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CONTRASTING EFFECTS OF REINDEER GRAZING ON CO2, CH4 AND N2O FLUXES ORGINATING FROM THE NORTHERN BOREAL FOREST FLOOR.

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Running Title: REINDEER GRAZING AND GREENHOUSE GAS FLUXES FROM FIELD LAYER.

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Abstract

Reindeer (*Rangifer tarandus* L.) are considered to be an important mammalian herbivore, strongly influencing Arctic lichen-dominated ecosystems. There is no wide knowledge about the effect of reindeer on greenhouse gas (GHG) fluxes in northern boreal forests. Ground vegetation plays an important role in absorbing nitrogen (N) and carbon dioxide (CO_2) from the atmosphere. Lately, it has also been found to be a significant source of nitrous oxide (N_2O) and a small source of methane (CH_4). We investigated the influence of reindeer grazing on field layer GHG (CO_2, CH_4 and N_2O) fluxes, ground vegetation coverage and biomass, soil physical properties (temperature and moisture) in a northern boreal forests. At our study site, the reindeer-induced replacement of lichen by mosses had contrasting effects on the GHG fluxes originating from the field layer. Field layer CO_2 efflux was significantly higher in grazed areas. The field layer was a CH_4 sink in all areas, but grazed areas absorbed more CH_4 compared to non-grazed areas. While total N_2O fluxes remained around zero in grazed areas, a small N_2O sink occurred in non-grazed areas with lower moss biomass. Our results indicated that grazing by reindeer in northern boreal forests affects GHG fluxes from the forest field layer both positively and negatively,

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and these emissions largely depend on grazing-induced changes in vegetation composition.

Keywords: Reindeer grazing, boreal forests, greenhouse gases, mosses, lichens

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Introduction

Over 35% (~415 000 km^2) of the land area in Scandinavia is grazed by reindeer (*Rangifer tarandus* L.) (Jernsletten & Klokov, 2002). They influence most of the Scandinavian Arctic, subarctic and northern boreal regions, which are also expected to be significantly influenced by the climate change (Anisimov *et al.,* 2007). Reindeer can strongly influence plant diversity and species composition, and consequently also the nutrient availability and carbon (C) balance of subarctic ecosystems (Väre *et al.*, 1996; Köster *et al.*, 2013; Akujärvi *et al.*, 2014). The number of reindeer has declined in northern boreal areas, except for Scandinavia where it has remained stable or has even increased over the last decades (Vors & Boyce, 2009).

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Reindeer grazing affects ground vegetation by trampling (Väre *et al.,* 1996; Suominen & Olofsson, 2000), selective grazing (Olofsson & Oksanen, 2002) and by returning nutrients in dung and urine (Barthelemy *et al.,* 2015). Van der Wal (2006) showed that in systems with low productivity, grazing changes the ground vegetation from lichen-rich to moss-rich. In more nutrient-rich systems, this change may be from moss-rich to graminoid-rich (Van der Wal, 2006). Heavy grazing increases the presence of bare patches of soil (Suominen & Olofsson, 2000), and grazing may therefore warm up and dry the soil (Väre *et al.*, 1996). Temperature and soil moisture are one of the key factors influencing activity of microbes, soil decomposition processes and the greenhouse gas (GHG) exchange between the field layer and atmosphere (Karhu *et al.*, 2014).

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Northern and high altitude soils have large soil organic matter (SOM) stores due to the slowly decomposing recalcitrant plant litter (Hobbie *et al.,* 2002). Soils can be both source or/and sink of three GHGs: carbon dioxide (CO_2), methane (CH_4) and nitrous oxide (N_2O) (Smith *et al.*, 2003). Effluxes of soil CO_2 can be originated from heterotrophic respiration (decomposition of SOM), and autotrophic respiration of roots and mycorrhizal fungi. Both of these are affected by the soil organic C composition, concentration and soil physical properties (Kirschbaum 2000). The CH_4 flux is a net effect of CH_4 methanogenesis and CH_4 oxidation (Le Mer & Roger, 2001). N_2O is a product or by-product in a series of microbial processes such as denitrification and nitrification (Wrage *et al.*, 2001). As both methanogenesis and denitrification are anaerobic processes, CH_4 and N_2O fluxes are sensitive to soil moisture content changes.

In addition, soil GHG fluxes are affected by cryptogams (lichens, bryophytes, etc.), which can fix CO_2 from the atmosphere through photosynthesis and also fix nitrogen (N) in symbiosis with N-fixing bacteria (Elbert *et al.*, 2012). The role of cryptogams as sources of N_2O and CH_4 has also been demonstrated recently (Lenhart *et al.*, 2015). By affecting ground vegetation composition and soil temperatures reindeer grazing could significantly impact the N_2O and CH_4 fluxes from the forest floor (Porada *et al.,* 2017).

Over half of the subarctic area is covered by forest, but the number of studies addressing the interactions between grazing and field layer GHG fluxes in northern boreal forests is low (Olofsson *et al.*, 2010; Köster *et al.*, 2013; Köster *et al.*, 2015b). Previous studies on reindeer grazing have mostly focused on tundra areas and grazing effect on CO_2 efflux, while the effects on other GHGs (CH_4 and N_2O) have not been studied. This study assesses the influence of reindeer on the fluxes of these three GHGs in the field layer of a northern boreal forests. We compared grazed and

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non-grazed areas and linked the GHG fluxes (CO_2 efflux from the field layer, the proportion of root respiration amongst the CO_2 production, the CH_4 and N_2O exchange between the field layer and atmosphere) to vegetation biomass, plant functional type and characteristics of soil (root biomass, soil temperature and moisture).

We hypothesized that by reducing lichen biomass, reindeer grazing will increase soil temperature and decrease soil moisture. We also hypothesized that these and the following soil microbiological changes in the soil affect field layer CO_2, CH_4 and N_2O fluxes: a) higher soil temperatures result in higher CO_2 emissions from the soil; b) decreased soil moisture negatively affects CH_4 and N_2O fluxes; c) differences in ground vegetation characteristics between grazed and non-grazed areas influence soil CH_4 and N_2O fluxes, as mosses and lichens can both fix and emit these GHGs.

Materials and methods

Study sites

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Our study areas situate in the Värriö Strict Nature Reserve (67°46' N, 29°35' E) of Finnish Lapland. The areas are situated close to the treeline (average altitude of the study area was 300 m a.s.l.), in a northern boreal forest, in the zone of the last intact subarctic Scots pine (*Pinus sylvestris* L.) forest landscapes in Fennoscandia (Potapov *et al.*, 2008). The area is characterized by the sub-continental climate. Snow cover persists for 200–225 days/year, and the average snow depth is approximately 0.7 m (Köster *et al.*, 2015b). The annual growing season varies between 105–120 days (Köster *et al.*, 2014; Köster *et al.*, 2015b). The soils belong to haplic podzol (FAO, 1990) with no permafrost, and the pH of the soil is 4.4 (Köster *et al.*, 2014). The study areas belong to the Pohjois-Salla reindeer herding district, with approximately 2.2 reindeer per km^2 (Turunen *et al.,* 2016).

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Experimental design

The experiment was established in a year 2013 as a split plot experiment with five plots. Each plot was separated to the grazed and non-grazed subplot (400 m^2). The areas are separated by the fence running between Finland and Russia, preventing

Finnish domesticated reindeer to cross the border (Köster *et al.,* 2017). The official border between Finland and Russia is a few hundred metres further east from the reindeer fence. The subplots (n=10) were situated along this fence. The Finnish side is mainly grazed during the wintertime, with an average density of 2.2 reindeer per km^{-2}, while the non-grazed areas on the Russian side of the fence have been excluded from heavy reindeer grazing for nearly a century (Stark *et al*., 2003).

Biomass measurements and vegetation coverage

Stand characteristics and ground vegetation and root biomass measurements were conducted in 2013, and the description of the methods used is published in Köster *et al.* (2015b) and in Supporting experimental procedures: Methods S1. The ground vegetation biomass measurements were repeated according to the same protocols in 2014 at the same time as GHG measurements. Four 0.5m x 0.5m quadrats placed systematically inside each subplot were photographed and the ground vegetation species composition, species coverage and possible area of bare ground were visually estimated from these photos. As shown in Köster *et al.* (2015b), total ground

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vegetation and lichen biomasses were higher and moss biomasses lower in the areas with no reindeer, while the dwarf shrub and grass biomasses were similar for both areas (Table 1). The differences in ground vegetation and tree regeneration caused differences in root biomasses between the non-grazed and grazed areas. Both ground vegetation root biomasses and tree root biomasses were higher in non-grazed areas (Table 1) (Köster *et al.*, 2015b).

Chamber measurements of CO_2, CH_4 and N_2O.

Soil GHG fluxes were measured using the static chamber method with 50 polyvinyl chloride (PVC) collars (five collars per subplot; h = 0.05 m, Ø = 0.22 m) installed permanently in the soil during the spring of 2013 one year before the flux measurements. To avoid the leakage of air to the collar we installed collars in the litter layer and sealed them with sand. The ground vegetation was left intact inside the chamber in course of measurements. GHG measurements were performed monthly (second week of each month) in June, July and August in 2014, with a portable opaque chamber (h = 0.24 m, Ø = 0.22 m) (Pumpanen *et al.*, 2015).

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CO_2 concentration in the chamber headspace was registered for a 5-minute chamber deployment time at 5-sec intervals with a CO_2 probe (GMP343, Vaisala Oyj, Vantaa, Finland); temperature and air humidity were recorded with a temperature and relative humidity sensor (HM70, Vaisala Oyj, Vantaa, Finland) (Köster *et al.*, 2015a).

The CH_4 and N_2O flux measurements were performed using the same collars and the same chamber as in the CO_2 efflux measurements by collecting air samples from the chamber with a polypropylene syringe (50-ml) (BD Plastipak 60, BOC Ohmeda, Helsingborg, Sweden). The samples were collected 0, 1, 5, 10 and 15 min after the chamber was installed, and immediately stored into glass vials (Soda glass (12 ml) Labco Exetainer®, Labco Limited, UK). We analysed the samples by an Agilent Gas Chromatograph model 7890A (GC, Agilent Technologies, USA). The linear regression between the measurement time and GHG concentration change within the chamber was used to calculate the fluxes of CO_2, CH_4 and N_2O. Outliers from the CH_4 and N_2O concentrations measured during each chamber deployment were filtered using Grubbs' test for outliers (Stefansky, 1972).

During the GHG measurements, soil moisture was determined with a ML2 sensor (Delta-T Devices, UK) and soil temperature (top 10 cm) with a P 300w temperature

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probe (Dostmann Electronic GmbH, Germany). In addition, soil temperature was measured continuously at every subplot with iButton temperature sensors (Maxim Integrated, San Jose, California, U.S.A.) and soil moisture at two subplots with an ML2x soil moisture sensor (Delta-T Devices Ltd., Cambridge, England) installed under the organic layer and connected to a data logger.

The proportion of root respiration

Five soil cores (h = 0.15 m, Ø = 0.05 m) were collected from each subplot for the incubation study and stored at +4 ˚C for two weeks. Soil cores were incubated in cylinders (h = 0.3 m, Ø = 0.075), and CO_2 exchange was followed with CO_2 and water vapour analysers (Licor LI-840 and Licor LI-7000, Li-Cor Inc., Lincoln, Nebraska). The system temperature was constantly +12 °C, and differences of CO_2 concentrations were measured from the incoming and outgoing air. The proportion of root respiration was calculated from one time point (the beginning of June) by comparing the field layer CO_2 efflux measurements (corrected to the rates occurring at +12 ˚C) in the field to the lab incubation measurements. Field layer CO_2 efflux was

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used as total respiration (heterotrophic + autotrophic respiration). Lab incubation measurements provided us with the heterotrophic respiration values.

Data analysis

Normality check for the data was done with the Shapiro–Wilk test ($P > 0.05$) and logarithm transformations were calculated for the measured CO_2 fluxes. The other parameters did not need transformation. We used the linear mixed effects model (PROC MIXED) for testing the effects of various factors (grazed or non-grazed area, subplot, collar location, measurement time, root biomass, various ground vegetation biomasses and coverage, etc.) on soil GHG emissions as follows:

$$Y_{P,S} = \beta_0 + \beta_1 A + b_p + b_{C*P} + b_T + \epsilon_S \qquad (1)$$

$$b_p \sim N\left(0, \delta_p^2\right) \qquad (2)$$

$$b_{C*P} \sim N(0, \delta_{C*P}^2) \qquad (3)$$

$$b_T \sim N(0, \delta_T^2) \qquad (4)$$

$$\epsilon_S \sim N(0, \delta_S^2) \qquad (5)$$

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Where β_0 is the intercept and β_1 is the regression slope. b_P is the random intercept of the regression for plots, b_{C*P} is the random intercept for collars within a plot, b_T is the random intercept for measurement times and ϵ_S is the sample residual. δ^2_{C*P} and δ^2_T are the variances between the plots (p) and collars (s) within the plots. We assumed unstructured covariance between all random factors. The subplots were treated as random factors and the three GHG measurements conducted in June, July and August at each collar were used as repeated random factors. We treated grazing (grazed or non-grazed) as a fixed factor.

A similar approach was used for all three GHGs. The first estimation of the model was done using all existing co-variates: soil moisture, soil temperature, root biomass, lichen biomass, moss biomass, shrub biomass, lichen coverage, moss coverage, area (grazed or non-grazed). We therefore dropped the non-significant terms one by one and separate model based Akaike values (AIC) were calculated (Table S1). Factor area (grazed or non-grazed) was forced to stay in each tested model. The best model to explain factor effects on different GHGs was selected based on the lowest AIC value. For quantifying the fit of the linear mixed effects model, we calculated the coefficient of determination (r^2):

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$$r^2 = 1 - \left(\frac{V(m)}{V(r)}\right) \tag{6}$$

Where *V(m)* is the sum of squared residuals from the model and *V(r)* is the sum of squared residuals from the intercept-only model (Nakagawa & Schielzeth 2013).

The Pearson correlation coefficients were calculated between the fluxes and explanatory effects (same co-variates as in model) to evaluate the direction of different effects (Table S2).

Tukey's HSD post hoc test was employed to compare the grazing effects on different months. All statistical analyses compared grazed and non-grazed areas, and the significance level was *P* = 0.05. SAS version 9.3 (SAS Institute Inc., Cary, NC, USA) was used for statistical analyses.

Results

Vegetation structure and environmental factors

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Grazing did not create patches of bare soil in our study areas (Table 1). Lichen coverage was on average 77% higher in the areas where reindeer were not present ($P < 0.01$), and grazing resulted in 94% loss of lichen cover (Table 1). The effect of reindeer grazing was the opposite for moss coverage: 66% of the ground was covered with mosses in the grazed areas, whereas mosses covered only 22% of the ground in the non-grazed areas ($P = 0.0042$) (Table 1). Similar patterns were observed when biomasses of various vegetation types (lichens, mosses, dwarf shrubs, grass) were compared between grazed and non-grazed areas (Table 1) (Köster *et al*., 2015b).

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Average soil temperatures during the measuring period were +10.2 °C in grazed areas and +9.4 °C in the non-grazed areas ($P = 0.2527$). Coldest soil temperatures were measured in June and the warmest in July (Figure 1), and a significant difference in temperature between the areas was observed only in July ($P = 0.0218$), the temperatures being 0.9 °C warmer in grazed areas.

Soil was driest in July and wettest in June (Figure 1) in both areas. In August, soil water content in the grazed area was lower compared to the non-grazed area ($P < 0.0001$). A negative correlation was detected between soil water content and soil temperature (Table S2: $R = -0.835$, $P < 0.0001$).

Field layer CO_2 efflux

The highest field layer CO_2 effluxes were measured in July and August and the lowest in June (Figure 2), and there was a positive correlation between soil temperature and field layer CO_2 emission ($R = 0.44$, $P < 0.0001$). In general, CO_2 effluxes were higher in grazed areas, but the differences were statistically significant only in June and August (Figure 2).

Based on the linear mixed model effect, soil temperature ($P < 0.0001$) and lichen coverage ($P = 0.0411$) were the most important factors affecting the CO_2 efflux (Table 2). The effect of grazing on the CO_2 efflux from the field layer was not statistically significant ($P = 0.1566$) (Table 2). The CO_2 efflux increased with warmer soil temperatures (Table S2: $R = 0.665$, $P < 0.0001$) and decreased with higher

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lichen coverage (Table S2: $R = -0.223$, $P = 0.0565$). Approximately 50–79% of the total field layer CO_2 efflux originated from root and rhizosphere respiration, but no significant difference was observed between grazed and non-grazed areas (Table 1).

Soil CH_4 flux

Soils in our study areas were CH_4 sinks throughout the entire measuring period, and the sink was significantly higher ($P = 0.0108$) in grazed areas (Figure 3). The grazed areas were larger sinks for CH_4 in June and August ($P < 0.0001$), but there was no difference between the areas detected in July (Figure 3). Based on the linear mixed effect model, soil temperature ($P = 0.0009$) and moss coverage ($P = 0.0042$) were the most important factors affecting the CH_4 flux (Table 2). Higher moss coverage in grazed areas resulted in a higher CH_4 sink (Table S2: $R = -0.406$, $P = 0.0003$), but at the same time warmer soils decreased the field layer CH_4 sink (Table S2: $R = 0.330$, $P = 0.0041$). The effects of grazing and soil moisture on the CH_4 flux were not statistically significant (Table 2).

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Soil N_2O flux

A difference ($P = 0.0116$) in N_2O fluxes was observed between the areas grazed and non-grazed. The non-grazed areas acted as N_2O sinks throughout the entire measuring period, while the trend was not as clear in the grazed areas (Figure 4). In June and August, we observed no significant differences between the treatments, whereas in July the non-grazed areas were larger sinks for N_2O. Moss biomass was the only factor affecting the N_2O fluxes ($P = 0.0494$) (Table 2), while N_2O consumption (sink) was larger with lower moss biomass (Table S2: $R = 0.528$, $P < 0.0001$).

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Discussion

We studied the impact of reindeer grazing on field layer GHG (CO_2, CH_4 and N_2O) fluxes in a northern boreal coniferous forest, and linked these fluxes to grazer-induced changes in ground vegetation coverage and biomass along with soil temperature and soil moisture. Areas grazed by reindeer consumed more CH_4 in June and August, and there were significantly higher CO_2 effluxes from these areas at the same time. Non-grazed areas were a sink for N_2O. Our study indicates that grazing caused changes in soil temperature and lichen coverage affect field layer CO_2 emissions. Concurrently, grazing-induced changes in moss coverage, soil moisture content and temperature affected the CH_4 fluxes, and changes in moss biomass affected the N_2O fluxes.

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We observed that field layer CO_2 effluxes were generally higher in areas grazed by reindeer. As hypothesized, the linear mixed effect model showed that the important factor explaining the CO_2 efflux was the soil temperature (Table 2). Together with soil temperature lichen coverage also significantly influenced the CO_2 efflux as there was a negative correlation between soil CO_2 efflux and lichen coverage (Table 2). Our study detected significant grazing effects on the CO_2 efflux only in June and August (Figure 2), and the reason for that could be that the CO_2 measurements in July were performed directly after a few rainy days, and the low temperature and high soil moisture possibly influencing the CO_2 efflux (Figure 1).

Previous studies from boreal pine forests have showed grazing to have no effect (Köster *et al.,* 2015b) or only a minor effect (Köster *et al.,* 2017) on the field layer CO_2

efflux. Stark *et al.* (2003) documented lower soil respiration and microbial activity in the grazed areas in the northern boreal forest soils. These outcomes were explained by decreased activity of microbes and Scots pine root biomass. As our study deals with field layer respiration that encompasses both soil respiration and the respiration by vegetation, also the changed species composition and the altered environmental conditions induced by it may explain the difference.

The results of our study reviled also that grazed areas were stronger CH_4 sinks (i.e. increased CH_4 uptake) in June and August. The results of the mixed effect model analysis indicated that soil temperature and moss coverage together with soil moisture explained most of the CH_4 fluxes (Table 2).

Based on the model, colder and drier soils acted as stronger CH_4 sinks. Another explanation for higher CH_4 uptake in the grazed areas was the grazing induced differences in ground vegetation, as the field layer CH_4 sink correlated positively with the moss coverage. Lichens and bryophytes contain methane-producing cyanobacteria (Lenhart *et al.,* 2015). Higher moss coverage (and smaller lichen coverage) is likely to have increased the capacity of the ground layer to act as a CH_4

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sink. Our results therefore suggest, as hypothesized, that changes in the CH_4 flux depend on the changes in ground layer vegetation.

The forest field layer was a clear N_2O sink in non-grazed areas, but the trends were not as clear in grazed areas. Our hypothesis that differences in ground vegetation characteristics might influence the N_2O fluxes was confirmed by our model analysis, which showed moss biomass to be the only factor which affected the N_2O fluxes in our study (Table 2). Lichens and bryophytes are one of the main N_2O sources in Arctic regions (Zhuang *et al.*, 2012), where the N_2O release also depends on temperature (Lenhart *et al.*, 2015). Non-grazed areas have less mosses, which probably emit less N_2O. As the soil acts as an N_2O sink regardless of grazing, the higher moss biomass on the grazed area likely negated this and turned the field layer to be smaller N_2O sink. However, other reasons may exist behind the difference between grazed and non-grazed areas, e.g. temperature and soil moisture content. Supporting the observations by Olofsson *et al.* (2010), soil temperatures in our study were slightly higher in grazed areas (although no statistically significant difference

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was observed in our case). Soil warming goes along with changes in species composition in our study, where lichens were replaced with mosses, and these darker surfaces absorb more solar radiation.

Our previous study (Köster *et al.,* 2015b) documented significant effect of grazing on the biomass of lichens and mosses, but no effect was observed on dwarf shrub and grass biomasses. Lichens are the main winter forage for reindeer, and similarly to other studies (Akujärvi *et al.*, 2014; Susiluoto *et al.,* 2008; Olofsson *et al.,* 2010; Köster et al., 2013), reindeer grazing reduced the lichen biomass by more than 90% in our study areas. One additional important finding in our study was that grazing by reindeer did not create patches of bare soil, which was shown to be the case in studies conducted in tundra areas (Suominen and Olafson, 2000; Väre *et al.,* 1996). In our study areas, mosses were occupying the areas grazed by reindeer and bare patches of soil were uncommon. Also, previous studies (Köster *et al.*, 2013: Väre *et al.,* 1996) have showed mosses to quickly invade grazed areas, probably due to decreased competition by lichens. Thus, through the promotion of mosses and the

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reduction in tree regeneration (Köster *et al.*, 2013), grazing changes the vegetation composition and its functions.

Grazing by reindeer increases nutrient cycling (Olofsson & Oksanen, 2002) by changing the litter quality and abiotic conditions (temperature and moisture) relevant for litter decomposition (Olofsson & Oksanen, 2002; Stark & Väisänen, 2014). It has been found that reindeer grazing in areas grazed during summer has a strong positive effect on ecosystem nutrient cycling, as dung and urine deposits provides resources that are highly decomposable (Olofsson *et al.,* 2004; Barthelemy *et al.,* 2015), and have positive effect on net N mineralization (Stark *et al.,* 2000) and GHG fluxes (Turunen *et al.* 2013). Still, our study areas are located in the winter ranges, where dung and urine depositions are partly wasted away with snowmelt, and thereby, they do not affect microbial activity in a similar manner as in the summer grazing areas.

Grazing may also affect belowground C dynamics through changes in ground vegetation. A substantial proportion of assimilated C is allocated to both tree and belowground plant root biomass and/or root-associated mycorrhizal fungi, which are

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an important contributors to soil respiration. Moreover, the recently assimilated C may also increase SOM decomposition by providing energy for decomposing microorganisms and possibly affect GHGs (Högberg et al., 2002). Ground vegetation root biomasses were slightly higher in non-grazed areas, but the CO_2 efflux was concurrently higher in the grazed areas, thus changes in root and rhizhosphere respiration of ground vegetation did not explain the higher CO_2 efflux in the grazed areas. The amount of litter in the grazed area could also be expected to be smaller when ground vegetation biomass was reduced due to grazing, and this would result in smaller decomposition rates. However, the main litter input in forested areas comes from trees, but as shown by Köster *et al.* (2015b), no differences were observed in the aboveground biomasses between the treatments.

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Our study showed that grazing significantly reduced lichen coverage and biomass. The biomass and coverage of mosses concurrently increased significantly in grazed areas. Our results indicated that grazing-induced changes in vegetation composition both positively and negatively affect GHG fluxes from the forest field layer in a northern boreal forests. Our results showed clearly higher CO_2 emissions from grazed areas, and these were affected by soil temperature and lichen coverage. Our results also clearly demonstrated that CH_4 and N_2O fluxes were dependent on shifts in aboveground vegetation communities. Soil temperature and moss coverage together with soil moisture explained most of the CH_4 fluxes, and grazed areas consumed more CH_4. Non-grazed areas with lower moss biomass were concurrently a small N_2O sink. The results presented in our study are collected from a single experiment with similar site characteristics (same soil, tree species, grazing practices, etc.), and thus it would be difficult to extrapolate our results to entire forested areas in Arctic regions. Overall, our results show for the first time that besides influencing the CO_2 fluxes from the northern boreal forest floor, reindeer grazing has an impact on the fluxes of other GHGs. Thus, reindeer may have a significant role in determining the GHG balance of northern boreal forests.

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Supporting Information:

Supporting experimental procedures: Methods S1

Supporting tables: Table S1, Table S2

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561 Table 1. Average ground vegetation biomasses (kg m^{-2}), root biomasses (kg m^{-2}), 562 number of trees per hectare (referred from Köster et al., 2015b). Average vegetation 563 coverages (%), patches of bare soil (%) and values for root respiration (%) in grazed 564 and non-grazed areas. The given values are the mean and SE in parentheses.

	Grazed	Non-grazed
Total ground vegetation biomass (kg m^{-2})	0.61 (±0.09)	0.94 (±0.07)*
Ground vegetation root biomass (kg m^{-2})	0.52 (±0.02)	0.66 (±0.02)*
Tree root biomass (kg m^{-2})	2.2 (±0.12)	2.5 (±0.2)
Nr of trees per ha (h<1.3)	3892 (±839)	7133 (±233)*
Nr of trees per ha (h>1.3)	583 (±79)	558 (±33)
Lichen biomass (kg m^{-2})	0.04 (±0.02)	0.45 (±0.09)*
Moss biomass (kg m^{-2})	0.36 (±0.07)	0.28 (±0.04)*
Dwarf shrub biomass (kg m^{-2})	0.21 (±0.02)	0.21 (±0.03)
Grass biomass (kg m^{-2})	0.01 (±0.01)	0.01 (±0.01)
Lichen coverage (%)	4.2 (±0.9)	76.7 (±8.6)*
Moss coverage (%)	65.9 (±12.3)	22.2 (±8.8)*
Dwarf shrub coverage (%)	49.9 (±7.9)	38.3 (±6.4)
Patches of bare soil (%)	< 1	< 1
Grass coverage (%)	< 1	< 1
Root respiration (%)	65.6 (±4.3)	61.1 (±4.9)

565 *$P \leq 0.01$

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Table 2. Parameter values of the linear mixed effect models that best explained the GHG fluxes. The tested models and their selection based on AIC criteria are shown in Table S1.

	CO_2 Model 7	CH_4 Model 6	N_2O Model 10
r^2	0.6517	0.245	0.249
AIC	70.3	-1686.3	-1827.5
Intercept	-2.248	-0.000015	-4.4×10^{-7}
(stderr, P)	(0.245, $P = 0.0116$)	(4.4×10^{-6}, $P = 0.0729$)	(7.9×10^{-8}, $P < 0.0001$)
Soil temperature	0.167	7.8×10^{-7}	
(stderr, P)	(0.016, $P < 0.0001$)	(2.2×10^{-7}, $P = 0.009$)	
Lichen coverage	-0.005		
(stderr, P)	(0.002, $P = 0.0167$)		
Soil moisture		1.3×10^{-7}	
(stderr, P)		(8.2×10^{-8}, $P = 0.0945$)	
Moss coverage		-2.8×10^{-8}	
(stderr, P)		(9.7×10^{-9}, $P = 0.0042$)	
Moss biomass			1.3×10^{-6}
(stderr, P)			(2.5×10^{-7}, P < 0.0001)
Area (grazed or non-grazed)	0.259	-7.1×10^{-7}	
(stderr, P)	(0.181, $P = 0.1566$)	(7.7×10^{-7}, $P = 0.3480$)	

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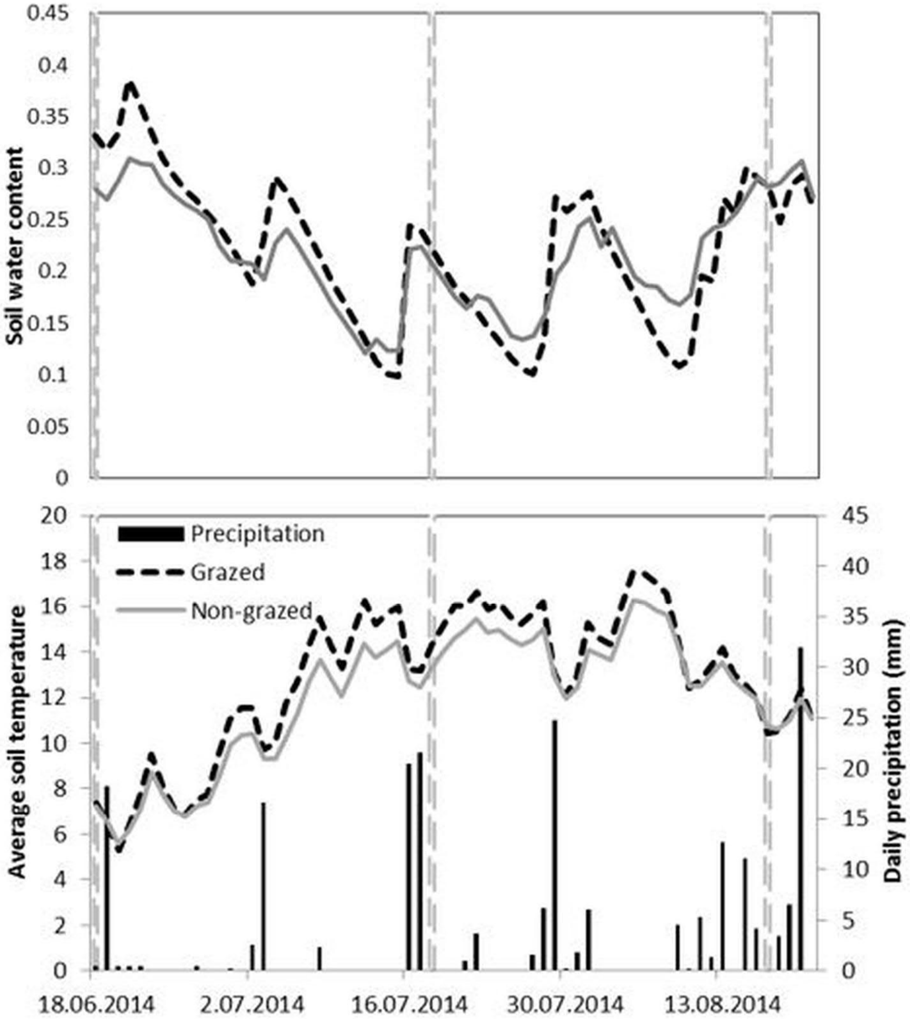

Figure 1. Soil water content (m^3 m^{-3}) and average soil temperature (°C) and precipitation (mm) during the measuring period (June–August). Doted vertical lines represent the GHG flux measurement days.

156x181mm (300 x 300 DPI)

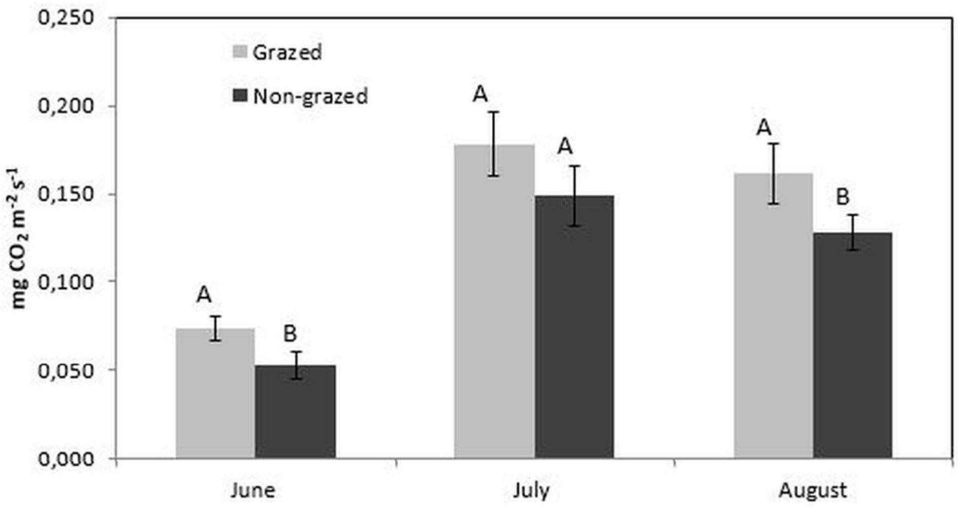

Figure 2. Average field layer CO_2 effluxes (mg CO_2 m^{-2} s^{-1}) throughout the growing season in areas grazed by reindeer and in non-grazed areas. Error bars represent SE. Statistically significant differences between the grazed and non-grazed areas during separate months are denoted by letters above the bars.

84x49mm (300 x 300 DPI)

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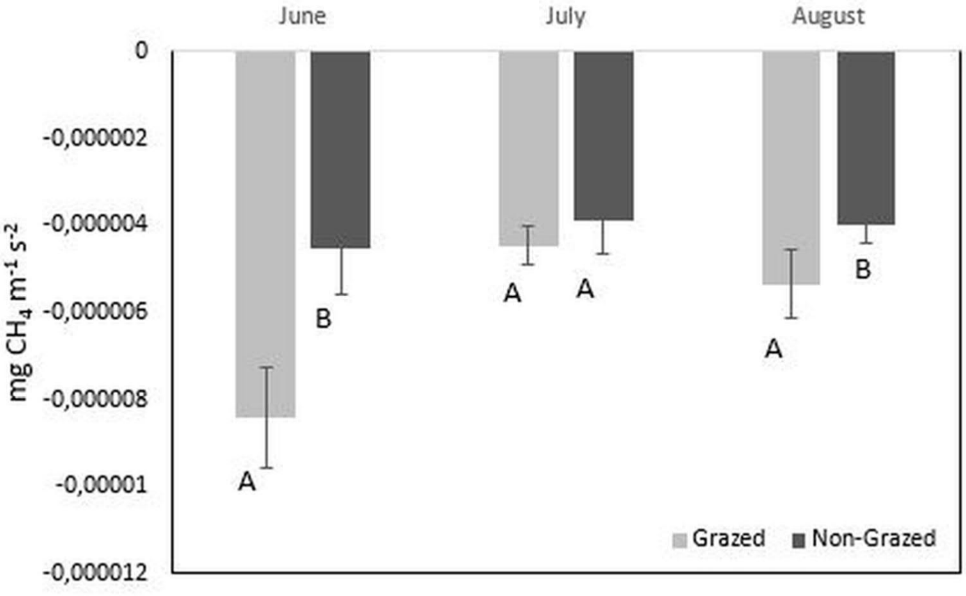

Figure 3. Average field layer methane fluxes (mg CH$_4$ m^{-2} s^{-1}) throughout the growing season in areas grazed and not grazed by reindeer. Error bars represent SE. Statistically significant differences between the grazed and non-grazed areas during separate months are denoted by letters above the bars.

74x44mm (300 x 300 DPI)

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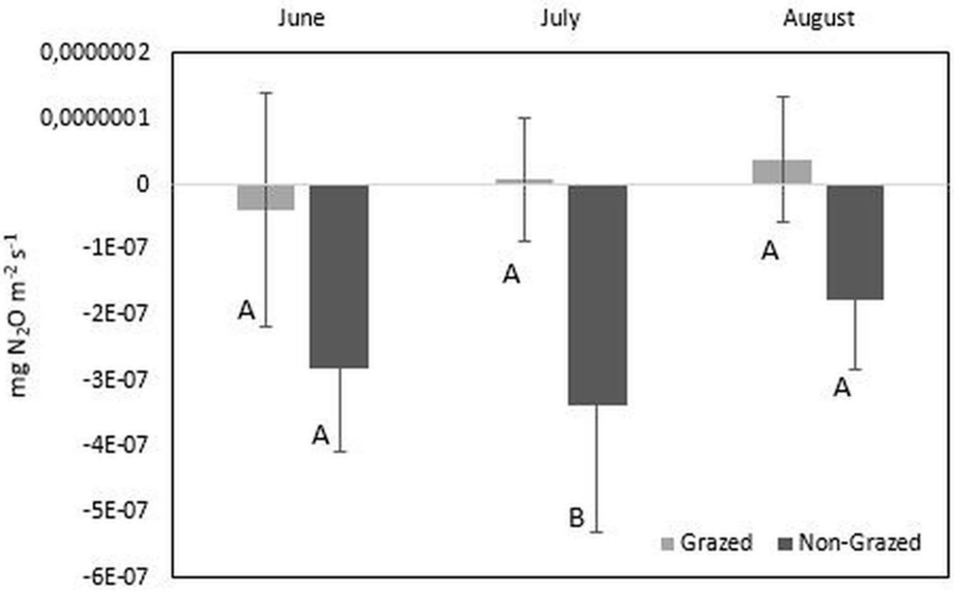

Figure 4. Average field layer fluxes of nitrous oxide (mg N_2O m^{-2} s^{-1}) throughout the growing season in areas grazed by reindeer and in non-grazed areas. Error bars represent SE. Statistically significant differences between grazed and non-grazed areas during separate months are denoted by letters above the bars.

75x45mm (300 x 300 DPI)

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