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Distinguishing Rapid and Slow C Cycling Feedbacks to Grazing in Sub-arctic Tundra

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Abstract

Large grazers are known to affect ecosystem functioning even to the degree where ecosystems transition to another vegetation state. Alongside the vegetation change, several features of ecosystem functioning, such as ecosystem carbon sink capacity and soil carbon mineralisation rates, may be altered. It has remained largely uninvestigated how the grazing effects on carbon cycling processes depend on the duration of grazing. Here, we hypothesised that grazing affects ecosystem carbon sink through plant-driven processes (for example, photosynthesis) on shorter time-scales, whereas on longer time-scales changes in soil-driven processes (for example, microbial activity) become more important contributing to a decreased carbon sink capacity. To test this hypothesis, we investigated key processes behind ecosystem carbon cycling in an area that recently had become dominated by graminoids due to a high reindeer grazing intensity and compared these to the processes in an area of decades old grazing-induced graminoid dominance and in an area of shrub dominance with little grazer influence. In contrast to our hypothesis, areas of both old and recent grassification showed a similar carbon sink capacity. Yet the individual fluxes varied depending on the time passed since the vegetation shift: ecosystem respiration and mid-season photosynthesis were higher under old than recent grassification. In contrast, the extracellular enzyme activities for carbon and phosphorus acquisition were similar regardless of the time elapsed since grazer-induced vegetation change. These results provide novel understanding on how ecosystem processes develop over time in response to changes in the intensity of herbivory. Moreover, they indicate that both autotrophic and heterotrophic processes are controlled through multiple drivers that likely change depending on the duration of herbivory.

Key words: herbivory; reindeer; carbon balance; CO_2 flux; extracellular enzyme activities; microbial respiration.

Highlights

- Reindeer-induced vegetation change affects ecosystem CO_2 fluxes with a time-lag
- Soil C:N ratio and most enzyme activities changed parallel to the vegetation change
- Grazer control over plant- and soil-driven processes changes with the duration of grazing

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Author Contributions SS and HY concieved the study. HY performed field sampling and processed field CO_2 flux data. SS analysed enzymatic activities and microbial respiration. HY conducted statistical analyses. Both authors jointly wrote the text.

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Introduction

A line of evidence demonstrates that herbivores are an important component of ecosystem carbon (C) cycling (Hobbs 1996; Augustine and McNaughton 1998; Bardgett and Wardle 2003; Wardle and others 2004) to the extent that their regional effects on C sequestration have been compared to the anthropogenic greenhouse gas emissions of different countries (Schmitz and others 2014). By consuming plant biomass and inducing disturbance through trampling, herbivores induce changes in the community composition and overall abundance of vegetation, which reflect on the capacity of ecosystems to fix C (Cahoon and others 2012; Metcalfe and Olofsson 2015). Yet, herbivores also control a range of processes behind ecosystem C release: plant respiration reacts to biomass loss, and microbial activity and C mineralisation processes react to grazer-induced changes in the soil environment (Pastor and others 1996; Olofsson and Oksanen 2002; Stark and others 2007). Ultimately, herbivory-induced changes in C uptake and release equal to amount the C sink capacity of the ecosystem, referred to as net ecosystem exchange (NEE). These effects may range from neutral to positive and negative (Schmitz and others 2014).

A wide array of herbivory impacts on C cycling act through changes in soil nutrient cycles and altered soil properties. These are indirectly modified by vegetation changes that alter plant water uptake and albedo, as well as the quantity and quality of plant litter and exudates entering the decomposer subsystem (Olofsson and others 2004; Haynes and others 2014; te Beest and others 2016). Additionally, through the trampling of soil and the deposition of urine and faeces, herbivores compact the soil, provide patches of increased nutrient availability (Sirotnak and Huntly 2000; van der Wal and Brooker 2004; Barthelemy and others 2015) and relocate nutrients from the feeding to the resting places of herbivores (Abbas and others 2012; Stark and others 2015a; Sitters and others 2017). These changes may be substantial, and for example the impact of herbivory on soil temperatures and nutrient availability may even exceed the projected, global warming-induced changes (Olofsson and others 2004; Stark and others 2015b). In some cases, the changes result in a positive effect of herbivory on plant productivity and soil nitrogen (N) availability (Andriuzzi and Wall 2017) with consequences for soil nutrient stoichiometry and phosphorus (P) availability (Stark and Väisänen 2014; Sitters and others 2017). As nutrient availability is a strong determinant for both plant productivity, that is, C uptake by vegetation, and soil microbial activity in tundra (Weintraub and Schimel 2003; Schimel and Bennett 2004), grazing-induced changes in soil N cycling could feedback on ecosystem C cycling. Yet, in other cases, herbivory exerts the exact opposite effect and decreases productivity and nutrient cycling (Bardgett and Wardle 2003). Regardless of the direction of the herbivore effect, this may promote a vegetation shift into a different vegetation type (Bardgett and Wardle 2003; van der Wal 2006; Zimov and others 2012). When this takes place, the grazing effect on both C uptake and release may become independent of the actual grazing event and instead be driven by long-term changes in vegetation and soil C quality (Stark and Väisänen 2014).

Although the grazing-induced ecosystem consequences are well known, we still lack understanding on how the relative magnitude of the different cascading herbivore effects varies in time during a grazer-induced shift in vegetation. Contrasting with the direct effects of herbivory, the indirect soil feedbacks could act with different response times, be of transient or slow nature and they may accelerate or stabilise the rapid herbivory effects. Eventually, the effects of herbivory in decadal time-scales could be both quantitatively and qualitatively different from the short-term effects (that is, the first 5–10 years), because they derive from different mechanisms (Väisänen and others 2014). Within the first years, herbivore-induced changes in gross ecosystem production (GEP) might dominate the net effect of herbivory on NEE (as in Cahoon and others 2012; Metcalfe and Olofsson 2015), whereas on longer time-scales, the indirect changes in nutrient availability and soil microbial activity could become more important.

Here, we investigated the time scale of different grazing impacts on sub-arctic tundra ecosystem by comparing ecosystem processes among a shrub-dominated lightly grazed tundra and two areas with different-aged grazer-induced vegetation shifts ($>$ 60 years and $<$ 15 years). We used a reindeer pasture rotation fence in northern Norway, along which a yearly grazing pulse by reindeer (*Rangifer tarandus* L.) has replaced shrub-dominated tundra with graminoids (Olofsson and others 2001, 2004) over 60 years ago. Parallel to the *grassification* of vegetation, soil nutrient availability, microbial activity for C cycling (Olofsson and Oksanen 2002; Stark and others 2002; Olofsson and others 2004; Stark and Väisänen 2014), and ecosystem respiration had increased leading to a weaker net ecosystem C sink (that is, less negative NEE; Väisänen and others 2014). These chan-

ges have been detected decades after the change in grazing pressure. Now, we monitored ecosystem processes also in a third area, which was still dominated by shrubs 14 years earlier (Olofsson and others 2001, 2004), but has since gained dominance of graminoids (Ylänne and others 2018). The comparison of zones with decadal old graminoid dominance (Olofsson and others 2001), recent graminoid dominance (Ylänne and others 2018) and a control zone dominated by shrubs with decadal history of little reindeer influence provided unique means for investigating how grazer-induced shifts in the vegetation and soil processes contribute to the grazing effect on the C sink.

We quantified growing season C sink (NEE), photosynthesis (GEP), ecosystem respiration, C:N ratios of different ecosystem compartments, and soil microbial activities for C cycling. We expected that the plant-driven processes (that is, GEP) would represent more rapid responses to grazer-induced changes in vegetation, whereas the soil-driven processes (that is, microbial activities) would represent slow responses. More specifically, we hypothesised that ecosystem C uptake (GEP) would be similar in both graminoid-dominated areas and thereby not depend on the time since vegetation change. However, in terms of the soil microbial activity for C cycling, we hypothesised that the old vegetation type would control differences in soil C quality, and therefore, that soil C:N ratio and soil microbial activities under recent grassification would still be similar to those under shrub dominance. Furthermore, although ecosystem respiration is a result of both autotrophic and heterotrophic respiration, we expected it to follow the same trend as soil microbial activity and be lower under shrub dominance and recent grassification than under old grassification. Finally, this temporal discrepancy in grazer effects on plant-driven and soil-driven processes was expected to result in a higher net ecosystem C sink (that is, more negative NEE) under recent grassification than under old grassification.

Materials and Methods

Study Area and Experimental Set-Up

This study was conducted in Raisduoddar, northern Norway, approximately 100 m above the treeline (69°31′29 N, 21°19′16 E; altitude 430–570 m a.s.l.), where the dominant vegetation is of the *Empetrum–Dicranum*–Lichens type (Oksanen and Virtanen 1995). A reindeer pasture rotation fence built in the 1960s bisects the site separating the coastal summer ranges from the autumn, spring and winter ranges further inland. During late summer, reindeer start to migrate towards their autumn range, but they become halted by the fence, since it is not legal to enter autumn ranges at the time. This results in reindeer staying at one side of the fence for approximately 2–3 weeks. As a consequence, the summer range side of the fence is heavily grazed and trampled, which has resulted in graminoids gaining dominance over bryophytes, lichen and the deciduous and evergreen shrubs (Olofsson and others 2001). In contrary, the autumn–spring range near the fence is only sporadically used during the spring and autumn migrations, and the vegetation consists of both deciduous and evergreen shrubs underlain by a thick bryophyte layer (Olofsson and others 2001). Previously, the reindeer-induced vegetation transition had been limited to the immediate vicinity of the fence (Olofsson and others 2001) resulting from the tendency of reindeer to follow fences. However, between the years 2002 and 2014, the vegetation further away from the fence had gained graminoid dominance (Ylänne and others 2018).

To compare the ecosystem processes under recent and decades old grassification, we used eight geologically and topographically homogenous transects that bisected the reindeer fence 100 m apart from each other (Olofsson and others 2004; Ylänne and others 2018). The shrub-dominated control zone (LG) located approximately 10 m from the fence on the autumn-spring range, the zone with decades old reindeer-induced grassification (HG) located 10 m from the fence on the summer range, and the zone with recent reindeer-induced grassification (MG; Ylänne and others 2018) located 100 m from the fence in the summer range. Here, we refer to the zones with the same acronyms that have been used for the site before, where the letters denote the previous intensity of grazing (low, high, moderate). Notably, in the year of this study, 2014, reindeer activity analysed with trampling indicators did not differ between MG and HG (Ylänne and others 2018) although in 2000, it had been approximately 30% higher in HG than MG (Olofsson and others 2004). One plot of 1×1 m was set to each zone along the eight transects yielding 24 study plots.

Prevalent Vegetation and C:N Ratios in Different Ecosystem Compartments

In 2014, at the time of the reported results, graminoids and forbs were the dominant plant group in HG, whereas vegetation in LG was characterised

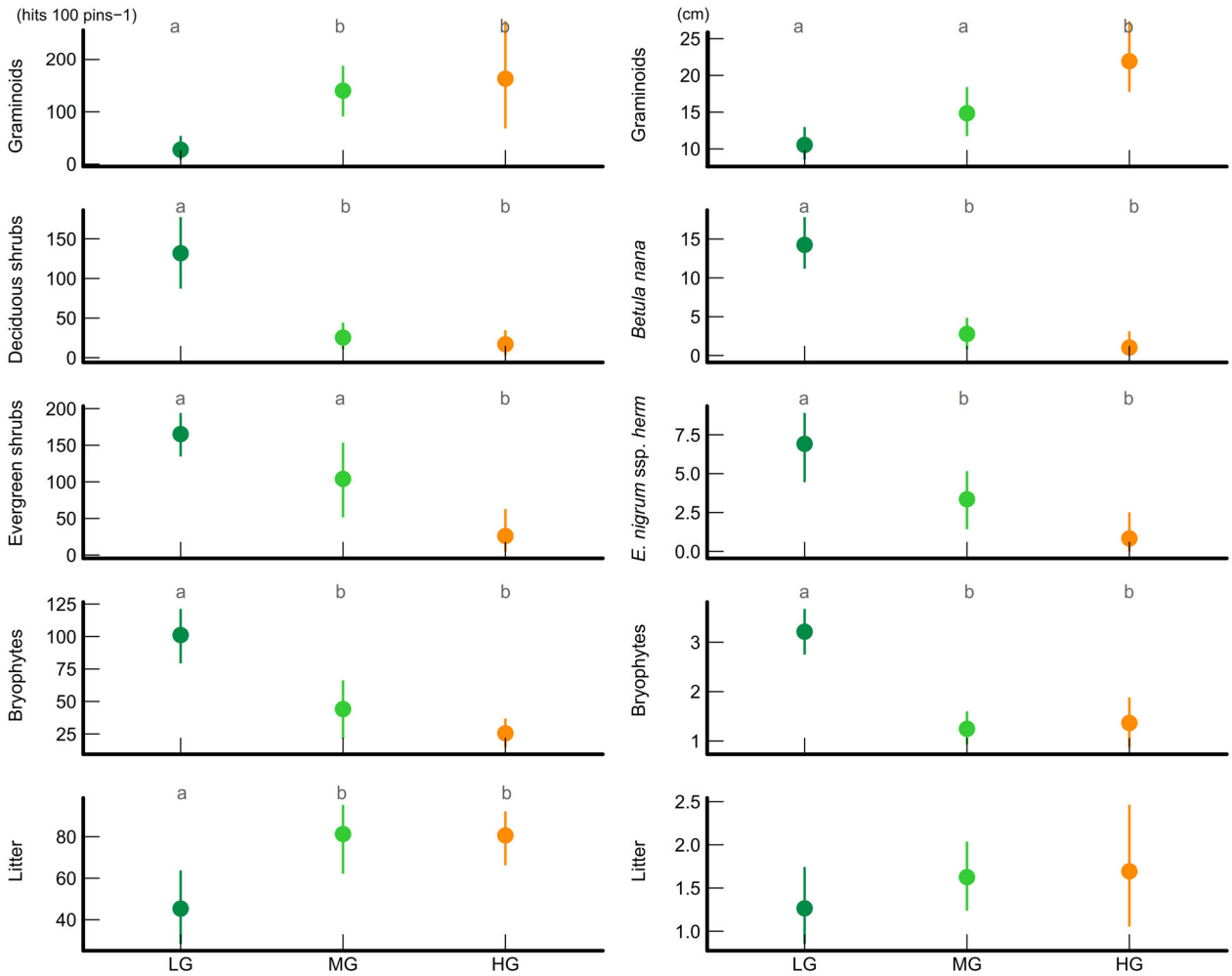

Figure 1. The average abundance (left) and height (right) of graminoids, deciduous shrubs, evergreen shrubs, bryophytes and the litter layer in the three grazing zones. The values represent mean ± 95% confidence intervals in different grazing zones (LG = light grazing, MG = recent grazer-induced grassification, HG = old grazer-induced grassification). The letters above the charts denote the significant differences among grazing zones as identified by Least Squares comparison. The abundance was measured as hits 40 pins^{-1} during the peak growing season (July 18th–19th, 2014). From vascular vegetation, all hits were recorded, whereas from the ground layer (that is, bryophytes and lichens) only the first hit for each species. The maximum height of graminoids, *Betula nana* and *Empetrum nigrum ssp. hermaphroditum* represents the average height of the five tallest individuals. The average depth of bryophyte and litter layers is derived from five measurements placed randomly on the study plots. Data partly redrawn from Ylänne and others (2018).

by a mosaic of evergreen and deciduous dwarf shrubs underlain by a thick moss carpet (Ylänne and others 2018). In MG, graminoids had gained dominance and replaced the deciduous shrubs and bryophytes prevalent in 2000 (Olofsson and others 2001, 2004); yet, patches of evergreen shrubs persist in the area (Ylänne and others 2018). As a result of grazing, in both HG and MG, the abundance and height of deciduous shrubs was similarly low (Figure 1, Supplementary table S1) the cover and depth of the bryophyte layer was lower and the cover of litter was higher when compared to LG. Also graminoid abundance was similar in MG and HG, yet, graminoids grew taller in HG than MG (Figure 1). There were more evergreen dwarf shrubs in MG than HG, but no difference in the abundance and height of the dominant evergreen dwarf shrub species, *Empetrum nigrum* ssp. *hermaphroditum*.

To assess the C:N ratio in different ecosystem compartments, we collected biomass samples from aboveground and belowground vascular vegetation as well as the litter layer. All aboveground vascular vegetation was clipped from an area of 50 × 50 cm and divided to growth forms (for example, evergreen shrubs, deciduous shrubs, graminoids and forbs) and subsequently, dried, weighed, milled

(25 revs s^{-1} for 20 s, Retsch MM301 mill) and analysed for C:N ratio with a CHNS–O Elemental analyser (EA1110, CE Instruments). We used two intact vegetation-soil cores (Ø 11.95 cm) to obtain litter biomass and 5–10 soil cores (Ø 2.9 cm) per plot to obtain vascular belowground biomass. Litter was hand picked from the cores, whereas the vascular belowground biomass was washed from soil remains (sieve mesh 0.5 mm). Samples from both compartments were dried, weighed and milled for the C:N analysis.

Field-Layer Carbon Dioxide Flux

We analysed net ecosystem C exchange (NEE), gross ecosystem productivity (GEP) and ecosystem respiration (ER) using a closed system composed of a custom-built acrylic chamber (Ø 30 cm, 39 cm height) coupled with a Vaisala carbon dioxide probe (GMP343), a Vaisala humidity and temperature probe (HMP75), a Vaisala Measurement Indicator (MI70) and a quantum-photo-radiometer (HD 9021). The measurements were conducted within 3 h of midday on five occasions during the growing season of 2014 (June 12, June 24, July 16, August 2 and August 30). Each transect was measured at the same time by seven consecutive measurements at each plot; four with gradually decreasing light intensity (ambient light, 35%, 50% and 65% shading) and three in the dark to account for ecosystem respiration (ER). Between each measurement, the chamber was vented to allow the CO_2 concentration to return to ambient. The gradual shading was implemented with hoods made of single-, double- and triple-layer white mosquito nets and the dark measurements were obtained by covering the chambers with an opaque white hood that did not permit light to the plots. We logged the CO_2 concentration, temperature and humidity inside the chambers at 5 s intervals for 90 s, during which photosynthetically active radiation (PAR) within the chamber was monitored. The CO_2 flux was corrected for changes in the water vapour pressure (Hooper and others 2002) with the following formula:

$$\mathrm{CO_2flux} = -\left[Cf \times \frac{Pf}{273.16 + Tf} - Cb \times \frac{Pb}{273.16 + Tb}\right] \times \frac{V}{t \times 8.314 \times s}$$

where C_b and C_f are the CO_2 concentrations at the beginning and end of measuring period, respectively (µmol CO_2 mol^{-1} air), Pb and Pf are the atmospheric pressures at beginning and end of measuring period, respectively (mb), Tb and Tf are the temperatures (°C) at beginning and end of measuring period, respectively, V is the volume of the system (ml), t is the elapsed time (s) and s is the surface area (m^2). The fluxes are shown as µmol CO_2 m^{-2} s^{-1} and NEE is presented from the atmospheric perspective (that is, a negative flux indicates net CO_2 uptake by the ecosystem).

We counted GEP as NEE–ER and standardised it to a common irradiance (PAR = 600 µmol m^{-2} s^{-1}) based on light-response curves generated for every plot during each occasion to fit a Michaelis–Menten model (Ritz and others 2015). Due to the small number of measurements, we used the raw CO_2 flux data in the statistical analysis and accounted for the random effects of temperature for ER and irradiance for NEE and GEP. We also present the light-standardised values (GEP_{600}, NEE_{600}) and use these to calculate average daytime flux rates over the growing season as weighted means for the period June 1st–September 15th. Weighed means were obtained by plotting the fluxes against the measurement days and deriving an estimate for each day by local polynomial regression fitting (R Core Team 2012). This procedure takes into account uneven intervals between the CO_2 measurements.

Microbial Respiration, Enzyme Activities and Their Temperature Sensitivity in the Organic Soil Layer

To depict microbial potential for soil C and nutrient cycling, we analysed microbial respiration (that is, the release of CO_2 from the soil) and the activities of key extracellular enzymes responsible for soil C degradation. We collected soil samples on three sampling dates (June 11th, June 25th and July 19th) with 5–10 soil cores (Ø 2.9 cm) extending the entire soil organic layer (average depth = 4.35 ± 0.30). The depth of each sample was recorded, and the samples were subsequently combined to form one composite sample per plot. The samples were sieved (2 mm mesh) in the laboratory, stored in 4 °C and analysed within a week of sampling. For background information, we analysed soil moisture (105 °C, 12 h), organic matter content (loss on ignition at 475 °C, 4 h) and bulk density (dry weight of soil per sample volume) from the sieved samples. Soil ammonium (NH_4^+–N) was extracted with 0.5 M K_2SO_4 and analysed colorimetrically (SFS 3032, Shimadzu UV-1700 spectrophotometer). We did not analyse soil nitrate (NO_3^-–N) concentrations as previous investigations at the same site had shown very low concentrations (for example, Stark and others 2002) indicating a minor importance in the N cycle.

Microbial respiration was analysed to depict the rate of C release from soil organic matter. At the site, soil temperatures differ depending on grazing, being highest in HG, and higher in MG than LG (Ylänne and others 2018), with further feedbacks on the temperature sensitivity of the soil microbial activity (Stark and others 2015b). For this reason, we analysed soil microbial activities at a range of temperatures. Soil CO_2 release (microbial respiration) and its temperature sensitivity were analysed by incubating fresh soil samples in 100 ml incubation bottles sealed with rubber stoppers at four temperatures (4, 9, 14 and 19 °C). The bottles were pre-incubated for 48 h and aired before the actual incubation time of 72 h. We collected airsamples from the headspace of the bottles and analysed those for the concentration of microbially released CO_2 with a gas chromatograph (HP 6890). The microbial respiration is reported as mg CO_2 g OM^{-1} h^{-1}.

Further, we analysed the potential activities of three hydrolytic extracellular enzymes that catalyse the degradation of soil C: *β*-glucosidase (BG) that releases glucose from cellulose, *β*-*N*-acetylglucosaminidase (NAG) that hydrolyses *N*-acetyl glucosamine residues from chitin-derived oligomers, and acid-phosphatase (AP) that catalyses the release of phosphate by hydrolysing the phosphoric ester bonds of phosphate groups in organic molecules. BG can be regarded a proxy for C turnover, AP for P acquisition, and NAG for N acquisition through the breakdown of fungal derived chitin (Sinsabaugh and others 2008). The potential activities were extracted with the corresponding chromogenic substrates (Boerner and others 2000): 5 mmol paranitrophenyl(pNP)-*β*-glucopyranoside for BG, 3 mmol pNP-*β*-*N*-acetylglucosaminide for NAG, and 5 mmol pNP-phosphate for AP. We conducted all assays in sodium acetate buffer (50 mM) that corresponds to the study site soil pH (5.0), and incubated the samples at four temperatures (4, 9, 14 and 19 °C). Following the incubations, the samples were centrifuged, after which we transferred 100 ml of the supernatant into a 96-well plate; added 5 ml of 1.0 M NaOH, and analysed the absorbance at 410 nm using a Multiscan FC microplate reader (Thermo Scientific). We corrected the assay absorbance to account for homogenate and substrate absorbance by subtracting those. We used standard curves for paranitrophenol to calculate the extinction coefficients for the potential activities and reported those as μmol h^{-1} g OM^{-1}.

We calculated the temperature sensitivity (Q_{10}) of microbial respiration and enzyme activities by plotting the natural logarithm of CO_2-C release/activity against the incubation temperature and using the slope (k) of the linear regression in the following formula: $Q_{10} = e^{(10 \times k)}$ (for example, Wallenstein and others 2009).

Statistical Analyses

We tested for the effects of measurement time, grazing and their interaction on the ecosystem processes with a repeated measures mixed effects model (Pinheiro and others 2014). For GEP_{600} and NEE_{600} and the Q_{10} values of microbial respiration and enzyme activities, measurement time, grazing and their interaction were set as fixed factors and transect was kept as a random factor. For microbial respiration and enzyme activities, we also included the incubation temperature and its interactions to the fixed factors. We used the same test without the repeated measures design for the growing seasonal weighed averages of CO_2 fluxes. In all models, the pairwise differences between grazing intensities were subsequently tested with the least squares means post hoc test (Lenth 2016).

For ecosystem CO_2 fluxes, we used the lme4 package (Bates and others 2015), where also the random effect of temperature (for ER) or PAR (for GEP and NEE) were included in the models. We used Satterthwaite approximation to estimate the degrees of freedom (Kuznetsova and others 2016) and tested the pairwise differences between grazing intensities on each measurement occasion with the least squares means post hoc test. All data processing and statistical analyses were performed with R software for statistical computing (R Core Team 2012) and the package ggplot2 (Wickham 2009) was used for drawing the figures.

Results

Grazing Effects on Ecosystems C:N Ratios

The C:N ratios in the above- and belowground biomass of vascular vegetation were highest in the shrub-dominated LG and did not differ between HG and MG (Figure 2, Table 1). Grazing had similarly decreased the C:N ratio in litter. However, litter C:N ratio was even lower on HG than on MG. Similarly, grazing had increased NH_4^+-N in organic soil in both HG and MG, so that the C:N ratios of HG and MG were significantly lower than that of LG (Table 1; data from Ylänne and others 2018).

Ecosystem CO_2 Fluxes

We found no significant grazing effect on the growing seasonal average fluxes of light-standard-

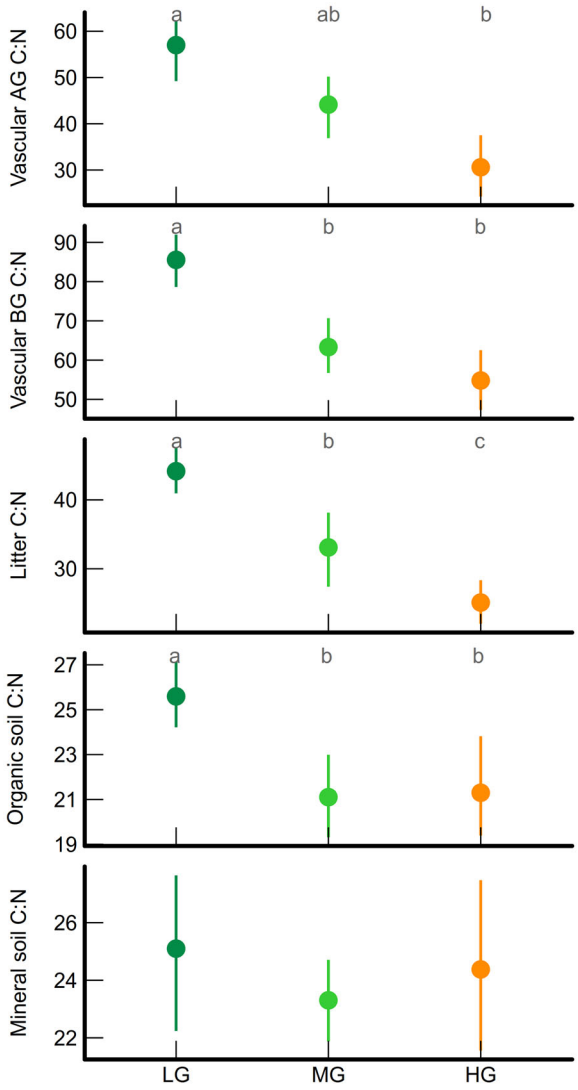

Figure 2. Carbon-to-nitrogen ratios in aboveground vascular vegetation, belowground vascular vegetation, litter, organic soil and mineral soil. The values display average C:N ratio (%) with a 95% confidence interval in different grazing zones (LG = light grazing, MG = recent grazer-induced grassification, HG = old grazer-induced grassification). The letters above the charts denote the significant differences among grazing zones as identified by Least Squares comparison. Organic and mineral soil C:N ratios drawn after Ylänne and others (2018).

ised ecosystem productivity ($GEP_{600\text{-}wm}$) and respiration (ER; Table 1; Figure 3). Yet, the weighed mean of NEE_{600} was indicatively less negative in HG and MG than LG ($P = 0.070$), indicating a lower CO_2 sink potential in both graminoid-dominated areas compared to the shrub-dominated LG.

Despite similarities in the average values of GEP and ER, seasonal differences among the grazing zones were found (see pairwise differences in

Table 1. Grazing Effects on C:N Ratios and the Average CO_2 Fluxes

	num d.f.	*den d.f.*	*F*	*P*
Vascular AG C:N	2	14	**12.03**	**< 0.001**[a]
Vascular BG C:N	2	14	**19.62**	**< 0.001**[b]
Litter C:N	2	14	**20.35**	**< 0.001**[c]
Organic soil C:N	2	14	**6.27**	**0.011**[b]
Mineral soil C:N	2	14	0.46	0.642
ER_{wm}	2	14	1.31	0.301
GEP_{600wm}	2	14	2.71	0.101
NEE_{600wm}	2	14	**3.24**	**0.070**[b]

The abreviations AG and BG stand for above- and belowground, respectively. The average values for ecosystem respiration (ER_{wm}), gross ecosystem production (GEP_{600wm}) and net ecosystem exchange (NEE_{600wm}) were calculated based on five measurements, where a weighed-mean approach was used to correct for the uneven time-intervals between the measurement occasions. Statistically significant differences are shown in bold and the pairwise differences between grazing zones were obtained by the least squares comparison and are shown in small letters.
[a]HG diff to LG.
[b]LG diff from HG and MG.
[c]All differ from each other.

Table S2 in the Supplementary material). More often, ecosystem respiration was higher in HG than in LG and MG (Table 2; Figure 3). In the beginning of the growing season, all CO_2 fluxes were similar among the grazing zones. Towards mid-July, ecosystem respiration and gross ecosystem production were both higher on HG than on LG or MG. Yet, when looking at NEE, both HG and MG functioned as a stronger CO_2 sink than LG. In the beginning of August, both graminoid-dominated areas, HG and MG, had higher ecosystem respiration when compared to LG with no significant difference among the grazing intensities in NEE. After the reindeer grazing pulse, the gross ecosystem productivity dropped in both HG and MG, being significantly lower than in LG. In MG, also ecosystem respiration decreased notably after grazing, whereas in HG, ecosystem respiration remained high. As a result, ecosystem respiration was lower in MG than HG and LG. Despite the differences in ecosystem respiration, NEE in August did not differ significantly between HG and MG, although both areas functioned as weaker CO_2 sinks than LG.

Microbial Activity

The seasonal development of soil microbial activity was opposite to the seasonal trend in plant activity. Microbial respiration and the potential activities of *B*-glucosidase (BG) and *N*-acetyl-glucosane (NAG) in the organic soil layer were the highest in the beginning of the growing season, and became

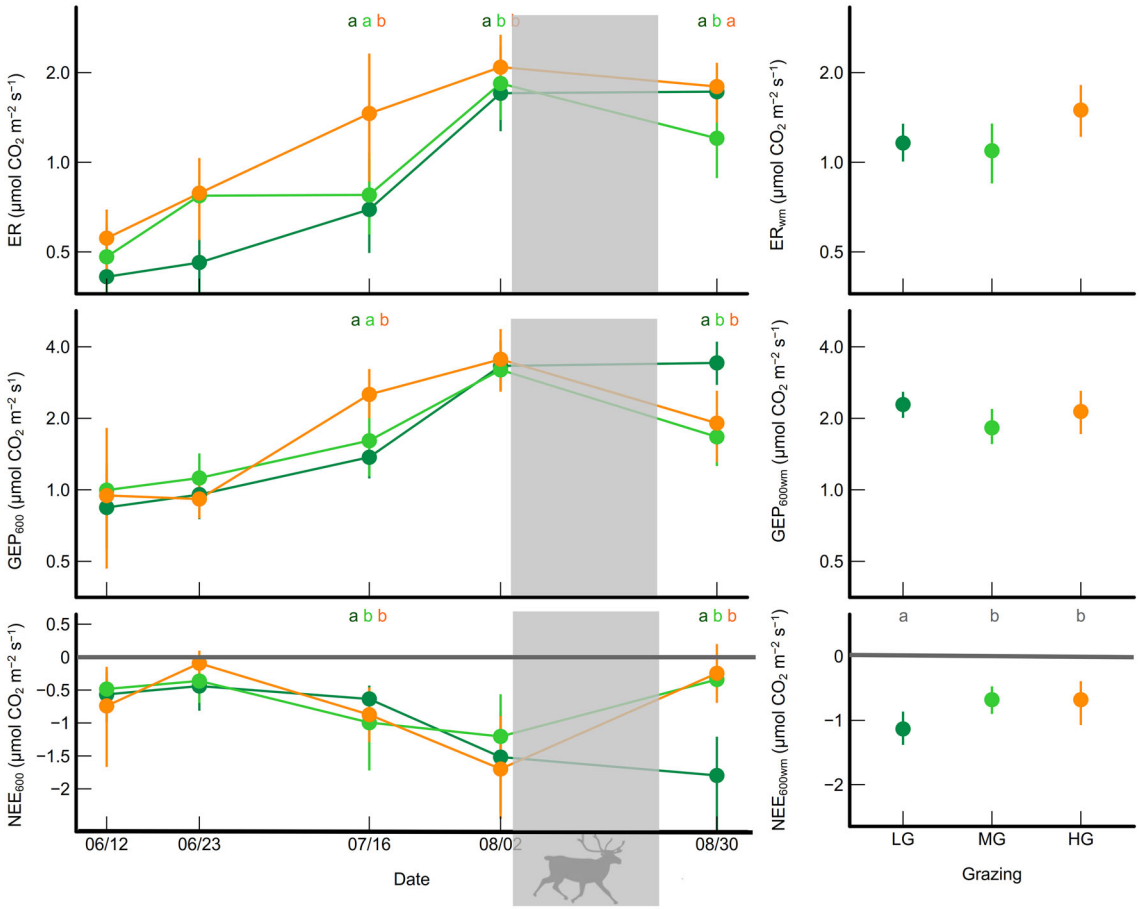

Figure 3. Ecosystem–atmosphere CO_2 fluxes in different grazing zones. Left panel represents the raw values of GEP, ER and NEE on the measurement occasions during the growing season of 2014. The right panel represents the weighed means of GEP_{600}, ER and NEE_{600}. The values display mean with a 95% confidence interval in different grazing zones (dark green = light grazing, light green = recent grazer-induced grassification, orange = old grazer-induced grassification). The letters above the charts denote the significant differences among grazing zones as identified by Least Squares comparison. On the left panel, the significant differences are shown separately at each measurement occasion (Color figure online).

Table 2. The Effects of Grazing and Measurement Time on CO_2 Fluxes

	Num d.f.	ER			GEP			NEE		
		den d.f.	*F*	*P*	*den d.f.*	*F*	*P*	*den d.f.*	*F*	*P*
Time	4	334.53	103.17	< 0.001	270.93	101.15	< 0.001	316.19	25.57	< 0.001
Grazing	2	21.12	**5.25**	**0.014**[a]	13.93	0.87	0.442	13.69	1.67	0.224
Time:Grazing	8	309.67	**10.04**	< **0.001**	389.36	**17.39**	**0.001**	385.02	**8.32**	< **0.001**

The table presents the results of a repeated measures mixed effects model on the effects of measurement time, grazing and their interaction on ecosystem respiration (ER), gross ecosystem productivity (GEP) and net ecosystem exchange (NEE) when the effect of light and temperature have been accounted for. The pairwise differences between grazing intensities at different measurement times are found in Table S1.
Statistically significant differences are shown in bold.
[a]*HG diff to LG and MG.*

smaller towards the mid of growing season (Figure 4 and Supplementary figure 1). Yet, the potential activity of acid-phosphatase (AP) increased with the advance of the summer (Figure 4), alike the temperature sensitivities (Q_{10}) of microbial respiration and BG and NAG activities (Figure 4).

Microbial activities and their temperature sensitivities varied depending on grazing irrespective of the measurement time (Tables 3 and 4). Microbial

respiration was higher in LG than HG (Table 3), and NAG activity followed the same pattern tentatively, although the grazing effect was not statistically significant ($P = 0.057$). Notably, microbial respiration or NAG activity in MG did not differ significantly from that in LG. In contrast to NAG and microbial respiration, the potential activities of BG and AP were higher in the graminoid-dominated MG and HG when compared to LG (Table 3). Yet their temperature sensitivities were highest in LG (Table 4). The temperature sensitivity (Q_{10}) of NAG was higher in HG than in LG and there was no difference in the temperature sensitivity of micro-

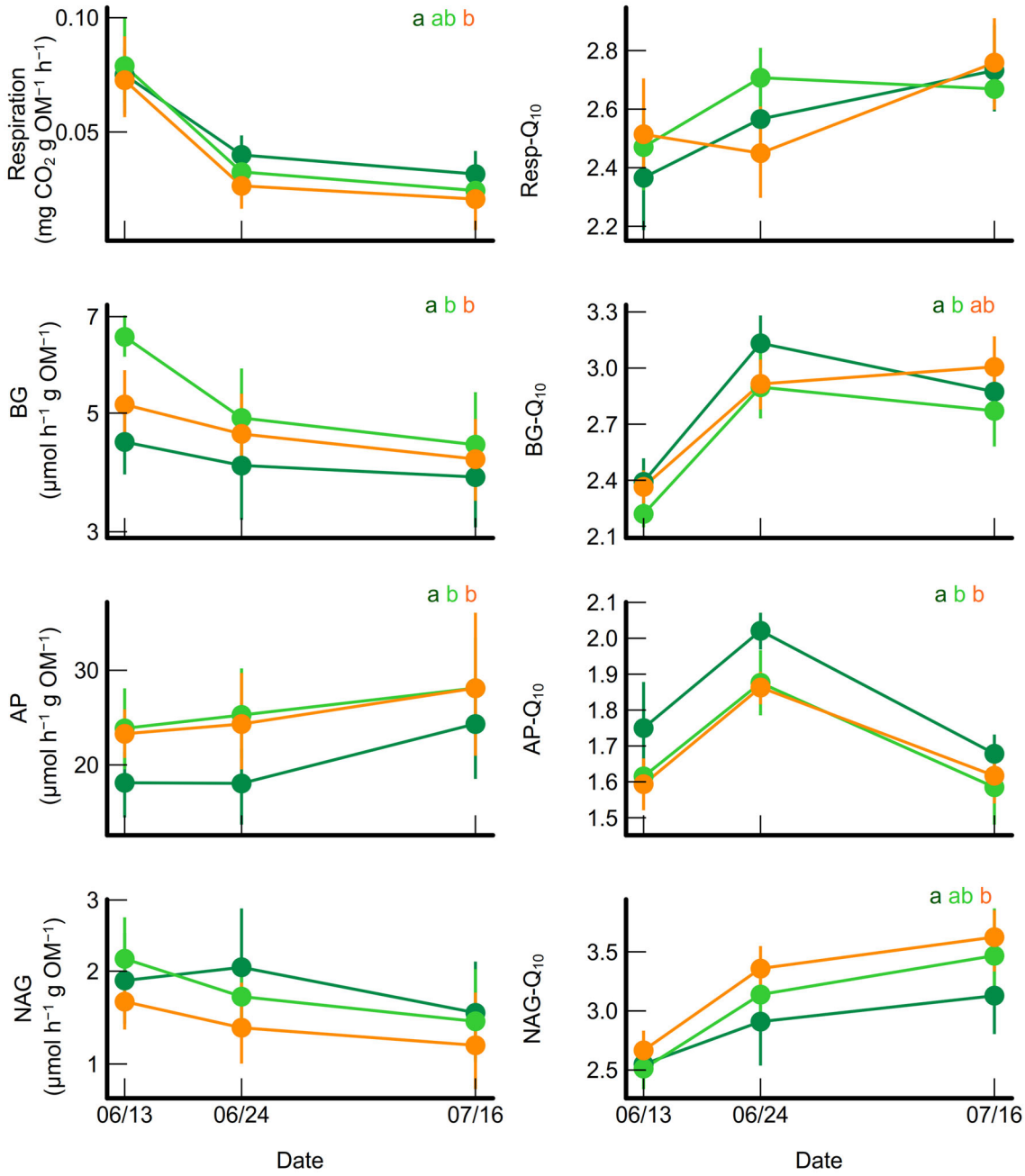

Figure 4. Microbial respiration and the potential activities of *B*-glucosidase (BG), acid-phosphatase (AP) and *N*-acetyl-glucosane (NAG) at 9 °C (left) and their temperature sensitivities (right) on the three measurement occasions in 2014. The values represent mean ± 95% confidence intervals in different zones (dark green = light grazing, light green = recent grazer-induced grassification, orange = old grazer-induced grassification). The letters above the charts mark the significant differences among grazing intensities across all measurement dates (Color figure online).

bial respiration among the grazing intensities (Figure 4; Table 4).

Discussion

In this paper, we quantified how C cycling under recent grazer-induced *grassification* relates to C cycling under an area with a long history of graminoid dominance and on a shrub tundra with low reindeer influence. We expected both old and recent graminoid-dominated areas to maintain similar rates of gross ecosystem productivity (GEP), whereas we expected the soil microbial activities for C cycling and ecosystem respiration under recent *grassification* to be more similar to those under shrub dominance, resulting in a higher C sink capacity. In contrast to our expectations, we found that the net ecosystem exchange (NEE) over the growing season did not differ between old and recent grassification, but it was tentatively less negative in both graminoid-dominated areas than under shrub dominance. Yet, the duration of grazing altered the processes governing the NEE, as the seasonal trends of both ecosystem respiration and the mid-season photosynthesis differed between old and recent grassification. Interestingly, these temporal differences balanced each other and led to a similar outcome on the C sink. Likewise, contrasting our expectations, we observed both similarities and differences in the soil processes between the graminoid-dominated areas: the potential enzymatic activities of BG and AP were higher on both graminoid-dominated zones than under shrub dominance whereas the potential activity of NAG was the same under recent grassification as under shrub dominance. Put together, our results revealed that different ecosystem processes respond to herbivory with different timescales and indicate that both autotrophic and heterotrophic processes are controlled through multiple drivers that vary depending on the herbivory history.

Grazing Effect on Ecosystem Respiration and Photosynthesis Depended on the Age of Vegetation Shift

Our results revealed that the impact of grazing-induced grassification on ecosystem CO_2 sink was similar irrespective of the age of the vegetation shift: in both grazed areas, grazing contributed to a tentatively less negative NEE when compared to the adjacent area with shrub dominance. Grazing effects on C sink were particularly obvious on two occasions: in the middle of the growing season, when grazed areas functioned as stronger CO_2 sinks, and after the yearly grazing event, when the CO_2 sink in HG and MG had decreased. Noteworthy, the decrease in CO_2 sink during late growing season dominated the grazing effect on the growing seasonal average NEE (as in Väisänen and others 2014, Supplementary material).

Even though the age of the vegetation shift did not alter the grazing effect on CO_2 sink, the seasonal differences in C uptake and release varied depending on the duration of grazing. More commonly, we found higher ecosystem respiration and mid-season photosynthesis under old than recent *grassification*, which indicates that the higher respiration under graminoid dominance evolves with

Table 3. The Effects of Grazing on Microbial Respiration and Potential Enzymatic Activities

	Num d.f.	*den d.f.*	Microbial respiration		BG		AP		NAG	
			F	*P*	*F*	*P*	*F*	*P*	*F*	*P*
(Intercept)	1	176	9099	< 0.001	945	< 0.001	1401	< 0.001	299	< 0.001
Time	2	176	320.79	< 0.001	35.41	< 0.001	28.90	< 0.001	6.64	0.002
Grazing	2	60	**3.27**	**0.045**[a]	**13.68**	< **0.001**[b]	**5.40**	**0.007**[b]	3.01	0.057
Temp	1	2	290.10	0.003	88.17	0.011	12.48	0.072	190.27	0.005
Time:Grazing	4	176	1.07	0.372	2.07	0.087	1.34	0.256	2.07	0.086
Time:Temp	2	176	1.85	0.160	10.87	< 0.001	5.94	0.003	6.07	0.003
Grazing:Temp	2	60	0.03	0.971	0.29	0.746	0.21	0.809	0.23	0.793
Time:Grazing:Temp	4	176	0.37	0.831	0.17	0.954	0.05	0.996	0.15	0.964

The table presents the results of repeated measures mixed effect model on the effects of measurement time, grazing and incubation temperature, and their interactions on microbial respiration and the potential activities of B-glucosidase (BG), acid-phosphatase (AP) and N-acetyl-glucosamine (NAG) in the organic soil layer. Statistically significant differences are shown in bold and the pairwise differences between grazing zones were obtained by the least squares comparison and are shown in small letters.
[a]*HG diff to LG.*
[b]*LG diff to HG and MG.*

Table 4. Grazing Effects on the Temperature Sensitivity of Microbial Activity

	num d.f.	*den d.f.*	Resp-Q_{10}		BG-Q_{10}		AP-Q_{10}		NAG-Q_{10}	
			F	*P*	*F*	*P*	*F*	*P*	*F*	*P*
(Intercept)	1	41	6198	< 0.001	12668	< 0.001	11330	< 0.001	1289	< 0.001
Time	2	41	11.03	< 0.001	71.38	< 0.001	49.44	< 0.001	43.07	< 0.001
Grazing	2	14	0.31	0.737	**4.51**	**0.031**[b]	**6.65**	**0.009**[a]	**5.08**	**0.022**[c]
Time:Grazing	4	41	2.27	0.078	1.46	0.231	0.46	0.76	1.11	0.366

The table presents the results of repeated measures mixed effect model on the effects of measurement time, grazing and their interactions on the temperature sensitivities of microbial respiration (Resp-Q_{10}), and B-glucosidase (BG-Q_{10}), acid-phosphatase (AP-Q_{10}) and N-acetyl-glucosane (NAG-Q_{10}) potential activities in the organic soil layer. Statistically significant differences are shown in bold and the pairwise differences between grazing zones were obtained by the least squares comparison and are shown in small letters.

[a] *LG diff to HG and MG.*

[b] *LG diff to MG.*

[c] *LG diff to HG.*

time. Yet, we also found that, by the end of the growing season, grazing-induced decrease in productivity contributed to the grazing effect on the CO_2 sink. In both graminoid-dominated areas, GEP dropped after the grazing pulse leading to a decreased CO_2 sink strength, which likely depicts the immediate effect of plant consumption on GEP (Cahoon and others 2012; Metcalfe and Olofsson 2015). Under recent *grassification*, ecosystem respiration decreased at the same time, whereas under old *grassification*, respiration rates remained high even after the grazing pulse. The continuously high ecosystem respiration under the old graminoid dominance indicates that respiration was not solely a function of autotrophic processes. As microbial respiration in the organic soil layer was the same under both recent and old grassification, we suggest that the differences in ecosystem respiration in response to grazing likely derived from microbial respiration in the litter layer.

The Age of Vegetation Shift had Divergent Influence on Soil Microbial Activities

Contrasting with our hypotheses, the differences among grazing regimes in soil processes were not uniform: microbial respiration and the potential activities of BG and AP were the same under both recent and old grassification, whereas NAG activity was as high under recent grassification as under shrub dominance. These results demonstrate that the indirect effects of herbivory on the different soil microbial processes may have largely differing response times and be jointly governed by the stoichiometric C and nutrient demand of microbes as well as the substrate availability (Wallenstein and others 2009; Koyama and others 2013; Sistla and others 2014; Stark and others 2015a). As soil microorganisms synthesise enzymes to meet their own resource requirement, the high N availability in the grazed areas could downregulate the activities for N acquisition (Sinsabaugh and others 2008; Sinsabaugh and Follstad Shah 2012). Here, we found higher NAG activity under recent than old grassification although the organic soil C:N ratio or mineral N availability did not differ between the graminoid-dominated areas. We suggest the higher NAG activity to be induced by higher fungal biomass and thus, higher levels of chitin in the soil (Hernández and Hobbie 2010; Kielak and others 2013; Zeglin and others 2013). As chitin supply mainly controls chitin degradation (Beier and Bertilsson 2013), a delayed shift of the soil microbes from chitin-containing fungi to bacteria after the vegetation change could likely explain the slow response time of NAG activity to grazer-induced change in vegetation and soil N availability.

In contrast to NAG activity, the potential activities of BG and AP were similar in MG and HG, being significantly higher than the activities in LG. According to the theory of stoichiometric regulation of enzyme activities, enhanced BG activity could result from the grazer-induced increase in soil N; and reflect a higher microbial demand for C (Sinsabaugh and others 2008). However, a previous investigation at the study site showed that BG activity did not respond to increased N availability connected with the reindeer grazing pulse (Stark and Väisänen 2014) indicating that microbial saturation of N is likely not the main driver behind BG activity. Instead, the higher BG activity under graminoid dominance could derive from altered substrate availability (Stark and Väisänen 2014) as graminoid litter contains labile compounds that are rapidly degraded by soil microorganisms (De Deyn and others 2008). On the other hand, the higher AP activity in graminoid-dominated areas could

derive from the microbial stoichiometric demand, and demonstrate the tendency of soil microorganisms to allocate more resources for P mineralisation to balance changes in the soil N:P stoichiometry (Stark and Väisänen 2014; Sitters and others 2017). These results are in line with the general observation that microbial enzyme activities are closely governed by the soil N:P stoichiometry, whereas the relationship between enzyme activities and soil C:N stoichiometry is not equally clear (Sinsabaugh and Follstad Shah 2012).

Interestingly, soil NH_4-concentrations further away from the pasture rotation fence increased even before vegetation *grassification* (38, 78 and 87 μg m^{-2} in 2000 in LG, MG and HG, respectively; Olofsson and others 2004). Thus, many of the soil-driven processes may have changed even before graminoids gained dominance in the vegetation as a response to the combined effects of increased N availability and the gradual change in vegetation. We suggest that one of the triggering forces for the ecosystem shift could have been the decline in bryophytes. Notably, in 2000, the bryophyte biomass was equally high in both MG and LG (99 ± 36 g, and 97 ± 42 g, compared to the lower biomass, 19 ± 11 g, in HG), whereas in 2014, there was no difference in bryophyte biomass between HG and MG (Ylänne and others 2018). It has been shown that bryophytes may trap nutrients from urine and thereby prevent nutrient enrichment in the soil (Barthelemy and others 2018). Thus, a gradual decline of the bryophyte layer could permit higher nutrient availability into the soils and, through the loss of insulation, alter soil physical environment and increase soil temperatures. These mechanisms may have enhanced soil decomposition rates and—in combination with the trampling-induced disturbance to the deciduous and evergreen shrubs—opened up a window of opportunity for graminoids to increase in abundance.

Implications for Understanding the Temporal Dynamics of Grazer-Induced Ecosystem Changes

In this paper, we showed that the effect of grazing on ecosystem C sink was similar regardless of the time passed since the vegetation state shift. Yet, the time passed after graminoids gained dominance affected which processes governed the grazing effect on the C sink (Figure 5). We found that high rates of photosynthesis evolve with time after graminoid dominance as mid-season GEP was not as high under recent than old grassification (< 12 years vs > 60 years). Yet, this difference was not reflected on the ecosystem C sink as the mid-season ecosystem respiration was also lower under recent graminoid dominance. We also found that the grazing-induced changes in soil processes varied depending on the duration of grazing. The

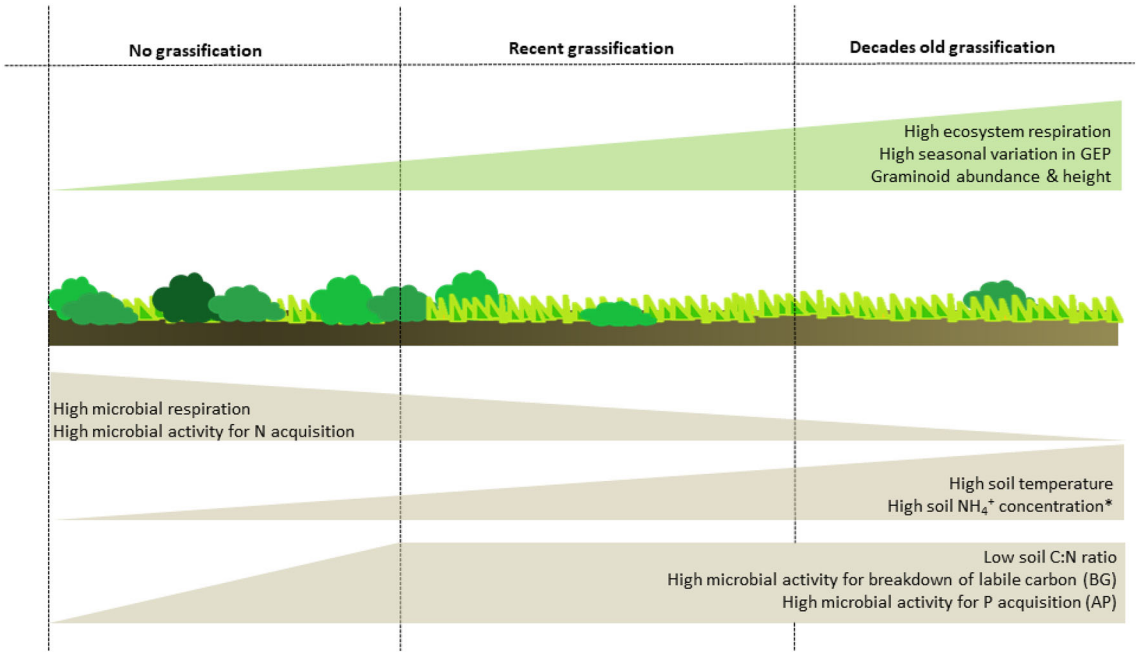

Figure 5. Graphical presentation on how carbon cycling rates under recent grazer-induced *grassification* relate to the rates in an area with a long history of graminoid dominance and on a shrub tundra with low reindeer influence.

activities of BG and AP under recent grassification were already the same as under old grassification, and in contrast, NAG activity was still as high as under the shrub dominance. The differences in microbial activities suggest a rapid response of microbes to the changed litter quality and N:P stoichiometry, and at the same time, a possibly high chitin availability as a legacy of the old vegetation.

Taken together, our findings confirmed the initial hypothesis that the different processes influenced by herbivory have different response times, and revealed unexpected variation within the plant- and soil-driven processes. Still, this data should not be generalised to represent long- and short-term effects of grazing on the C sink across the tundra, as a vegetation shift alike the described one is unlike to take place across all grazed sites. Indeed, previous studies report that there are no consistent vegetation trends caused by reindeer grazing (Bernes and others 2015) and indicate that, at the landscape level, grazing-induced increase in evergreen vegetation may be more common than the increase in graminoids (Bråthen and others 2007). As evergreen shrubs have low rates of litter fall and high concentrations of phenolic compounds in their tissues, the consequences of grazer-induced increase in evergreens for decomposition and nutrient availability are not the same as in cases where grazing increases graminoid dominance (Ylänne and others 2015). Furthermore, even in cases when grazing promotes a higher abundance of graminoids, nutrient availability might not necessarily increase (Haynes and others 2014; Ricca and others 2016) and the consequences for soil C cycling might depend on the initial vegetation type (Ylänne and others 2018).

Our results are, however, consistent with earlier studies showing that the long-term, for example, decadal, effects of grazing on both vegetation (Saccone and Virtanen 2016) and the ecosystem C sink (Väisänen and others 2014) differ from the initial effects within a timeframe of a couple of years. This highlights that process rates in any given time, may only present a time window of processes under a constant change driven by herbivory. We believe this to be irrespective of the type of vegetation change induced by herbivory. Partly, the timeframe of change could also constitute one of the factors explaining the bidirectional grazing effects on productivity and soil C and nutrient cycling in different ecosystems (sensu Wardle and others 2004). How the different ecosystem processes change along with the duration of herbivory should therefore be incorporated into the general theoretical framework describing the role of herbivory in ecosystems.

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