoal record is very sparse throughout the Holocene period (Eide and others 2006; H. H. Birks unpublished data) suggesting that fires have been of very low frequency and importance in this highly oceanic region. Ecological systems on islands may also differ from those in land-locked situations due to the influence of water on local climatic conditions. Furthermore, the islands in this study were of generally lower elevation than the exclosures/grazed pairs (see above). To check the sensitivity of our findings to the influence of lakes on local climate, and the minor difference in elevation, we repeated all analyses comparing the islands only to the lower elevation and lakeside mainland plots (plots 1–5, Figure 1).

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

### Field-Layer Vegetation

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

On the islands, three locations were selected in similar south facing slopes to the mainland plots, again avoiding bogs, wetlands and exposed rocks. At each of the three locations, two quadrats were positioned within 5 m of each other, one immediately under the birch canopy and one not immediately under the birch canopy (thus six quadrats

per island). The field-layer vegetation composition and biomass harvests were carried out in the same way as in the grazed and exclosed quadrats. Based on species-accumulation curves, our sample number was not adequate for estimating diversity. However, in terms of C dynamics, the dominant species are the most important, and these are well sampled with six quadrats per island. We also know from experience that the quadrat size is adequate (see Austrheim and others 2007). Furthermore, power-of-test analyses suggest that to detect a difference of 0.05 in relative abundance (5%) of a given species at the  $P < 0.05$  level, a sample size of 3 is adequate (given the average standard deviation across species). For the more abundant (and hence higher standard deviation) *N. stricta* and *D. flexuosa*, a mean difference of 0.4 (the actual difference is 0.57) can be detected with a sample size of six quadrats.

### Birch

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

## Soil

Soils were sampled immediately adjacent to the field-layer vegetation quadrats in the grazed and exclosed plots and on the islands. Soil samples were collected using a 5.2 cm diameter auger. The soil was sampled by genetic horizon and the depth recorded. To obtain enough material for analysis, two to six soil samples from the horizons at each site were taken. These were bulked prior to analysis. The organic soil layer (as sub-horizons  $O_i$ ,  $O_e$ ,  $O_a$  representing little, moderately and highly decomposed soil organic matter, respectively, or the total organic layer  $O_{ica}$ ) was sampled from a location adjacent to each of the three field-layer quadrats within each grazed or exclosed plot (a total of 60 locations) or island (a total of 18 locations). Soil profiles (a total of 31 locations) were excavated on the mainland (10 of the grazed plots and 8 of the exclosures with 1 or 2 replicates per plot) and at all sites on the islands for soil characterization. On the mainland, the mineral soil (E, B/C or A/C horizons) was sampled at 22 locations with Gleysols or Podzols (IUSS Working Group 2006). The profile at nine of these locations consisted of organic material only (Histosols). On the islands mineral soil (E, B/C or A/C horizons) was sampled at ten locations with Gleysols or Podzols. Eight locations (including all locations at island 2) had Histosols. Data from the different soil types were analyzed together, and soil type was used as a covariate in analyses of soil parameters. Soils were stored cold and dark prior to drying (40°C in a drying cabinet, Wascator, type NV-97-1).

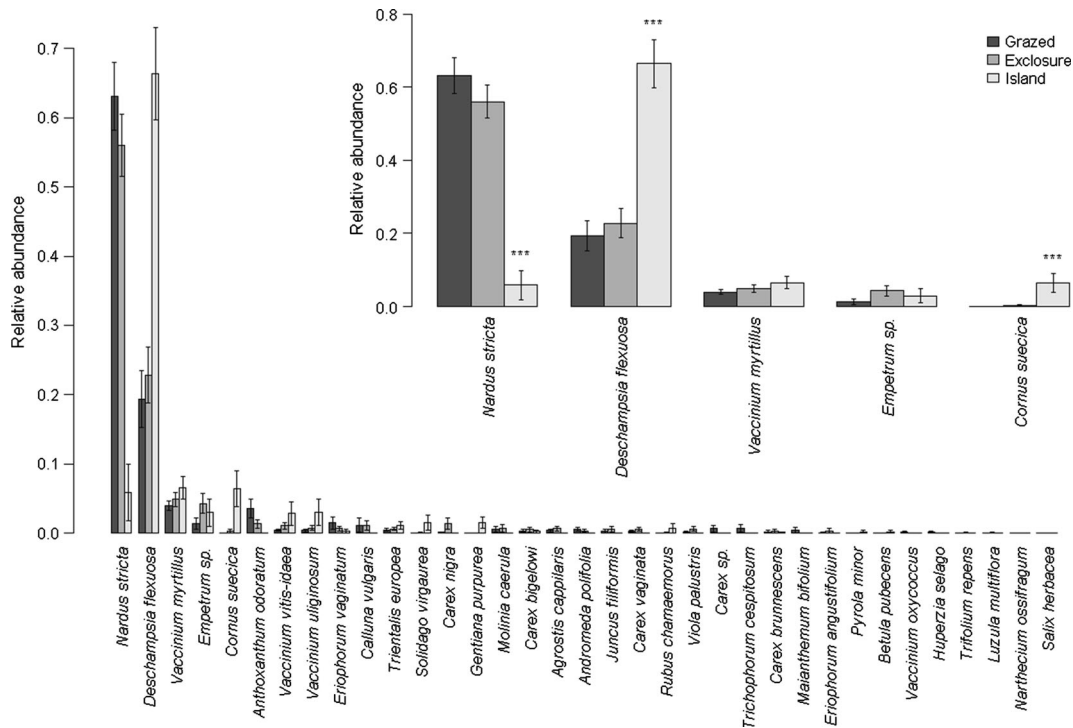
The dry matter mass (corrected for amount of roots and gravel) of the soils samples with a known volume was used to determine bulk density (BD,  $g\ cm^{-3}$ ). Roots with a diameter of over 2 mm are thus not included in estimates of C pools. Subsamples of the dried and sieved samples were dried at 60°C and milled prior to determination of total C and N concentration. Total C and N were determined by dry combustion (Leco CHN-1000; Leco Corporation, Sollanduna, Sweden) (Nelson and Sommers 1982) and the Dumas method (Bremmer and Mulvaney 1982), respectively. The carbon to nitrogen ratio (C:N) was calculated as total C (%) divided by total N (%). Due to the low pH (mean  $pH_{H_2O}$  at the grazed or exclosed plots = 4.7 and 4.6 in the O- and mineral horizon, respectively, and mean  $pH_{H_2O}$  at island plots = 4.4 and 4.7 in the O- and mineral horizon, respectively), total C represents organic C, because acid soils do not contain carbonates. Soil C and C:N ratio for the O horizon were estimated based on measured values for the

bulk O horizons ( $O_{ica}$ ), whereas depth-weighted mean values were used for O horizons where  $O_i$ ,  $O_e$  and  $O_a$  were analyzed separately. Carbon stocks were calculated by multiplying horizon depth, BD and C-concentration (Martinsen and others 2011) and expressed as  $kg\ C\ m^{-2}$ .

## Biomass and Carbon Assessment

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

Birch carbon content and C:N were assessed on both the main stem and small twigs (<10 mm diameter). The birch biomass was ground and homogenized in a plant mill (Laboratory mill 3100, Falling number) and dried at 60°C prior to determination of total C and N. Carbon content and C:N were pooled across tissue types. There was a strong quadratic relationship between birch stem biomass and stem diameter (Figure B2 in Appendix B, Supplementary material 2). This relationship was used to estimate the biomass of all birch stems on the islands. The carbon content (%C) of birch did not vary with stem diameter of birch ( $F_{1,25} = 1.36$ ,  $P = 0.25$ ), nor per island ( $F_{1,25} = 2.81$ ,  $P = 0.11$ ), so



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

birch C content was averaged across all trees, then multiplied by the biomass estimated at the individual stem level. This was summed and divided by the circle sector area to estimate the aboveground birch carbon pool ( $\text{g C m}^{-2}$ ).

## STATISTICAL ANALYSES

To test whether carbon concentrations and stocks varied between grazed and ungrazed ecosystems, we used Gaussian family mixed effect models to test whether the parameters varied between the three treatments (grazed, exclosures and islands). Variables and model residuals were visually checked for normality and homoscedasticity. Random intercepts were fitted to account for the nesting of quadrats and soil samples within plots and islands (further details in Appendix “C”, Supplementary material3). Islands ( $n = 3$ ) were equivalent to plots on the mainland ( $n = 10$ ), in the experimental design, with three vegetation quadrats and soil samples nested within each. Likelihood ratio tests (Wald  $F$ ) were used to test whether parameters varied with treatment and contrasts are presented between each of

the short-term (exclosures) and long-term (islands) grazer exclusion and grazed plots. Analyses were carried out in the R statistical environment (R Development Core Team 2012) and the nlme package (Pinheiro and others 2009).

## RESULTS

### Field Layer

The three dominant species across treatments were *N. stricta* (relative abundance of  $0.47 \pm 0.04$  of total intercepts, mean  $\pm$  standard error), *D. flexuosa* ( $0.32 \pm 0.03$ ) and *Vaccinium myrtillus* ( $0.05 \pm 0.01$ ) (Figure 2). *N. stricta* was particularly abundant in the grazed quadrats ( $0.63 \pm 0.05$ ), and to a lesser extent in the exclosures ( $0.56 \pm 0.05$ ), but on the islands it was much more sparse ( $0.06 \pm 0.04$ , Figure 2). On the islands, *D. flexuosa* was the dominant species ( $0.66 \pm 0.07$ ), whilst the same species was significantly less abundant in the exclosures ( $0.23 \pm 0.04$ ) and where grazed ( $0.19 \pm 0.04$ , Figure 2), where it was the second most abundant species after *N. stricta*. The shrubs *Vaccinium myrtillus* and *Empetrum sp.* did not significantly differ in relative abundance

between the treatments, but *Cornus suecica* was the third most abundant species on the islands, but absent from grazed plots and rarely encountered within the exclosures (Figure 2).

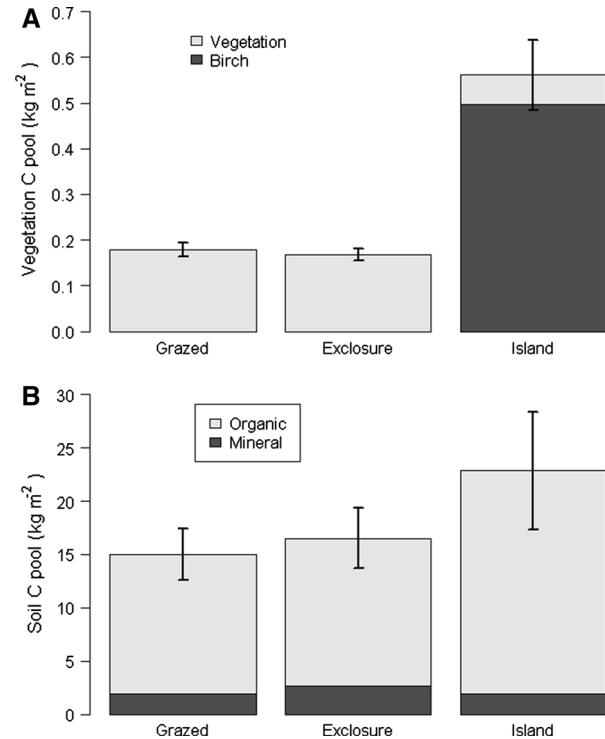
On the islands, there was no significant difference in vegetation composition between the island canopy and non-canopy plots (permutated ANOVA of RDA constrained on canopy/non-canopy  $F_{1,16} = 0.23$ ,  $P = 0.87$ ). There was also no significant difference in vegetation biomass (ANOVA  $F_{1,16} =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

Vegetation biomass and carbon pool of the field layer was significantly lower on the islands (biomass =  $140.7 \text{ g m}^{-2} \pm 19.6$ ; C =  $65.2 \text{ g m}^{-2} \pm 8.9$ ) than where grazed (biomass =  $385.6 \text{ g m}^{-2} \pm 31.2$ ; C =  $178.5 \text{ g m}^{-2} \pm 15.0$ , Figure 3A), but vegetation biomass and carbon pool did not significantly differ between the exclosures and where grazed (Table 1). Carbon to nitrogen (C:N) ratio was significantly lower in the field-layer vegetation on the islands ( $17.7 \pm 2.4$ ) than where grazed ( $29.5 \pm 1.5$ , Table 1), due to the higher relative abundance of *D. flexuosa* (species C:N of  $23.8 \pm 0.64$ ) and lower relative abundance of *N. stricta* (C:N of  $34.7 \pm 0.88$ ). C:N ratio did not differ between the exclosures ( $32.45 \pm 1.26$ ) and the grazed plots (Table 1). The analyses of vegetation composition, biomass and carbon concentration were not sensitive to the removal of mainland sites that were not on the lakeshore (Appendix "D", Supplementary material 4). However, after excluding the sites away from the lakeshore, the exclosed vegetation carbon stock was significantly lower in both exclosures ( $122.25 \pm 9.58$ ) and islands ( $65.19 \pm 8.88$ ) than where grazed ( $171.84 \pm 19.25$ ).

## Birch

The mean density of birch individuals on the three islands ranged from 0.2 to 0.3  $\text{m}^{-2}$ , and the mean stem density (given that the majority of individuals were polycormic) ranged between 0.4 and 0.9  $\text{m}^{-2}$ . Birch was completely absent from the grazed plots, and a total of one individual sapling was present within the ten exclosures (but not sampled). Thus, the mean density within the exclosures is 0.0001  $\text{m}^{-2}$  and for the purpose of this study is assumed equal to 0.

The median height of the birch on the islands was 151 cm (quartiles 106 and 196 cm). The esti-



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

mated median age of the birch (based on relationship between stem diameter and age, Figure B1 in Appendix B, Supplementary material 2) was between 33 and 35 years with the maximum being 69, 65 and 66 years on islands 1–3, respectively (Figure B3 in Appendix B, Supplementary material 2). The age distributions of the birch on the three islands were uni-modal (Figure B3 in Appendix B, Supplementary material 2). The aboveground birch carbon pool on the islands ranged between 309 and 666  $\text{g m}^{-2}$ , with an overall mean of 496  $\text{g m}^{-2}$  (SE = 104,  $n = 3$ , Table 1; Figure 3A). The total vegetation carbon stock (field-layer vegetation plus birch) was significantly higher on the islands ( $561.3 \text{ g m}^{-2} \pm 7.7$ ) than where grazed ( $178.5 \text{ g m}^{-2} \pm 15.0$ , Figure 3A).

## Soil

Organic-horizon depth was highly variable between plots but tended to be deeper on the islands ( $21.5 \text{ cm} \pm 8.0$ ) than either the grazed ( $16.4 \text{ cm} \pm 3.3$ ) or

**Table 1.** Carbon Stocks of Field Vegetation (All Aboveground Vegetation Other Than Trees), Birch and Organic Soil in Quadrats with a Long History of Grazing, Following 12 Years of Large-herbivore Exclusion and on Large-Herbivore Free Islands

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>
	<i>F</i> <sub>2,53</sub> = 5.48, <i>P</i> = 0.007	<i>F</i> <sub>2,53</sub> = 1.26, <i>P</i> = 0.293	<i>F</i> <sub>2,54</sub> = 9.30, <i>P</i> < 0.001	<i>F</i> <sub>2,53</sub> = 5.54, <i>P</i> = 0.007
Birch ( <i>n</i> )	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>
<b>Organic soil (<i>n</i>)</b>	<b>Organic soil depth<sup>a</sup> (cm)</b>	<b>C content (%)</b>	<b>C:N</b>	<b>C stock (kg m<sup>-2</sup>)</b>
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
	<i>F</i> <sub>2,23</sub> = 0.87, <i>P</i> = 0.432	<i>F</i> <sub>2,23</sub> = 5.12, <i>P</i> = 0.014	<i>F</i> <sub>2,23</sub> = 5.09, <i>P</i> = 0.015	<i>F</i> <sub>2,23</sub> = 1.68, <i>P</i> = 0.208
Soil type	<i>F</i> <sub>2,23</sub> = 31.06, <i>P</i> < 0.001	<i>F</i> <sub>2,23</sub> = 2.25, <i>P</i> = 0.127	<i>F</i> <sub>2,23</sub> = 1.25, <i>P</i> = 0.304	<i>F</i> <sub>2,23</sub> = 21.75, <i>P</i> < 0.001

The C content and C:N ratio of each fraction are presented along with biomass of field vegetation and birch, and the depth of organic soil. Mean and standard errors are shown estimated after pooling pseudo-replicates within each site or island (*n* = 10 for the grazed and exclosures, and 3 for the islands, reduced to *n* = 8 for the exclosed sites for soil depth and soil C stock). Likelihood ratio Wald *F* tests are shown for treatment in a mixed effects model with site as a random intercept. For the organic soil, soil type was included as a covariate in the models and likelihood ratio Wald *F* tests are shown for soil type in addition. Variables that significantly differ in exclosures or islands from the grazed plots are denoted by bold text. Note that C stock units vary between vegetation and soil pools.

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

exclosed (14.0 cm ± 3.0) treatments (Table 1). Similarly, the organic-horizon soil carbon pool tended to be higher on the islands (20.9 kg m<sup>-2</sup> ± 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 variability (Table 1; Figure 3B), and the difference was not significant. If island 2 was omitted (because the soils were Histosols), the total soil organic carbon pool on the islands was 13.53 ± 5 kg C m<sup>-2</sup> (depth 14.55 ± 4.7 cm) which is in the same range as for the grazed and exclosed plots (Table 1). Neither organic-horizon soil depth (*F*<sub>2,18</sub> = 0.61, *P* = 0.6) nor organic-horizon soil carbon pool (*F*<sub>2,18</sub> = 0.78, *P* = 0.5) differed significantly between the grazing treatments after accounting for differences in soil type. Organic-horizon soil depth and carbon pools were more influenced by soil type than by sheep exclusion (Table 1). However, the C:N ratio of the organic-horizon soil was significantly higher on the islands (20.1 ± 0.9) than where grazed (15.0 ± 0.5, Table 1, *F*<sub>2,54</sub> = 7.5, *P* = 0.001). Soil C:N was not associated with vegetation C:N (Pearson's product moment correlation: *r* = -0.16, *t*<sub>67</sub> = -1.28, *P* = 0.20). When the analyses were repeated with inclusion of only the five lakeside and low-elevation mainland sites (sites 1–5, Figure 1), the same patterns were apparent. However, the higher C:N ratio on the islands than where grazed was not significant (although margin-

ally so) when the non-lakeshore plots were excluded (Appendix "D," *F*<sub>2,12</sub> = 3.67, *P* = 0.057).

## DISCUSSION

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

To assess the importance of our findings to the global carbon cycle, we extrapolated our findings across the whole of Norway. Land-use change could lead to forest expansion in Norway of a total



land area of 48,800 km<sup>2</sup>, of which 10,992 km<sup>2</sup> is above 800 m in elevation (Bryn and others 2013). The mean difference in aboveground carbon stock shown in our study between the long-term grazed and long-term ungrazed treatments is 0.38 kg m<sup>-2</sup> (SE = 0.14) in the aboveground pool (Figure 3). If Norwegian forest expansion was to meet its potential following cessation of sheep grazing, and our study is representative of the vegetation response across the region of potential forest expansion in Norway (Bryn and others 2013), we roughly estimate that the carbon storage in Norwegian alpine ecosystems could increase by up to 4.2 million ton C in the aboveground vegetation pool. This would represent an increase of only 2% on the total aboveground C stocks in Norwegian forests (Kjønaas and others 2000). However, a cessation of sheep grazing is in conflict with the policy goal of increasing food production within Norway by 20% by 2020 (Norwegian Ministry of Agriculture and Food 2011).

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

Herbivores are known to play a role in ecosystem C dynamics (Frank and Groffman 1998; Olofsson

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

It has been suggested that the lower carbon pool in forest than tundra is driven by high plant activity during the peak growing season within birch forests, priming the decomposition of older soil organic matter and hence reduction in forest soil carbon (Hartley and others 2012). However, a reduction in soil carbon stocks following an increase in grazing intensity (as well as an increase in soil carbon stocks following a decrease in grazing intensity) has also been observed in an alpine ecosystem independently of birch colonisation (Martinsen and others 2011); this was driven by grazers at high density increasing the breakdown of particulate organic matter, and reducing litter quantity (Martinsen and others 2011) indicating that grazing is a key driver of carbon storage in tundra ecosystems. We observed that the soil C:N ratio was higher under a forest canopy than where grazing livestock prevented forest establishment, probably due to a greater fraction of woody mate-

rial under forests. We did not find an association between the field-layer vegetation C:N and the soil C:N across samples, however, the birch C:N ratio was unsurprisingly far higher than the field vegetation. Thus, birch litter quality and quantity may also play a role in regulating carbon dynamics in our system, potentially compensating for decomposition of old organic matter driven by birch colonisation.

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

### Forest Development

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

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

### Short- and Long-Term Changes

Although birch recruitment in the short term did not reflect the longer term forest development, the short-term change in the rest of the vegetation did reflect the longer term change. Following 12 years of grazer exclusion, the grazing-resistant *N. stricta* was lower in abundance and the highly palatable *D. flexuosa* was higher in abundance than where grazed. Although the relative abundances were not significantly different at this point, the rates of change in these species did significantly differ after just 4 years of livestock exclusion (Austrheim and others 2007). The short-term vegetation change was associated with a decrease in aboveground vegetation biomass and carbon content. Short-term change appears to be in the same direction as long-term change, with *D. flexuosa* being the dominant field-layer vascular plant on the islands, and a lower abundance of *N. stricta*. Herb species, notably *C. suecica* were also relatively abundant on the islands with similarities in vegetation composition

to the dwarf cornel birch forest described by Wehberg and others (2005). The trend for short-term changes in vegetation to be indicative of long-term changes following herbivore removal, albeit with a lag time, has also been reported in the case of reindeer exclusion in sub-arctic tundra ecosystems (Olofsson 2006). However, it is important to note that the abandonment of livestock grazing may lead to the alpine tundra becoming a carbon source in the short term as the field-layer transitions from a *Nardus* dominated state to a *Deschampsia* dominated state with lower carbon content, before birch forest establishment occurs.

## CONCLUSIONS

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

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