<https://helda.helsinki.fi>

Contrasting effects of reindeer grazing on CO₂, CH₄, and N₂O fluxes originating from the northern boreal forest floor

Köster, Kajar

2018-02

Köster , K , Köster , E , Berninger , F , Heinonsalo , J & Pumpanen , J 2018 , ' Contrasting effects of reindeer grazing on CO₂, CH₄, and N₂O fluxes originating from the northern boreal forest floor ' , Land Degradation and Development , vol. 29 , no. 2 , pp. 374-381 . <https://doi.org/10.1002/ldr.2868>

<http://hdl.handle.net/10138/309202>

<https://doi.org/10.1002/ldr.2868>

---

cc_by_nc

submittedVersion

Downloaded from Helda, University of Helsinki institutional repository.

This is an electronic reprint of the original article.

This reprint may differ from the original in pagination and typographic detail.

Please cite the original version.

This is the pre-peer reviewed version of the following article: CONTRASTING EFFECTS OF REINDEER GRAZING ON CO₂, CH₄ AND N₂O FLUXES ORIGINATING FROM THE NORTHERN BOREAL FOREST FLOOR, which has been published in final form at <https://doi.org/10.1002/ldr.2868>. This article may be used for non-commercial purposes in accordance with Wiley Terms and Conditions for Use of Self-Archived Versions.

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

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

4   Kajar Köster^{1*}, Egle Köster¹, Frank Berninger¹, Jussi Heinonsalo^{1,2,3}, Jukka
5   Pumpanen⁴

6
7   ¹ Department of Forest Sciences, University of Helsinki, P.O. Box 27, FI-00014
8   Helsinki, Finland

9   ²Department of Food and Environmental Sciences, University of Helsinki, PO Box 56
10   (Viikinkaari 9) FI-00014 Helsinki, Finland

11   ³Finnish Meteorological Institute, P.O. Box 503, 00101 Helsinki, Finland

12   ⁴ Department of Environmental and Biological Sciences, University of Eastern
13   Finland, PL 1627, FI-70211 Kuopio, Finland

14
15   * Corresponding author:

16   Kajar Köster, PhD

17 Address:

18 University of Helsinki

19 Department of Forest Sciences

20 P.O. Box 27, FI-00014 Helsinki

21 Tel: +37253439598

22 E-mail: kajar.koster@helsinki.fi

23

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

26

27

28

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

29   **Abstract**

30   Reindeer (*Rangifer tarandus* L.) are considered to be an important mammalian
31   herbivore, strongly influencing Arctic lichen-dominated ecosystems. There is no wide
32   knowledge about the effect of reindeer on greenhouse gas (GHG) fluxes in northern
33   boreal forests. Ground vegetation plays an important role in absorbing nitrogen (N)
34   and carbon dioxide (CO₂) from the atmosphere. Lately, it has also been found to be a
35   significant source of nitrous oxide (N₂O) and a small source of methane (CH₄). We
36   investigated the influence of reindeer grazing on field layer GHG (CO₂, CH₄ and N₂O)
37   fluxes, ground vegetation coverage and biomass, soil physical properties
38   (temperature and moisture) in a northern boreal forests. At our study site, the
39   reindeer-induced replacement of lichen by mosses had contrasting effects on the
40   GHG fluxes originating from the field layer. Field layer CO₂ efflux was significantly
41   higher in grazed areas. The field layer was a CH₄ sink in all areas, but grazed areas
42   absorbed more CH₄ compared to non-grazed areas. While total N₂O fluxes remained
43   around zero in grazed areas, a small N₂O sink occurred in non-grazed areas with
44   lower moss biomass. Our results indicated that grazing by reindeer in northern boreal
45   forests affects GHG fluxes from the forest field layer both positively and negatively,

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

47 composition.

48

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

50

For Peer Review

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

51   **Introduction**

52   Over 35% (~415 000 km²) of the land area in Scandinavia is grazed by reindeer
53   (*Rangifer tarandus* L.) (Jernsletten & Klokov, 2002). They influence most of the
54   Scandinavian Arctic, subarctic and northern boreal regions, which are also expected
55   to be significantly influenced by the climate change (Anisimov *et al.*, 2007). Reindeer
56   can strongly influence plant diversity and species composition, and consequently
57   also the nutrient availability and carbon (C) balance of subarctic ecosystems (Väre *et*
58   *al.*, 1996; Köster *et al.*, 2013; Akujärvi *et al.*, 2014). The number of reindeer has
59   declined in northern boreal areas, except for Scandinavia where it has remained
60   stable or has even increased over the last decades (Vors & Boyce, 2009).
61
62   Reindeer grazing affects ground vegetation by trampling (Väre *et al.*, 1996;
63   Suominen & Olofsson, 2000), selective grazing (Olofsson & Oksanen, 2002) and by
64   returning nutrients in dung and urine (Barthelemy *et al.*, 2015). Van der Wal (2006)
65   showed that in systems with low productivity, grazing changes the ground vegetation
66   from lichen-rich to moss-rich. In more nutrient-rich systems, this change may be from
67   moss-rich to graminoid-rich (Van der Wal, 2006). Heavy grazing increases the

1
2
3 68 presence of bare patches of soil (Suominen & Olofsson, 2000), and grazing may
4
5
6 69 therefore warm up and dry the soil (Väre *et al.*, 1996). Temperature and soil moisture
7
8
9
10 70 are one of the key factors influencing activity of microbes, soil decomposition
11
12
13 71 processes and the greenhouse gas (GHG) exchange between the field layer and
14
15
16 72 atmosphere (Karhu *et al.*, 2014).
17
18
19
20 73 Northern and high altitude soils have large soil organic matter (SOM) stores due to
21
22
23 74 the slowly decomposing recalcitrant plant litter (Hobbie *et al.*, 2002). Soils can be
24
25
26 75 both source or/and sink of three GHGs: carbon dioxide (CO₂), methane (CH₄) and
27
28
29 76 nitrous oxide (N₂O) (Smith *et al.*, 2003). Effluxes of soil CO₂ can be originated from
30
31
32 77 heterotrophic respiration (decomposition of SOM), and autotrophic respiration of
33
34
35 78 roots and mycorrhizal fungi. Both of these are affected by the soil organic C
36
37
38 79 composition, concentration and soil physical properties (Kirschbaum 2000). The
39
40
41 80 CH₄ flux is a net effect of CH₄ methanogenesis and CH₄ oxidation (Le Mer & Roger,
42
43
44 81 2001). N₂O is a product or by-product in a series of microbial processes such as
45
46
47 82 denitrification and nitrification (Wrage *et al.*, 2001). As both methanogenesis and
48
49
50 83 denitrification are anaerobic processes, CH₄ and N₂O fluxes are sensitive to soil
51
52
53 84 moisture content changes.
54
55
56
57
58
59
60

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

85

86 In addition, soil GHG fluxes are affected by cryptogams (lichens, bryophytes, etc.),
87 which can fix CO₂ from the atmosphere through photosynthesis and also fix nitrogen
88 (N) in symbiosis with N-fixing bacteria (Elbert *et al.*, 2012). The role of cryptogams as
89 sources of N₂O and CH₄ has also been demonstrated recently (Lenhart *et al.*, 2015).
90 By affecting ground vegetation composition and soil temperatures reindeer grazing
91 could significantly impact the N₂O and CH₄ fluxes from the forest floor (Porada *et al.*,
92 2017).

93

94 Over half of the subarctic area is covered by forest, but the number of studies
95 addressing the interactions between grazing and field layer GHG fluxes in northern
96 boreal forests is low (Olofsson *et al.*, 2010; Köster *et al.*, 2013; Köster *et al.*, 2015b).
97 Previous studies on reindeer grazing have mostly focused on tundra areas and
98 grazing effect on CO₂ efflux, while the effects on other GHGs (CH₄ and N₂O) have
99 not been studied. This study assesses the influence of reindeer on the fluxes of these
100 three GHGs in the field layer of a northern boreal forests. We compared grazed and

1
2
3 101 non-grazed areas and linked the GHG fluxes (CO₂ efflux from the field layer, the
4
5
6 102 proportion of root respiration amongst the CO₂ production, the CH₄ and N₂O
7
8
9
10 103 exchange between the field layer and atmosphere) to vegetation biomass, plant
11
12
13 104 functional type and characteristics of soil (root biomass, soil temperature and
14
15
16 105 moisture).
17
18
19
20
21 106
22
23
24
25 107 We hypothesized that by reducing lichen biomass, reindeer grazing will increase soil
26
27
28 108 temperature and decrease soil moisture. We also hypothesized that these and the
29
30
31 109 following soil microbiological changes in the soil affect field layer CO₂, CH₄ and N₂O
32
33
34 110 fluxes: a) higher soil temperatures result in higher CO₂ emissions from the soil; b)
35
36
37 111 decreased soil moisture negatively affects CH₄ and N₂O fluxes; c) differences in
38
39
40 112 ground vegetation characteristics between grazed and non-grazed areas influence
41
42
43 113 soil CH₄ and N₂O fluxes, as mosses and lichens can both fix and emit these GHGs.
44
45
46
47
48 114
49
50
51
52

53 115 **Materials and methods**

54 55 56 57 116 *Study sites*

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

117 Our study areas situate in the Värriö Strict Nature Reserve (67°46' N, 29°35' E) of
118 Finnish Lapland. The areas are situated close to the treeline (average altitude of the
119 study area was 300 m a.s.l.), in a northern boreal forest, in the zone of the last intact
120 subarctic Scots pine (*Pinus sylvestris* L.) forest landscapes in Fennoscandia
121 (Potapov *et al.*, 2008). The area is characterized by the sub-continental climate.
122 Snow cover persists for 200–225 days/year, and the average snow depth is
123 approximately 0.7 m (Köster *et al.*, 2015b). The annual growing season varies
124 between 105–120 days (Köster *et al.*, 2014; Köster *et al.*, 2015b). The soils belong to
125 haplic podzol (FAO, 1990) with no permafrost, and the pH of the soil is 4.4 (Köster *et*
126 *al.*, 2014). The study areas belong to the Pohjois-Salla reindeer herding district, with
127 approximately 2.2 reindeer per km² (Turunen *et al.*, 2016).

128

129 *Experimental design*

130 The experiment was established in a year 2013 as a split plot experiment with five
131 plots. Each plot was separated to the grazed and non-grazed subplot (400 m²). The
132 areas are separated by the fence running between Finland and Russia, preventing

1
2
3 133 Finnish domesticated reindeer to cross the border (Köster *et al.*, 2017). The official
4
5
6 134 border between Finland and Russia is a few hundred metres further east from the
7
8
9
10 135 reindeer fence. The subplots (n=10) were situated along this fence. The Finnish side
11
12
13 136 is mainly grazed during the wintertime, with an average density of 2.2 reindeer per
14
15
16 137 km⁻², while the non-grazed areas on the Russian side of the fence have been
17
18
19
20 138 excluded from heavy reindeer grazing for nearly a century (Stark *et al.*, 2003).
21
22
23
24 139
25
26
27
28 140 *Biomass measurements and vegetation coverage*
29
30
31

32 141 Stand characteristics and ground vegetation and root biomass measurements were
33
34
35 142 conducted in 2013, and the description of the methods used is published in Köster *et*
36
37
38 143 *al.* (2015b) and in Supporting experimental procedures: Methods S1. The ground
39
40
41
42 144 vegetation biomass measurements were repeated according to the same protocols in
43
44
45 145 2014 at the same time as GHG measurements. Four 0.5m x 0.5m quadrats placed
46
47
48
49 146 systematically inside each subplot were photographed and the ground vegetation
50
51
52 147 species composition, species coverage and possible area of bare ground were
53
54
55 148 visually estimated from these photos. As shown in Köster *et al.* (2015b), total ground
56
57
58
59
60

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

149 vegetation and lichen biomasses were higher and moss biomasses lower in the
150 areas with no reindeer, while the dwarf shrub and grass biomasses were similar for
151 both areas (Table 1). The differences in ground vegetation and tree regeneration
152 caused differences in root biomasses between the non-grazed and grazed areas.
153 Both ground vegetation root biomasses and tree root biomasses were higher in non-
154 grazed areas (Table 1) (Köster *et al.*, 2015b).
155
Chamber measurements of CO₂, CH₄ and N₂O.
157 Soil GHG fluxes were measured using the static chamber method with 50 polyvinyl
158 chloride (PVC) collars (five collars per subplot; h = 0.05 m, Ø = 0.22 m) installed
159 permanently in the soil during the spring of 2013 one year before the flux
160 measurements. To avoid the leakage of air to the collar we installed collars in the
161 litter layer and sealed them with sand. The ground vegetation was left intact inside
162 the chamber in course of measurements. GHG measurements were performed
163 monthly (second week of each month) in June, July and August in 2014, with a
164 portable opaque chamber (h = 0.24 m, Ø = 0.22 m) (Pumpanen *et al.*, 2015).

1
2
3 165 CO₂ concentration in the chamber headspace was registered for a 5-minute chamber
4
5
6 166 deployment time at 5-sec intervals with a CO₂ probe (GMP343, Vaisala Oyj, Vantaa,
7
8
9
10 167 Finland); temperature and air humidity were recorded with a temperature and relative
11
12
13 168 humidity sensor (HM70, Vaisala Oyj, Vantaa, Finland) (Köster *et al.*, 2015a).

14
15
16 169 The CH₄ and N₂O flux measurements were performed using the same collars and the
17
18
19
20 170 same chamber as in the CO₂ efflux measurements by collecting air samples from the
21
22
23 171 chamber with a polypropylene syringe (50-ml) (BD Plastipak 60, BOC Ohmeda,
24
25
26 172 Helsingborg, Sweden). The samples were collected 0, 1, 5, 10 and 15 min after the
27
28
29
30 173 chamber was installed, and immediately stored into glass vials (Soda glass (12 ml)
31
32
33 174 Labco Exetainer®, Labco Limited, UK). We analysed the samples by an Agilent Gas
34
35
36
37 175 Chromatograph model 7890A (GC, Agilent Technologies, USA). The linear
38
39
40 176 regression between the measurement time and GHG concentration change within
41
42
43 177 the chamber was used to calculate the fluxes of CO₂, CH₄ and N₂O. Outliers from the
44
45
46 178 CH₄ and N₂O concentrations measured during each chamber deployment were
47
48
49
50 179 filtered using Grubbs' test for outliers (Stefansky, 1972).

51
52
53 180 During the GHG measurements, soil moisture was determined with a ML2 sensor
54
55
56
57 181 (Delta-T Devices, UK) and soil temperature (top 10 cm) with a P 300w temperature
58
59
60

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

182 probe (Dostmann Electronic GmbH, Germany). In addition, soil temperature was

183 measured continuously at every subplot with iButton temperature sensors (Maxim

184 Integrated, San Jose, California, U.S.A.) and soil moisture at two subplots with an

185 ML2x soil moisture sensor (Delta-T Devices Ltd., Cambridge, England) installed

186 under the organic layer and connected to a data logger.

187

188 *The proportion of root respiration*

189 Five soil cores ($h = 0.15\text{ m}$, $\varnothing = 0.05\text{ m}$) were collected from each subplot for the

190 incubation study and stored at $+4\text{ }^{\circ}\text{C}$ for two weeks. Soil cores were incubated in

191 cylinders ($h = 0.3\text{ m}$, $\varnothing = 0.075$), and CO_2 exchange was followed with CO_2 and

192 water vapour analysers (Licor LI-840 and Licor LI-7000, Li-Cor Inc., Lincoln,

193 Nebraska). The system temperature was constantly $+12\text{ }^{\circ}\text{C}$, and differences of CO_2

194 concentrations were measured from the incoming and outgoing air. The proportion of

195 root respiration was calculated from one time point (the beginning of June) by

196 comparing the field layer CO_2 efflux measurements (corrected to the rates occurring

197 at $+12\text{ }^{\circ}\text{C}$) in the field to the lab incubation measurements. Field layer CO_2 efflux was

198 used as total respiration (heterotrophic + autotrophic respiration). Lab incubation

199 measurements provided us with the heterotrophic respiration values.

200

201 *Data analysis*

202 Normality check for the data was done with the Shapiro–Wilk test ($P > 0.05$) and

203 logarithm transformations were calculated for the measured CO₂ fluxes. The other

204 parameters did not need transformation. We used the linear mixed effects model

205 (PROC MIXED) for testing the effects of various factors (grazed or non-grazed area,

206 subplot, collar location, measurement time, root biomass, various ground vegetation

207 biomasses and coverage, etc.) on soil GHG emissions as follows:

$$208 \quad Y_{p,s} = \beta_0 + \beta_1 A + b_p + b_{C*P} + b_T + \epsilon_S \quad (1)$$

$$209 \quad b_p \sim N(0, \delta_p^2) \quad (2)$$

$$210 \quad b_{C*P} \sim N(0, \delta_{C*P}^2) \quad (3)$$

$$211 \quad b_T \sim N(0, \delta_T^2) \quad (4)$$

$$212 \quad \epsilon_S \sim N(0, \delta_S^2) \quad (5)$$

213

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

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_{C*P}^2 and δ_T^2 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):

231

232
$$r^2 = 1 - \left(\frac{V(m)}{V(r)} \right) \quad (6)$$

233

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

236 The Pearson correlation coefficients were calculated between the fluxes and

237 explanatory effects (same co-variables as in model) to evaluate the direction of

238 different effects (Table S2).

239 Tukey's HSD post hoc test was employed to compare the grazing effects on different

240 months. All statistical analyses compared grazed and non-grazed areas, and the

241 significance level was $P = 0.05$. SAS version 9.3 (SAS Institute Inc., Cary, NC, USA)

242 was used for statistical analyses.

243

244 Results

245 *Vegetation structure and environmental factors*

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

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

255

256 Average soil temperatures during the measuring period were +10.2 °C in grazed
257 areas and +9.4 °C in the non-grazed areas ($P = 0.2527$). Coldest soil temperatures
258 were measured in June and the warmest in July (Figure 1), and a significant
259 difference in temperature between the areas was observed only in July ($P = 0.0218$),
260 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 CO₂ efflux

The highest field layer CO₂ 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 CO₂ emission ($R = 0.44$, $P < 0.0001$). In general, CO₂ 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 CO₂ efflux (Table 2). The effect of grazing on the CO₂ efflux from the field layer was not statistically significant ($P = 0.1566$) (Table 2). The CO₂ efflux increased with warmer soil temperatures (Table S2: $R = 0.665$, $P < 0.0001$) and decreased with higher

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

277 lichen coverage (Table S2: $R = -0.223$, $P = 0.0565$). Approximately 50–79% of the
278 total field layer CO₂ efflux originated from root and rhizosphere respiration, but no
279 significant difference was observed between grazed and non-grazed areas (Table 1).
280
281 *Soil CH₄ flux*
282 Soils in our study areas were CH₄ sinks throughout the entire measuring period, and
283 the sink was significantly higher ($P = 0.0108$) in grazed areas (Figure 3). The grazed
284 areas were larger sinks for CH₄ in June and August ($P < 0.0001$), but there was no
285 difference between the areas detected in July (Figure 3). Based on the linear mixed
286 effect model, soil temperature ($P = 0.0009$) and moss coverage ($P = 0.0042$) were
287 the most important factors affecting the CH₄ flux (Table 2). Higher moss coverage in
288 grazed areas resulted in a higher CH₄ sink (Table S2: $R = -0.406$, $P = 0.0003$), but at
289 the same time warmer soils decreased the field layer CH₄ sink (Table S2: $R = 0.330$,
290 $P = 0.0041$). The effects of grazing and soil moisture on the CH₄ flux were not
291 statistically significant (Table 2).

293 *Soil N₂O flux*

294 A difference ($P = 0.0116$) in N₂O fluxes was observed between the areas grazed and
295 non-grazed. The non-grazed areas acted as N₂O sinks throughout the entire
296 measuring period, while the trend was not as clear in the grazed areas (Figure 4). In
297 June and August, we observed no significant differences between the treatments,
298 whereas in July the non-grazed areas were larger sinks for N₂O. Moss biomass was
299 the only factor affecting the N₂O fluxes ($P = 0.0494$) (Table 2), while N₂O
300 consumption (sink) was larger with lower moss biomass (Table S2: $R = 0.528$, $P <$
301 0.0001).

302

303 **Discussion**

304 We studied the impact of reindeer grazing on field layer GHG (CO₂, CH₄ and N₂O)
305 fluxes in a northern boreal coniferous forest, and linked these fluxes to grazer-
306 induced changes in ground vegetation coverage and biomass along with soil
307 temperature and soil moisture. Areas grazed by reindeer consumed more CH₄ in
308 June and August, and there were significantly higher CO₂ effluxes from these areas

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

309 at the same time. Non-grazed areas were a sink for N₂O. Our study indicates that

310 grazing caused changes in soil temperature and lichen coverage affect field layer

311 CO₂ emissions. Concurrently, grazing-induced changes in moss coverage, soil

312 moisture content and temperature affected the CH₄ fluxes, and changes in moss

313 biomass affected the N₂O fluxes.

314

315 We observed that field layer CO₂ effluxes were generally higher in areas grazed by

316 reindeer. As hypothesized, the linear mixed effect model showed that the important

317 factor explaining the CO₂ efflux was the soil temperature (Table 2). Together with soil

318 temperature lichen coverage also significantly influenced the CO₂ efflux as there was

319 a negative correlation between soil CO₂ efflux and lichen coverage (Table 2). Our

320 study detected significant grazing effects on the CO₂ efflux only in June and August

321 (Figure 2), and the reason for that could be that the CO₂ measurements in July were

322 performed directly after a few rainy days, and the low temperature and high soil

323 moisture possibly influencing the CO₂ efflux (Figure 1).

324 Previous studies from boreal pine forests have showed grazing to have no effect

325 (Köster *et al.*, 2015b) or only a minor effect (Köster *et al.*, 2017) on the field layer CO₂

1
2
3 326 efflux. Stark *et al.* (2003) documented lower soil respiration and microbial activity in
4
5
6
7 327 the grazed areas in the northern boreal forest soils. These outcomes were explained
8
9
10 328 by decreased activity of microbes and Scots pine root biomass. As our study deals
11
12
13 329 with field layer respiration that encompasses both soil respiration and the respiration
14
15
16
17 330 by vegetation, also the changed species composition and the altered environmental
18
19
20 331 conditions induced by it may explain the difference.
21
22
23 332 The results of our study revealed also that grazed areas were stronger CH₄ sinks (i.e.
24
25
26
27 333 increased CH₄ uptake) in June and August. The results of the mixed effect model
28
29
30 334 analysis indicated that soil temperature and moss coverage together with soil
31
32
33 335 moisture explained most of the CH₄ fluxes (Table 2).
34
35
36
37 336 Based on the model, colder and drier soils acted as stronger CH₄ sinks. Another
38
39
40
41 337 explanation for higher CH₄ uptake in the grazed areas was the grazing induced
42
43
44 338 differences in ground vegetation, as the field layer CH₄ sink correlated positively with
45
46
47 339 the moss coverage. Lichens and bryophytes contain methane-producing
48
49
50
51 340 cyanobacteria (Lenhart *et al.*, 2015). Higher moss coverage (and smaller lichen
52
53
54 341 coverage) is likely to have increased the capacity of the ground layer to act as a CH₄

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

sink. Our results therefore suggest, as hypothesized, that changes in the CH₄ flux
depend on the changes in ground layer vegetation.

344

The forest field layer was a clear N₂O 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 N₂O fluxes was confirmed by our model analysis,
which showed moss biomass to be the only factor which affected the N₂O fluxes in
our study (Table 2). Lichens and bryophytes are one of the main N₂O sources in
Arctic regions (Zhuang *et al.*, 2012), where the N₂O release also depends on
temperature (Lenhart *et al.*, 2015). Non-grazed areas have less mosses, which
probably emit less N₂O. As the soil acts as an N₂O sink regardless of grazing, the
higher moss biomass on the grazed area likely negated this and turned the field layer
to be smaller N₂O 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

1
2
3 358 was observed in our case). Soil warming goes along with changes in species
4
5
6
7 359 composition in our study, where lichens were replaced with mosses, and these
8
9
10 360 darker surfaces absorb more solar radiation.
11
12
13
14 361
15
16
17 362 Our previous study (Köster *et al.*, 2015b) documented significant effect of grazing on
18
19
20 363 the biomass of lichens and mosses, but no effect was observed on dwarf shrub and
21
22
23 364 grass biomasses. Lichens are the main winter forage for reindeer, and similarly to
24
25
26
27 365 other studies (Akujärvi *et al.*, 2014; Susiluoto *et al.*, 2008; Olofsson *et al.*, 2010;
28
29
30 366 Köster *et al.*, 2013), reindeer grazing reduced the lichen biomass by more than 90%
31
32
33
34 367 in our study areas. One additional important finding in our study was that grazing by
35
36
37 368 reindeer did not create patches of bare soil, which was shown to be the case in
38
39
40 369 studies conducted in tundra areas (Suominen and Olafson, 2000; Väre *et al.*, 1996).
41
42
43
44 370 In our study areas, mosses were occupying the areas grazed by reindeer and bare
45
46
47 371 patches of soil were uncommon. Also, previous studies (Köster *et al.*, 2013; Väre *et*
48
49
50 372 *al.*, 1996) have showed mosses to quickly invade grazed areas, probably due to
51
52
53
54 373 decreased competition by lichens. Thus, through the promotion of mosses and the
55
56
57
58
59
60

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

374 reduction in tree regeneration (Köster *et al.*, 2013), grazing changes the vegetation
375 composition and its functions.
376
377 Grazing by reindeer increases nutrient cycling (Olofsson & Oksanen, 2002) by
378 changing the litter quality and abiotic conditions (temperature and moisture) relevant
379 for litter decomposition (Olofsson & Oksanen, 2002; Stark & Väisänen, 2014). It has
380 been found that reindeer grazing in areas grazed during summer has a strong
381 positive effect on ecosystem nutrient cycling, as dung and urine deposits provides
382 resources that are highly decomposable (Olofsson *et al.*, 2004; Barthelemy *et al.*,
383 2015), and have positive effect on net N mineralization (Stark *et al.*, 2000) and GHG
384 fluxes (Turunen *et al.* 2013). Still, our study areas are located in the winter ranges,
385 where dung and urine depositions are partly wasted away with snowmelt, and
386 thereby, they do not affect microbial activity in a similar manner as in the summer
387 grazing areas.
388 Grazing may also affect belowground C dynamics through changes in ground
389 vegetation. A substantial proportion of assimilated C is allocated to both tree and
390 belowground plant root biomass and/or root-associated mycorrhizal fungi, which are

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 CO₂ efflux was concurrently higher in the grazed areas, thus changes in root and rhizosphere respiration of ground vegetation did not explain the higher CO₂ 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.

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 CO₂ emissions from

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

408 grazed areas, and these were affected by soil temperature and lichen coverage. Our
409 results also clearly demonstrated that CH₄ and N₂O fluxes were dependent on shifts
410 in aboveground vegetation communities. Soil temperature and moss coverage
411 together with soil moisture explained most of the CH₄ fluxes, and grazed areas
412 consumed more CH₄. Non-grazed areas with lower moss biomass were concurrently
413 a small N₂O sink. The results presented in our study are collected from a single
414 experiment with similar site characteristics (same soil, tree species, grazing
415 practices, etc.), and thus it would be difficult to extrapolate our results to entire
416 forested areas in Arctic regions. Overall, our results show for the first time that
417 besides influencing the CO₂ fluxes from the northern boreal forest floor, reindeer
418 grazing has an impact on the fluxes of other GHGs. Thus, reindeer may have a
419 significant role in determining the GHG balance of northern boreal forests.

421 **Acknowledgements**

422 We acknowledge ICOS for supporting our study. This study was funded by grants
423 from the Kone Foundation and by the Academy of Finland projects (grants nr.

424 307222, 294600, 286685). Our gratitude belongs to the staff at Värriö Research

425 Station supported by the Academy of Finland Centre of Excellence programme (grant

426 no. 307331).

427

428 Supporting Information:

429 Supporting experimental procedures: Methods S1

430 Supporting tables: Table S1, Table S2

431

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

References

Anisimov OA, Vaughan DG, Callaghan TV et al. 2007. Polar regions (Arctic and Antarctic). In: Parry ML, Canziani OF, Palutikof JP, van der Linden PJ, Hanson CE, Eds. Climate change 2007: impacts, adaptation and vulnerability. Contribution of working group II to the fourth assessment report of the intergovernmental panel on climate change, Cambridge University Press, Cambridge, pp. 653–85.

Akujärvi A, Hallikainen V, Hyppönen M, Mattila E, Mikkola K, Rautio P. 2014. Effects of reindeer grazing and forestry on ground lichens in Finnish Lapland. *Silva Fennica* **48** (3): article id 1153. DOI: 10.14214/sf.1153

Barthelemy H, Stark S, Olofsson J. 2015. Strong Responses of Subarctic Plant Communities to Long-Term Reindeer Feces Manipulation. *Ecosystems* **18**: 740-751. DOI: 10.1007/s1002

Elbert W, Weber B, Burrows S, Steinkamp J, Budel B, Andreae MO, Poschl U. 2012. Contribution of cryptogamic covers to the global cycles of carbon and nitrogen. *Nature Geoscience* **5**: 459-462. DOI: 10.1038/ngeo1486

181.

- 449 Fao 1990. Soil Map of the World, revised legend. World Soil Resources Report No.
450 60. FAO, Rome, Italy.
- 451 Hobbie SE, Nadelhoffer KJ, Xf, Gberg P. 2002. A synthesis: The role of nutrients as
452 constraints on carbon balances in boreal and arctic regions. *Plant and Soil*
453 **242**: 163-170. DOI: 10.1023/A:101967073
- 454 Högberg P, Nordgren A, Ågren G. 2002. Carbon allocation between tree root growth
455 and root respiration in boreal pine forest. *Oecologia* **132**: 579-581. DOI:
456 10.1007/s00442-002-0983-8
- 457 Jernsletten J, Klokov K. 2002. Sustainable Reindeer Husbandry. Centre for Saami
458 Studies. University of Tromsø. 157pp
- 459 Karhu K, Auffret MD, Dungait JA, Hopkins DW, Prosser JI, Singh BK, Subke JA,
460 Wookey PA, Agren GI, Sebastia MT, Gouriveau F, Bergkvist G, Meir P,
461 Nottingham AT, Salinas N, Hartley IP. 2014. Temperature sensitivity of soil
462 respiration rates enhanced by microbial community response. *Nature* **513**: 81-
463 84. DOI: 10.1038/nature13604

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

464 Kirschbaum MUF. 2000. Will chnages in soil organic carbon act as a positive or
465 negative feedback on global warming? *Biogeochemistry* **48**: 21-51. DOI:
466 10.1023/A:1006238902976

467 Köster E, Köster K, Aurela M, Laurila T, Berninger F, Lohila A, Pumpanen J. 2013.
468 Impact of reindeer herding on vegetation biomass and soil carbon content: A
469 case study from Sodankylä, Finland. *Boreal Environment Research* **18**: 35-42.

470 Köster E, Köster K, Berninger F, Pumpanen J. 2015a. Carbon dioxide, methane and
471 nitrous oxide fluxes from podzols of a fire chronosequence in the boreal
472 forests in Värriö, Finnish Lapland. *Geoderma Regional* **5**: 181-187. DOI:
473 10.1016/j.geodrs.2015.07.001

474 Köster K, Berninger F, Köster E, Pumpanen J. 2015b. Influences of Reindeer
475 Grazing on Above- and Belowground Biomass and Soil Carbon Dynamics.
476 *Arctic, Antarctic, and Alpine Research* **47**: 495-503. DOI: 10.1657/AAAR0014-
477 062

478 Köster K, Berninger F, Lindén A, Köster E, Pumpanen J. 2014. Recovery in fungal
479 biomass is related to decrease in soil organic matter turnover time in a boreal

- 1
2
3 480 fire chronosequence. *Geoderma* **235–236**: 74-82. DOI:
4
5
6
7 481 10.1016/j.geoderma.2014.07.001
8
9
10 482 Köster K, Köster E, Kulmala L, Berninger F, Pumpanen J. 2017. Are the climatic
11
12
13 483 factors combined with reindeer grazing affecting the soil CO₂ emissions in
14
15
16
17 484 subarctic boreal pine forest? *Catena* **149**: 616-622. DOI:
18
19
20 485 10.1016/j.catena.2016.06.011
21
22
23 486 Le Mer J, Roger P. 2001. Production, oxidation, emission and consumption of
24
25
26
27 487 methane by soils: A review. *European Journal of Soil Biology* **37**: 25-50. DOI:
28
29
30 488 10.1016/S1164-5563(01)01067-6
31
32
33 489 Lenhart K, Weber B, Elbert W, Steinkamp J, Clough T, Crutzen P, Pöschl U, Keppler
34
35
36
37 490 F. 2015. Nitrous oxide and methane emissions from cryptogamic covers.
38
39
40 491 *Global Change Biology* **21**: 3889-3900. DOI: 10.1111/gcb.12995
41
42
43 492 Nakagawa S, Schielzeth H. 2013. A general and simple method for obtaining R² from
44
45
46
47 493 generalized linear mixed-effects models. *Methods in Ecology and Evolution* **4**:
48
49
50 494 133-142. DOI: 10.1111/j.2041-210x.2012.00261.x
51
52
53 495 Olofsson J, Stark S, Oksanen L. 2004. Reindeer influence on ecosystem processes
54
55
56
57 496 in the tundra. *Oikos* **105**: 386-396. DOI: 10.1111/j.0030-1299.2004.13048.x
58
59
60

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

Olofsson J, Moen J, Östlund L. 2010. Effects of reindeer on boreal forest floor
vegetation: Does grazing cause vegetation state transitions? *Basic and
Applied Ecology* **11**: 550-557. DOI: 10.1016/j.baae.2010.03.004

Olofsson J, Oksanen L. 2002. Role of litter decomposition for the increased primary
production in areas heavily grazed by reindeer: a litterbag experiment. *Oikos*
96: 507-515. DOI: 10.1034/j.1600-0706.2002.960312.x

Porada P, Pöschl U, Kleidon A, Beer C, Weber B. 2017. Estimating global nitrous
oxide emissions by lichens and bryophytes with a process-based productivity
model. *Biogeosciences* **14**: 1593-1602. DOI: 10.5194/bg-14-1593-2017

Potapov P, Yaroshenko A, Turubanova S, Dubinin M, Laestadius L, Thies C,
Aksenov D, Egorov A, Yesipova Y, Glushkov I, Karpachevskiy M, Kostikova A,
Manisha A, Tsybikova E, Zhuravleva I. 2008. Mapping the World's Intact
Forest Landscapes by Remote Sensing. *Ecology and Society* **13**: 51.

Pumpanen J, Kulmala L, Lindén A, Kolari P, Nikinmaa E, Hari P. 2015. Seasonal
dynamics of autotrophic respiration in boreal forest soil estimated by
continuous chamber measurements. *Boreal Environment Research* **20**: 637-
650.

- Smith KA, Ball T, Conen F, Dobbie KE, Massheder J, Rey A. 2003. Exchange of greenhouse gases between soil and atmosphere: interactions of soil physical factors and biological processes. *European Journal of Soil Science* **54**: 779-791. DOI: 10.1046/j.1351-0754.2003.0567.x
- Stark S, Tuomi J, Strömmer R, Helle T. 2003. Non-parallel changes in soil microbial carbon and nitrogen dynamics due to reindeer grazing in northern boreal forests. *Ecography* **26**: 51-59. DOI: 10.1034/j.1600-0587.2003.03336.x
- Stark S, Väisänen M. 2014. Insensitivity of Soil Microbial Activity to Temporal Variation in Soil N in Subarctic Tundra: Evidence from Responses to Large Migratory Grazers. *Ecosystems* **17**: 906-917. DOI: 10.1007/s10021-014-9768-2
- Stark S, Wardle DA, Ohtonen R, Helle T, Yeates GW. 2000. The effect of reindeer grazing on decomposition, mineralization and soil biota in a dry oligotrophic Scots pine forest. *Oikos* **90**: 301-310. DOI: 10.1034/j.1600-0706.2000.900210.x
- Stefansky W. 1972. Rejecting Outliers in Factorial Designs. *Technometrics* **14**: 469-479. DOI: 10.1080/00401706.1972.10488930

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

531 Suominen O, Olofsson J. 2000. Impacts of semi-domesticated reindeer on structure
532 of tundra and forest communities in fennoscandia: A review. *Annales Zoologici*
533 *Fennici* **37**: 233-249.

534 Susiluoto S, Rasilo T, Pumpanen J, Berninger F. 2008. Effects of grazing on the
535 vegetation structure and carbon dioxide exchange of a fennoscandian fell
536 ecosystem. *Arctic, Antarctic, and Alpine Research* **40**: 422-431. DOI:
537 10.1657/1523-0430(07-035)[SUSILUOTO]2.0.CO;2

538 Zhuang Q, Lu Y, Chen M. 2012. An inventory of global N₂O emissions from the soils
539 of natural terrestrial ecosystems. *Atmospheric Environment* **47**: 66-75. DOI:
540 10.1016/j.atmosenv.2011.11.036

541 Turunen M, Oksanen P, Vuojala-Magga T, Markkula I, Sutinen ML, Hyvönen J. 2013.
542 Impacts of winter feeding of reindeer on vegetation and soil in the sub-Arctic:
543 Insights from a feeding experiment. *Polar Research* **32**: 18610. DOI:
544 10.3402/polar.v32i0.18610

545 Turunen MT, Rasmus S, Bavay M, Ruosteenoja K, Heiskanen J. 2016. Coping with
546 difficult weather and snow conditions: Reindeer herders' views on climate

- 1
2
3 547 change impacts and coping strategies. *Climate Risk Management* **11**: 15-36.
4
5
6
7 548 DOI: 10.1016/j.crm.2016.01.002
8
9
10 549 Van der Wal R. 2006. Do herbivores cause habitat degradation or vegetation state
11
12
13 550 transition? Evidence from the tundra. *Oikos* **114**: 177-186. DOI:
14
15
16
17 551 10.1111/j.2006.0030-1299.14264.x
18
19
20 552 Vors LS, Boyce MS. 2009. Global declines of caribou and reindeer. *Global Change*
21
22
23 553 *Biology* **15**: 2626-2633. DOI: 10.1111/j.1365-2486.2009.01974.x
24
25
26
27 554 Wrage N, Velthof GL, Van Beusichem ML, Oenema O. 2001. Role of nitrifier
28
29
30 555 denitrification in the production of nitrous oxide. *Soil Biology and Biochemistry*
31
32
33 556 **33**: 1723-1732. DOI: 10.1016/S0038-0717(01)00096-7
34
35
36
37 557 Väre H, Ohtonen R, Mikkola K. 1996. The effect and extent of heavy grazing by
38
39
40 558 reindeer in oligotrophic pine heaths in northeastern Fennoscandia. *Ecography*
41
42
43 559 **19**: 245-253. DOI: 10.1111/j.1600-0587.1996.tb01251.x
44
45
46
47 560
48
49
50
51
52
53
54
55
56
57
58
59
60

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

Table 1. Average ground vegetation biomasses (kg m⁻²), root biomasses (kg m⁻²), number of trees per hectare (referred from Köster et al., 2015b). Average vegetation coverages (%), patches of bare soil (%) and values for root respiration (%) in grazed 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)

*P≤0.01

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	CH ₄	N ₂ O
	Model 7	Model 6	Model 10
r ²	0.6517	0.245	0.249
AIC	70.3	-1686.3	-1827.5
Intercept	-2.248	-0.000015	-4.4 x 10 ⁻⁷
(stderr, P)	(0.245, P = 0.0116)	(4.4 x 10 ⁻⁶ , P = 0.0729)	(7.9 x 10 ⁻⁸ , P < 0.0001)
Soil temperature	0.167	7.8 x 10 ⁻⁷	
(stderr, P)	(0.016, P < 0.0001)	(2.2 x 10 ⁻⁷ , P = 0.009)	
Lichen coverage	-0.005		
(stderr, P)	(0.002, P = 0.0167)		
Soil moisture		1.3 x 10 ⁻⁷	
(stderr, P)		(8.2 x 10 ⁻⁸ , P = 0.0945)	
Moss coverage		-2.8 x 10 ⁻⁸	
(stderr, P)		(9.7 x 10 ⁻⁹ , P = 0.0042)	
Moss biomass			1.3 x 10 ⁻⁶
(stderr, P)			(2.5 x 10 ⁻⁷ , P < 0.0001)
Area (grazed or non-grazed)	0.259	-7.1 x 10 ⁻⁷	
(stderr, P)	(0.181, P = 0.1566)	(7.7 x 10 ⁻⁷ , P = 0.3480)	

Figure 1. Soil water content ($\text{m}^3 \text{m}^{-3}$) and average soil temperature ($^{\circ}\text{C}$) 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 CO₂ effluxes (mg CO₂ 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)

Figure 3. Average field layer methane fluxes (mg CH₄ 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)

Figure 4. Average field layer fluxes of nitrous oxide ($\text{mg N}_2\text{O m}^{-2} \text{s}^{-1}$) 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)