

Consequences of warming on tundra carbon balance determined by reindeer grazing history

Maria Väisänen^{1*}, Henni Yläne^{1,2}, Elina Kaarlejärvi³, Sofie Sjögersten⁴, Johan Olofsson³, Neil Crout⁴ and Sari Stark¹

Arctic tundra currently stores half of the global soil carbon (C) stock¹. Climate warming in the Arctic may lead to accelerated CO₂ release through enhanced decomposition and turn Arctic ecosystems from a net C sink into a net C source, if warming enhances decomposition more than plant photosynthesis². A large portion of the circumpolar Arctic is grazed by reindeer/caribou, and grazing causes important vegetation shifts in the long-term. Using a unique experimental set-up, where areas experiencing more than 50 years of either light (LG) or heavy (HG) grazing were warmed and/or fertilized, we show that under ambient conditions areas under LG were a 70% stronger C sink than HG areas. Although warming decreased the C sink by 38% under LG, it had no effect under HG. Grazing history will thus be an important determinant in the response of ecosystem C balance to climate warming, which at present is not taken into account in climate change models.

In northernmost Eurasia, the management of semi-domesticated reindeer (*Rangifer tarandus* L., the same species as wild caribou in North America) constitutes an important means of land-use, and reindeer husbandry exerts a strong control over ecosystem functioning³. Grazing often increases the proportion of graminoids at the expense of evergreen and deciduous shrubs, and may enhance litter and soil C decomposition^{4,5}. Previous studies have shown that reindeer grazing has the potential to mitigate the effects of climate warming on vegetation by suppressing the growth of deciduous shrubs that otherwise benefit from climate warming^{6,7}. Short-term grazer exclusion and warming studies have also indicated that Arctic grazers may limit the positive effect of warming on the gross ecosystem production (GEP), and therefore, grazed areas under warmer conditions are weaker C sinks (negative net ecosystem exchange; NEE) than ungrazed areas⁸. However, vegetation shifts after herbivore exclusion are highly transient in time^{5,9}; thus, assessments of the impact of long-term grazing regimes on the responses of ecosystem C balance to climate warming are needed. The key questions are how the vegetation shifts induced by long-term grazing alter the effects of warming on GEP, and how grazing interacts with the indirect mechanisms associated with warming, such as the expansion of deciduous shrubs, that greatly affect conditions for decomposition¹⁰.

We examined the effects of long-term grazing history on ecosystem responses to warming and fertilization in a subarctic tundra heath in northern Norway (69° 31' N, 21° 19' E) during 2010–2012. We addressed two main research questions. First, what is the effect of long-term grazing on C fluxes—NEE, GEP and ecosystem respiration (R_e ; mg CO₂-C m⁻² h⁻¹)—under

ambient conditions? Second, how do responses of C fluxes to warming and fertilization differ under different long-term grazing intensities? To answer these questions, factorial warming and fertilization experiments were established on two sides of a reindeer pasture rotation fence built in the 1960s. Differing grazing pressure over the past 50 years has formed two distinct types of vegetation on the different sides of the fence; the vegetation under light grazing (LG) is dominated by dwarf shrubs (*Empetrum nigrum* ssp. *hermaphroditum*, *Betula nana*, *Vaccinium vitis-idaea*, *V. myrtillus* and *V. uliginosum*), whereas the vegetation under heavy grazing (HG) is dominated by graminoids (*Carex* spp., *Deschampsia flexuosa*, *Festuca* spp. and *Juncus trifidus*) with rapid growth and high litter decomposition rates¹¹. In 2010, we also established short-term reindeer exclosures on HG tundra (HGexc) to test how a sudden termination of grazing would influence C fluxes and interact with warming and fertilization. We hypothesized the following: HG tundra is a weaker sink for C (NEE less negative) via increased R_e because grazing enhances litter and soil C decomposition; warming and fertilization increase the GEP to a greater extent under HG, where graminoids respond rapidly to environmental change. NEE is determined by the balance between GEP and R_e , thus, we expected the response of NEE to warming to be weaker under HG than LG; and excluding reindeer grazing on HG will amplify the effects of warming and fertilization on GEP, thus, we expected the response of NEE to warming to be weakest under HGexc.

Consistent with our first hypothesis, the midday seasonal averages showed that LG was a 70% stronger C sink than HG under ambient conditions (NEE more negative under LG; Fig. 1a, control plots; $F_{2,21} = 4.99$, $P = 0.017$). As predicted, NEE difference between long-term grazing intensities was explained by higher R_e under HG than LG (Fig. 1b, control plots; $F_{2,21} = 5.34$, $P = 0.013$) rather than a difference in the GEP (Fig. 1c, control plots; $F_{2,21} = 0.23$, $P = 0.8$). In contrast with long-term responses, the short-term exclusion of reindeer had no detectable effects on the tundra C balance (no difference between HGexc and HG; Fig. 1a–c). The higher C sink under LG is in agreement with studies showing a stronger C sink in shrub- than graminoid-dominated tundra^{12,13} and findings of increased C sink strength due to herbivore exclusion^{8,14}. However, short-term exclosure studies have linked the effects of geese¹⁴ and ungulates⁸ to shifts in the GEP, whereas our study found that the effect of grazing on NEE was driven by a shift in R_e . Higher R_e under HGexc and HG is probably mediated by increased decomposition. Grazing increases the proportion of graminoids in relation to evergreen and deciduous shrubs and bryophytes, increases the abundance of litter

¹Arctic Centre, University of Lapland, P.O. Box 122, FIN-96101 Rovaniemi, Finland, ²Department of Biology, University of Oulu, FIN-90014 Oulu, Finland, ³Department of Ecology and Environmental Science, University of Umeå, SE-901 87 Umeå, Sweden, ⁴School of Biosciences, University of Nottingham, Sutton Bonington Campus, Sutton Bonington, Leicestershire, LE12 5RD, UK. *e-mail: maria.vaisanen@ulapland.fi

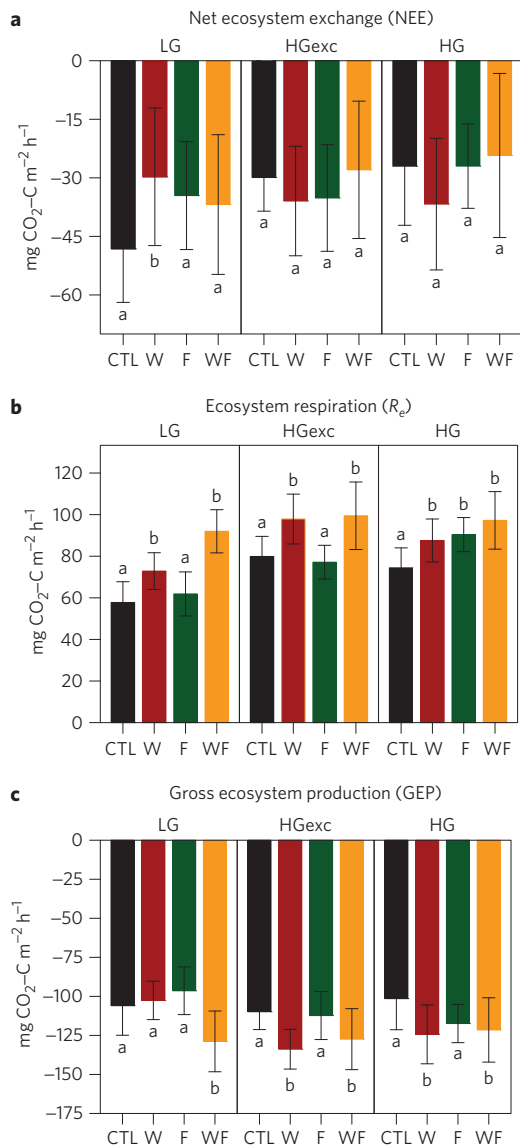


Figure 1 | Midday (08:00–18:00) CO₂-C flux rates averaged over growing seasons 2011–2012 in a subarctic tundra heath under light grazing (LG), short-term reindeer exclusion (HGexc) and heavy grazing (HG) by the reindeer. Differences in NEE (a), R_e (b) and GEP (c) in control (CTL), warmed (W), fertilized (F), and warmed and fertilized (WF) plots. Letters a and b denote significant differences among treatments within grazing intensities. LG was a stronger C sink than HGexc and HG, as a result of a similar GEP, but higher R_e under HGexc and HG than LG. Warming reduced the C sink under LG (NEE less negative) but not under HGexc and HG, because warming increased R_e similarly in all grazing intensities whereas it increased GEP only under HGexc and HG. Bars represent mean \pm s.e.m., $n=8$.

(Fig. 2a,b and Supplementary Table 1), and enhances litter¹⁵ and soil⁴ decomposition. Enhanced soil nitrogen¹⁶ and higher growing season soil temperatures (9.0 ± 0.3 and 7.5 ± 0.3 °C for HG and LG, respectively; Supplementary Table 2) may further intensify R_e under HG. Thus, long-term grazing simultaneously alters a number of ecosystem properties that have the potential to influence R_e . These ongoing grazer-mediated processes cannot be detected after short-term experimental herbivore exclusion. As the long-term and short-term effects of herbivory derive from different mechanisms and processes, the long-term effects of herbivory are both quantitatively and qualitatively different from the short-term effects.

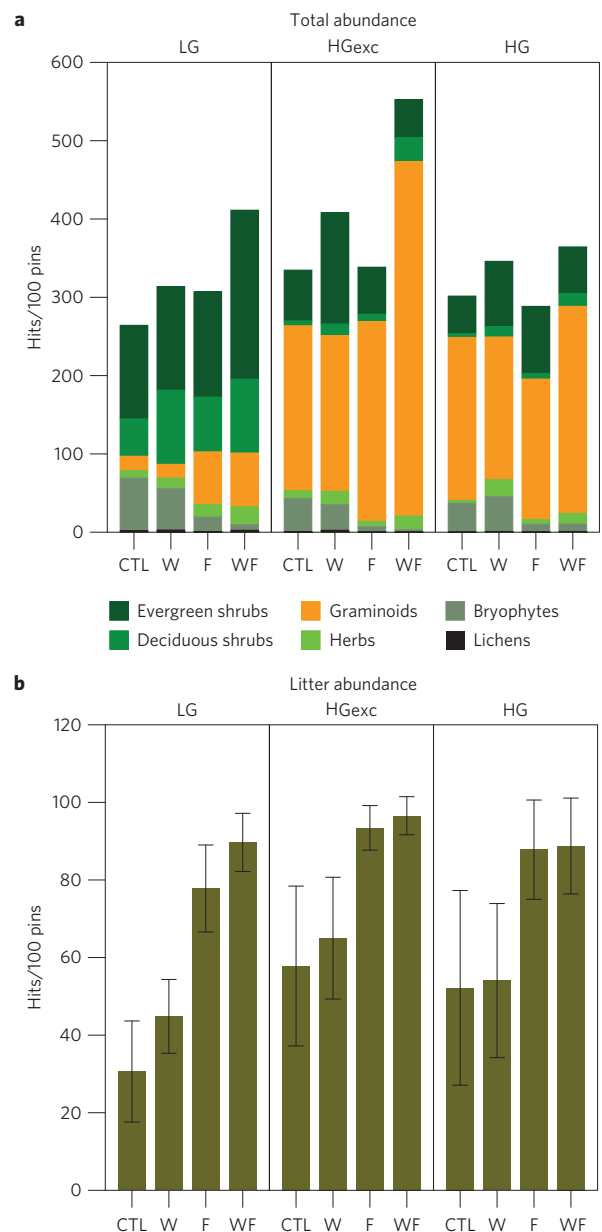


Figure 2 | The total abundance of vegetation and litter in a subarctic tundra heath under light grazing (LG), short-term reindeer exclusion (HGexc) and heavy grazing (HG) by the reindeer. Average abundances of plant functional groups (a) and litter (b) on the basis of point-intercept analysis in control (CTL), warmed (W), fertilized (F), and warmed and fertilized (WF) plots in August 2012 after three years of treatments. Evergreen and deciduous shrubs were more abundant under LG, whereas graminoids were more abundant under HGexc and HG. Warming increased plant abundance in all grazing intensities. The abundance of litter was higher under HGexc and HG than LG and significantly increased by fertilization (Supplementary Table 1). Bars represent the mean for plant abundance and mean \pm s.e.m. for litter abundance, $n=8$.

Consistent with our second hypothesis, warming increased GEP under HGexc and HG, and had no effect under LG (Fig. 1c; significant three-way $G \times W \times F$ interaction; Supplementary Table 3). The responses in R_e to warming were consistent at all grazing intensities (Fig. 1b and Supplementary Table 3), which in combination with the varying effects on the GEP had a major effect on the ecosystem C sink strength: warming under LG decreased the C sink by 38% (NEE less negative), whereas the NEE under HGexc

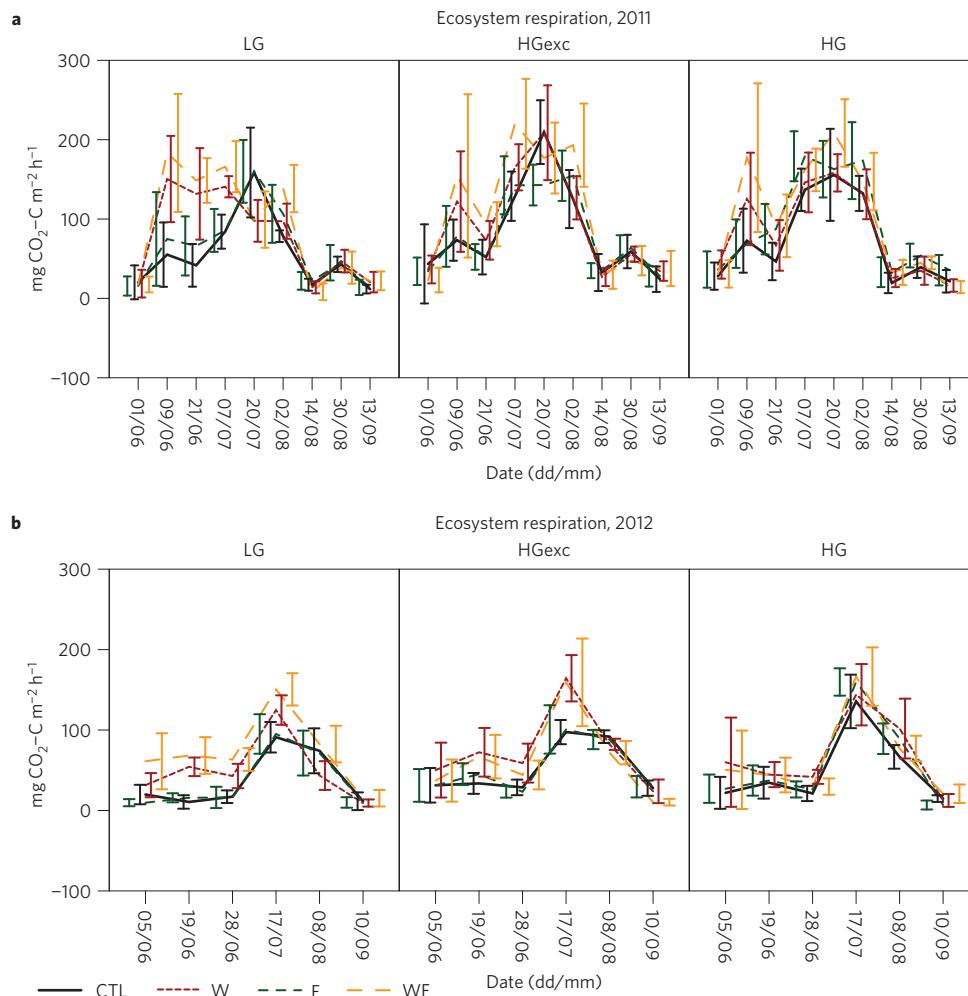


Figure 3 | Seasonal patterns in R_e in a subarctic tundra heath under light grazing (LG), short-term reindeer exclusion (HGexc) and heavy grazing (HG) by the reindeer. Rates were measured in control (CTL), warmed (W), fertilized (F) and warmed and fertilized (WF) plots simultaneously on different grazing intensities in varying weather conditions on nine occasions during growing season 2011 (a) and on six occasions during growing season 2012 (b). Warming increased R_e in the early growing season to a stronger extent under LG than HGexc and HG (Supplementary Tables 4 and 5). Lines represent the mean \pm s.e.m., $n=8$.

and HG remained unaffected (Fig. 1a; $G \times W \times F$ interaction; Supplementary Table 3). The warming effects on modelled seasonal sums of NEE, GEP and R_e agreed with the warming effects on midday seasonal averages (Supplementary Fig. 1). This finding is the first to demonstrate that the responses of the ecosystem C balance to global climate warming may differ drastically depending on the grazing history of the system. Another important finding was that existing differences in the NEE between the grazing intensities under ambient conditions were negated by warming; the NEE did not differ between grazing intensities in the warmed plots (Fig. 1a and Supplementary Table 3). The observed effects of grazing on C balances under the present climatic conditions may thus not be applicable in a warmer climate. Contrasting with our third hypothesis, the short-term grazer exclusion had no interaction with the effects of warming on C fluxes (Fig. 1a–c). Divergent short- and long-term effects of grazing on the responses of C fluxes to warming is a novel finding and shows that the short-term grazer exclusion is not necessarily adequate for evaluating the long-term ecosystem feedbacks due to grazing with respect to a changing climate.

In disagreement with our second hypothesis, experimental fertilization had weak effects on the ecosystem C fluxes at all levels of grazing intensity (Fig. 1 and Supplementary Table 3). As found in previous studies^{17,18}, fertilization exerted a modest increase in R_e ,

although this seemed to occur only on HG (c. 16%; Fig. 1b and Supplementary Table 3). Although the main effect of fertilization was weak, fertilization showed interactive effects on GEP and NEE with warming and grazing intensity that may provide insights into the mechanisms by which long-term grazing directs the effects of warming on C fluxes. Under LG, warming or fertilization alone had no effect on the GEP, whereas combined warming and fertilization increased it by 22% (Fig. 1c; significant $G \times W \times F$ interaction; Supplementary Table 3). As warming increased the GEP only after nitrogen (N) limitation was alleviated by fertilization, we suggest that GEP under LG was co-limited by low soil N availability and temperature. Increased GEP by combined warming and fertilization also negated the effect of warming on NEE (Fig. 1a). The lack of similar interactive effects of warming and fertilization under HGexc and HG indicates that GEP under high grazing intensity may not be limited by nutrients, probably as a result of the positive effect of long-term grazing on soil N availability¹⁶. These findings indicate that the indirect effect of herbivory on the soil nutrient cycling constitutes an important mechanism by which herbivores influence the ecosystem's response to warming.

Temporal patterns in the ecosystem C fluxes revealed a variation in the strength of the warming effects throughout the growing season; notably, the warming-induced increase in R_e was most

pronounced during the early growing season (Fig. 3a,b and Supplementary Tables 4 and 5), when the ecosystem also was a C source during midday (NEE positive; Supplementary Fig. 2). Although this did not affect the R_e averaged over the entire growing season, the early growing season responses of R_e to warming were significantly stronger under LG than HGexc and HG (significant $G \times W$ interactions; Supplementary Table 5). We propose that increased temperatures during the early growing season may enhance the maintenance and growth respiration of dwarf shrubs¹² and strongly affect R_e . As winter-time CO_2 fluxes are substantial in the annual C budget in northern ecosystems¹³, it was important to consider how grazing or experimental treatments influenced CO_2 release during the winter. We found no effects of grazing or treatments on the winter-time soil respiration in 2010–2011 (Supplementary Table 3; $0.07 \pm 0.001 \text{ g CO}_2\text{-C m}^{-2}$ averaged over all grazing intensities and treatments), indicating that the effects of grazing and warming were manifested only during the growing season.

Experimental warming increased the total plant biomass (Fig. 2a and Supplementary Table 1) and normalized difference vegetation index (NDVI; Fig. 4 and Supplementary Table 6) at all grazing intensities. The fact that warming similarly increased the aboveground plant biomass at all grazing intensities while increasing the GEP only under HGexc and HG most probably results from a high resource allocation to roots rather than shoot biomass^{5,19}. The plant biomass was higher, although not statistically significantly (Supplementary Table 1), in the short-term grazer exclosures (Fig. 2a), which agrees with the theoretical concept that herbivory may limit plant biomass in tundra²⁰. Supporting earlier findings that grazing drastically suppresses the warming-induced increase in evergreen dwarf shrubs^{6,7}, warming under HGexc more than doubled the abundance of evergreen dwarf shrubs while exerting weaker effects under HG (Fig. 2a and Supplementary Table 1). Fertilization under HGexc caused a strong increase in graminoids (Fig. 2a and Supplementary Table 1), which get suppressed by grazers under HG owing to the high palatability of graminoids for reindeer²¹. The responses of vegetation to the short-term exclusion highlight that a sudden termination of heavy grazing pressure at nutrient-rich tundra may cause rapid changes in the aboveground vegetation²².

Our study demonstrated for the first time that grazing history (at a timeframe of 50 years) may largely regulate the responses of the ecosystem balance to climate change. Given that most of the tundra biome is grazed by reindeer or caribou, our finding alters predictions regarding how a warmer climate will influence global C cycles and feedbacks in response to the future climate. Reindeer husbandry in northern Eurasia is an important traditional and contemporary means of land-use, with reindeer densities averaging between 1.2–1.7 reindeer km^{-2} (ref. 3). However, as grazing intensity at decadal and centennial timescales has varied greatly at different locations as a result of reindeer management practices or historical events influencing reindeer population sizes and migration routes²³, different tundra sites possess highly variable grazing histories that result from the combination of natural abiotic and biotic factors, cultural practices and political decisions. Studies on past reindeer grazing patterns at regional and pan-Arctic scales are extremely scarce^{24,25}, forming a large deficit in our ability to assess historical grazing pressures. Although grazing pressure by wild caribou in Northern America is lighter (approximately 0.25–1.3 caribou km^{-2}), it still exerts a major influence on vegetation^{21,26} and ecosystem responses to warming^{6,7,27}. Our results show that it is critical to know the grazing history before current tundra C balances and their responses to climate warming can be understood. A holistic approach that integrates the past grazing patterns and the future prospects of grazing intensity is needed to predict the effects of climate warming. Other major grazers of the Arctic (for example,

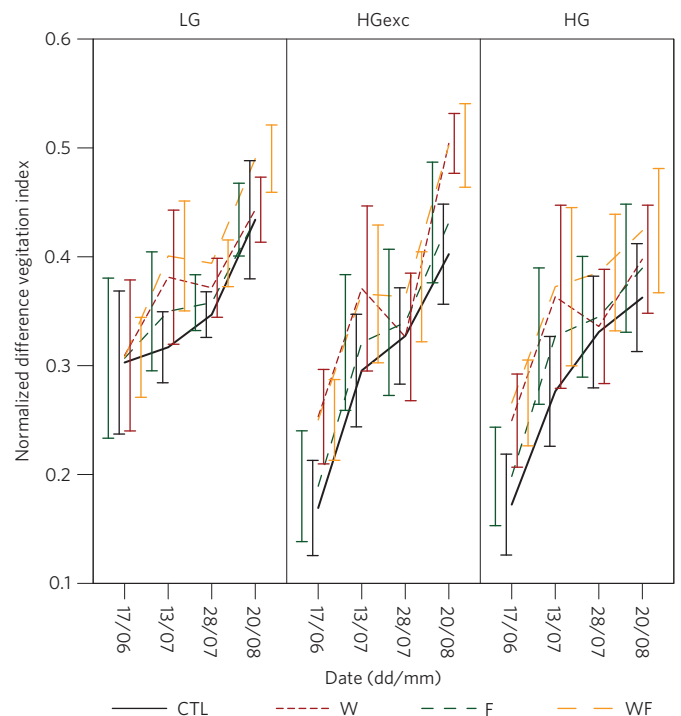


Figure 4 | Normalized difference vegetation index in a subarctic tundra heath under light grazing (LG), short-term reindeer exclusion (HGexc) and heavy grazing (HG) by the reindeer. NDVI was assessed in control (CTL), warmed (W), fertilized (F), and warmed and fertilized (WF) plots analysed on four occasions in growing season 2012. Warming increased NDVI in all grazing intensities (Supplementary Table 6). Lines present the mean \pm s.e.m., $n=8$.

moose, muskoxen, lemming, geese) also need to be considered. We propose that future research to further understanding of the relationship between grazing intensity and C balance under warming could potentially provide tools to counteract increases in C release from the tundra, which are at present subject to rigorous debate owing to their potential for climate feedback.

Methods

The site was located above the tree line (600–700 m asl) on a northern slope of Raisduoddar Fjell (69° 31' N, 21° 19' E) in suboceanic northern Norway. A pasture rotation fence built in the 1960s divides the area into a lightly grazed migration range (LG) and a heavily grazed summer range (HG) experiencing intensive grazing during reindeer migration in August. In 2010, eight blocks traversing the LG and HG side of the fence were selected with similar topography and altitude within blocks. Four plots on both LG and HG, were assigned to the following treatments: control (CTL), fertilized (F), warmed (W) and warmed and fertilized (WF). Warming was achieved using hexagonal open top chambers (OTCs) made from 1.5 mm thick and 0.4 m high polycarbonate deployed in the early growing season (16 June 2010, 31 May 2011, 5 June 2012) and removed just before reindeer arrival (7 August 2010, 4 August 2011, 8 August 2012). OTCs increase daytime air (1.2°–1.8 °C) and surface temperature (1 °C) corresponding to predicted climate in year 2050²⁷ but also affect humidity and wind²⁸. Here, OTCs increased surface temperatures by 0.9 °C on LG and by 1.8 °C on HG, with no effect on soil temperature (Supplementary Information). Fertilization was applied as ammonium nitrate (NH_4NO_3) equivalent to 10 g N m^{-2} in 11 of water in the early growing season (16 June 2010, 9 June 2011, 28 June 2012). There is a potential bias due to a single N application²⁹. Nitrogen dosage corresponds to the predicted soil N increase after a 7 °C increase in air temperature³⁰. Plots on HG were divided into grazed (HG) and ungrazed (HGexc) subplots protected from grazing by short-term exclosures (height 0.9 m, mesh 40 × 40 mm) established before reindeer migration and removed after all reindeer had left the area to avoid winter-time snow accumulation. Some browsing, trampling and fertilization were detected on HGexc due to early arrival of some reindeer. The experimental design did not include short-term exclosures on LG owing to very low grazing pressure. Mean temperature and precipitation in 2010 and 2012 were close to the

long-term average (-0.5°C , 500 mm–700 mm), whereas in 2011 the average temperature was $1.5^{\circ}\text{--}2.0^{\circ}\text{C}$ warmer and precipitation was 125% of the average.

Plant and litter abundance was recorded in mid-Aug 2010–2012. A modified point intercept method was used in positioning 50 cm wide rows of ten vertical pins at 10 cm distance from each other (eight rows on LG, four rows on HGexc and HG). The total number of hits per species was recorded, normalized to hits per 100 pins, and pooled into growth forms (evergreen dwarf shrubs, deciduous shrubs, graminoids, herbs, bryophytes and lichens).

NEE (light measurement) and R_e (dark measurement; chamber covered with an opaque white hood) were measured during growing seasons 2011 (nine times) and 2012 (six times) using custom-made cylinders (2 mm thick transparent polycarbonate, diameter 30 cm, height 39 cm) placed on plots and sealed to the ground with a plastic hem to create a closed system while avoiding damage to the vegetation. Air inside the chamber was mixed with a battery-driven fan. CO_2 -fluxes (ppm), relative humidity (%) and temperature ($^{\circ}\text{C}$) were recorded using a Vaisala Carbon Dioxide Probe (GMP343) and Humidity and Temperature Probe (HMP75) fitted to the cylinder top. Data was logged every 15 sec for 5 min using a Vaisala Measurement Indicator (MI70). Cylinders were vented between measurements to restore the CO_2 concentration to a basal level. GEP was obtained by subtracting R_e from NEE. The mean seasonal daytime fluxes ($\text{mg CO}_2\text{-C m}^{-2}\text{ h}^{-1}$) of NEE, GEP and R_e were calculated. The seasonal sum of C fluxes was assessed by a modelling approach (Supplementary Information).

Treatment effects on the midday average of NEE, GEP and R_e and vegetation were analysed by a mixed model with grazing (G), warming (W) and fertilization (F) as fixed factors, block nested with grazing as a random factor and year (Y) as a repeated factor. A Least Significant Difference (LSD) test was conducted to denote significant treatment effects within grazing intensities. To verify the main effect of grazing on CO_2 fluxes, analysis was separately conducted for control plots. Sampling date (D) was used as a repeated factor for the NDVI and daily CO_2 flux rates. Month (M) was used as a repeated factor for the soil temperature. The treatment effects on wintertime R_e were analysed without a repeated factor. In cases of significant interactions among factors, treatment effects were separately analysed for D, M or grazing intensity. Akaike's information criteria and residual plots were used to assess the model fit and transformations were made to meet the assumptions of a mixed model when necessary. The degrees of freedom are obtained by the Satterthwaite approximation. Statistical analyses were conducted using PASW Statistics 18.0 for Windows (PASW).

Received 22 October 2013; accepted 27 January 2014;
published online 16 March 2014

References

- Tarnocai, C. *et al.* Soil organic carbon pools in the northern circumpolar permafrost region. *Glob. Biogeochem. Cycle* **23**, GB2023 (2009).
- Davidson, E. A. & Janssens, I. A. Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. *Nature* **440**, 165–173 (2006).
- Forbes, B. C. & Kumpula, T. The ecological role and geography of reindeer (*Rangifer tarandus*) in northern Eurasia. *Geogr. Compass* **3**, 1356–1380 (2009).
- Stark, S., Strömmer, R. & Tuomi, J. Reindeer grazing and soil microbial processes in two suboceanic and two subcontinental tundra heaths. *Oikos* **97**, 69–78 (2002).
- Olofsson, J., Stark, S. & Oksanen, L. Reindeer influence on ecosystem processes in the tundra. *Oikos* **105**, 386–396 (2004).
- Post, E. & Pedersen, C. Opposing plant community responses to warming with and without herbivores. *Proc. Natl Acad. Sci. USA* **105**, 12353–12358 (2008).
- Olofsson, J. *et al.* Herbivores inhibit climate-driven shrub expansion on the tundra. *Glob. Change Biol.* **15**, 2681–2693 (2009).
- Cahoon, S. M., Sullivan, P. F., Post, E. & Welker, J. M. Large herbivores limit CO_2 uptake and suppress carbon cycle responses to warming in West Greenland. *Glob. Change Biol.* **18**, 469–479 (2012).
- Olofsson, J. Short- and long-term effects of changes in reindeer grazing pressure on tundra heath vegetation. *J. Ecol.* **94**, 431–440 (2006).
- Myers-Smith, I. H. *et al.* Shrub expansion in tundra ecosystems: Dynamics, impacts and research priorities. *Environ. Res. Lett.* **6**, 045509 (2011).
- Hobbie, S. E. Temperature and plant species control over litter decomposition in Alaskan tundra. *Ecol. Monogr.* **66**, 503–522 (1996).
- Cahoon, S. M., Sullivan, P. F., Shaver, G. R., Welker, J. M. & Post, E. Interactions among shrub cover and the soil microclimate may determine future Arctic carbon budgets. *Ecol. Lett.* **15**, 1415–1422 (2012).
- Euskirchen, E., Bret-Harte, M. S., Scott, G. J., Edgar, C. & Shaver, G. R. Seasonal patterns of carbon dioxide and water fluxes in three representative tundra ecosystems in northern Alaska. *Ecosphere* **3**, 1–19 (2012).
- Sjögersten, S., van der Wal, R., Loonen, M. J. J. E. & Woodin, S. J. Recovery of ecosystem carbon fluxes and storage from herbivory. *Biogeochemistry* **106**, 357–370 (2011).
- Olofsson, J. & Oksanen, L. Role of litter decomposition for the increased primary production in areas heavily grazed by reindeer: A litterbag experiment. *Oikos* **96**, 507–515 (2002).
- Olofsson, J., Kitti, H., Rautiainen, P., Stark, S. & Oksanen, L. Effects of summer grazing by reindeer on composition of vegetation, productivity and nitrogen cycling. *Ecography* **24**, 13–24 (2001).
- Volk, M. *et al.* Subalpine grassland carbon dioxide fluxes indicate substantial carbon losses under increased nitrogen deposition, but not at elevated ozone concentration. *Glob. Change Biol.* **17**, 366–376 (2011).
- Christiansen, C. T., Svendsen, S. H., Schmidt, N. M. & Michelsen, A. High Arctic heath soil respiration and biogeochemical dynamics during summer and autumn freeze-in-effects of long-term enhanced water and nutrient supply. *Glob. Change Biol.* **18**, 3224–3236 (2012).
- Hafner, S. *et al.* Effect of grazing on carbon stocks and assimilate partitioning in a Tibetan montane pasture revealed by ^{13}C pulse labeling. *Glob. Change Biol.* **18**, 528–538 (2012).
- Eskelinen, A. Herbivore and neighbour effects on tundra plants depend on species identity, nutrient availability and local environmental conditions. *J. Ecol.* **96**, 155–165 (2008).
- Post, E. S. & Klein, D. R. Relationships between graminoid growth form and levels of grazing by caribou (*Rangifer tarandus*) in Alaska. *Oecologia* **107**, 364–372 (1996).
- Ravolainen, V. T. *et al.* Rapid, landscape scale responses in riparian tundra vegetation to exclusion of small and large mammalian herbivores. *Basic Appl. Ecol.* **12**, 643–653 (2011).
- Tommervik, H., Dunfjeld, S., Olsson, G. A. & Ostby Nilsen, M. Detection of ancient reindeer pens, cultural remains and anthropogenic influenced vegetation in Byrkjje (Borgefjell) mountains, Fennoscandia. *Landscape Urban Plan.* **98**, 56–71 (2010).
- Josefsson, T., Hörnberg, G. & Östlund, L. Long-term human impact and vegetation changes in a boreal forest reserve: Implications for the use of protected areas as ecological references. *Ecosystems* **12**, 1017–1036 (2009).
- Räsänen, S., Froyd, C. & Goslar, T. The impact of tourism and reindeer herding on forest vegetation at Saariselkä, Finnish Lapland: A pollen analytical study of a high-resolution peat profile. *Holocene* **17**, 447–456 (2007).
- Zamin, T. J. & Grogan, P. Caribou exclusion during a population low increases deciduous and evergreen shrub species biomass and nitrogen pools in low Arctic tundra. *J. Ecol.* **101**, 671–683 (2013).
- Elmendorf, S., Henry, G. H. R., Hollister, R. D. & Björk, R. G. Global assessment of experimental climate warming on tundra vegetation: Heterogeneity over space and time. *Ecol. Lett.* **15**, 164–175 (2012).
- Bokhorst, S. *et al.* Microclimate impacts of passive warming methods in Antarctica: Implications for climate change studies. *Polar Biol.* **34**, 1421–1435 (2011).
- Phoenix, G. K. *et al.* Impacts of atmospheric nitrogen deposition: Responses of multiple plant and soil parameters across contrasting ecosystems in long-term field experiments. *Glob. Change Biol.* **18**, 1197–1215 (2012).
- Mack, M. C., Schuur, E. A. G., Bret-Harte, M. S., Shaver, G. R. & Chapin, F. S. Ecosystem carbon storage in Arctic tundra reduced by long-term nutrient fertilization. *Nature* **43**, 440–443 (2004).

Acknowledgements

We thank A. Niva and S. Aakkonen for their valuable help with the field experiments. We thank Su. Katves and Si. Katves for assisting with vegetation recording and J. Hyvönen for helping with the statistical analysis. This study was funded by the Academy of Finland (project numbers 218121 and 130507).

Author contributions

S.St. and M.V. initiated and managed the field experiment. J.O. and S.Sj. contributed to the planning of the experiment. M.V. and H.Y. carried out C flux measurements with contributions from S.St. and S.Sj. E.K. and J.O. were responsible for plant and NDVI analyses. N.C. was responsible for modelling C fluxes. M.V. carried out the statistical analyses. M.V. and S.St. wrote the manuscript, to which all other authors contributed with discussions and text.

Additional information

Supplementary information is available in the [online version of the paper](#). Reprints and permissions information is available online at www.nature.com/reprints. Correspondence and requests for materials should be addressed to M.V.

Competing financial interests

The authors declare no competing financial interests.