1 Response of vegetation and carbon fluxes to brown lemming herbivory
2 in Northern Alaska

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10 **Abstract.** The Arctic is warming at double the average global rate, affecting the carbon cycle of tundra ecosystems. Most research
11 on carbon fluxes from Arctic tundra ecosystems has focused on abiotic environmental controls (e.g. temperature, rainfall, or
12 radiation). However, Arctic tundra vegetation, and therefore the carbon balance of these ecosystems, can be substantially impacted
13 by herbivory. In this study we tested how vegetation consumption by brown lemmings (*Lemmus trimucronatus*) can impact carbon
14 exchange of a wet-sedge tundra ecosystem near Utqiaġvik, Alaska during the summer, and the recovery of vegetation during a
15 following summer. We placed brown lemmings in individual enclosure plots and tested the impact of lemmings' herbivory on
16 carbon dioxide (CO_2) and methane (CH_4) fluxes and the normalized difference vegetation index (NDVI) immediately after
17 lemming removal and during the following growing season. During the first summer of the experiment, lemmings' herbivory
18 reduced plant biomass (as shown by the decrease in the NDVI) and decreased CO_2 uptake, while not significantly impacting CH_4
19 emissions. Methane emissions were likely not significantly affected due to CH_4 being produced deeper in the soil and escaping
20 from the stem bases of the vascular plants. The summer following the lemming treatments, NDVI and CO_2 fluxes returned to
21 magnitudes similar to those observed before the start of the experiment, suggesting recovery of the vegetation, and a transitory
22 nature of the impact of lemming herbivory. Overall, lemming herbivory has short-term but substantial effects on carbon
23 sequestration by vegetation and might contribute to the considerable interannual variability in CO_2 fluxes from tundra ecosystems.

24 1 Introduction

25 The Arctic is warming at twice the rate of the global average (IPCC, 2014), impacting tundra vegetation and the carbon cycle.
26 Vegetation influences the carbon stored in the tundra ecosystem through the exchange of carbon dioxide (CO_2) and methane (CH_4)
27 from the soil into the atmosphere via respiration or by CO_2 uptake through photosynthesis. One of the largest natural reservoirs of
28 organic carbon in the world is stored within Arctic soils, containing approximately 1,300 Pg of carbon (Hugelius et al., 2014).
29 Once soils thaw, microbes can convert stored carbon into greenhouse gases that enter the atmosphere, contributing to global
30 warming (McGuire et al., 2009; Schuur et al., 2008). This positive feedback could have dramatic effects on warming rates, and
31 these effects are why most carbon cycle research in tundra systems focuses on abiotic controls on carbon fluxes (Kwon et al., 2019;
32 Oechel et al., 2014; Sturtevant et al., 2012; Zona et al., 2010). Most of the studies investigating the patterns and controls on the
33 carbon balance from Arctic ecosystems focused on the environmental controls on CO_2 and CH_4, while overlooking the role of
34 herbivory. Since herbivores remove photosynthetic tissues of vegetation, the ability of vegetation to photosynthesize and sequester
35 CO_2 should decrease substantially with herbivory (Metcalfe and Olofsson, 2015). The decrease in vascular plant cover should also
36 decrease CH_4 emissions, given that aerenchyma in sedges facilitate the escape of CH_4 into the atmosphere (McEwing et al., 2015).

37 Investigating the impacts of herbivory on Arctic vegetation and its recovery after herbivory can contribute to refining the

38 understanding of the response of tundra ecosystems to climate change.

39 Small rodents, especially lemmings, in the Arctic tundra of Alaska are important herbivorous consumers of plants and prey

40 species for larger animals (Le Vaillant et al., 2018). Compared to other ecosystems, lemmings in the Arctic tundra are

41 disproportionally common (Ims and Fuglei, 2005). Throughout the Arctic, few rodent species persist, of which lemmings are by

42 far the most abundant and widespread, and are consequently identified as keystone species in tundra environments (Krebs, 2011).

43 As dominant year-round grazers in the tundra, lemmings may heavily impact plant productivity (Olofsson et al., 2014). The site of

44 our research, Utqiaġvik, Alaska, was a perfect site for studying the impact of lemmings on vegetation, as it has been reported in

45 these Alaska tundra ecosystems that brown lemmings (*Lemmus trimucronatus*) deplete 100 times more primary production than

46 caribou, a much larger herbivorous mammal that migrates throughout the Alaskan Arctic (Batzli et al., 1980). Due to their life

47 history characteristics and abundance, lemmings can have a significant influence on the surrounding environment. Lemmings

48 experience cyclic population dynamics where their population density oscillates, changing community interactions (Soininen et

49 al., 2017). Lemming grazing during population peaks can dramatically affect vegetation (Olofsson et al., 2012), and therefore

50 greenhouse gas fluxes from Arctic tundra; given the amount of vegetation consumed by lemmings, their presence could have

51 substantial impacts on the carbon balance of tundra ecosystems. However, despite the role of lemmings as keystone herbivores,

52 the direct impact of their vegetation consumption on the carbon cycle of Arctic tundra in Alaska is still largely unknown, with only

53 few published studies evaluating the role of lemming herbivory on the Arctic carbon balance and vegetation (Lara et al., 2017;

54 Lindén et al., 2021; Metcalfe and Olofsson, 2015; Min et al., 2021).

55 Several methods for analyzing the effects of lemmings on Arctic vegetation have been documented. Most of these studies

56 focused on ecosystem functioning in the absence of lemmings (Lara et al., 2017; Lindén et al., 2021; Min et al., 2021), the impacts

57 of lemming waste products and carcasses on nutrient cycling and vegetation (McKendrick et al., 1980; Roy et al., 2020), the

58 disturbance to soil via turnover by burrowing and fecal production (McKendrick et al., 1980), and recruitment and loss of forest

59 vegetation (Ericson, 1977). This leaves a crucial gap in our understanding of how one of the main herbivores in a rapidly changing

60 ecosystem may affect carbon cycling. Since population cycles vary by species and region (Reid et al., 1995), qualitative predictions

61 on how brown lemmings would alter Arctic vegetation and carbon cycling are uncertain.

62 In this study, we used enclosures to directly quantify impacts of lemming herbivory on tundra carbon cycling, both immediately

63 after disturbance and the growing season following the disturbance to examine vegetation recovery after one year. Thus far, very

64 few studies (Johnson et al., 2011; Lara et al., 2017; Lindén et al., 2021; long-term exclosures) have investigated the effect of

65 lemming herbivory on the tundra carbon cycle, including the timing of recovery of vegetation after lemming disturbance. By using

66 enclosures to observe a direct impact of lemming presence during peak annual activity, our study quantified the short-term effects

67 of vegetation removal from lemming herbivory on carbon fluxes and the timing of vegetation recovery in the Alaskan Arctic.

68 The short-term effects of brown lemmings' herbivory on Arctic vegetation and carbon fluxes and their recovery are critical to

69 understand how lemmings might influence tundra environments. For this purpose, we measured the impact of brown lemmings on

70 vegetation in summer 2018 across a variety of plots in a wet-sedge tundra ecosystem in the Alaskan Arctic. Then, in summer 2019,

71 we measured control and treatment plots again to evaluate vegetation recovery from lemmings' grazing. The goal of this experiment

72 was to understand: (1) how brown lemmings affect vegetation through herbivory and disturbance, and therefore how they could

73 impact the Arctic tundra carbon cycle and photosynthetic capacity of vegetation, and (2) the rate of vegetation recovery after brown

74 lemming herbivory. We predicted that lemmings, given their high rate of vegetation consumption, would have a negative impact

75 on carbon sequestration, but due to the rapid regrowth of the annual, vascular plants they preferentially consume, the vegetation

76 would fully recover in terms of biomass and carbon sequestration the growing season following grazing. We expected CH_4
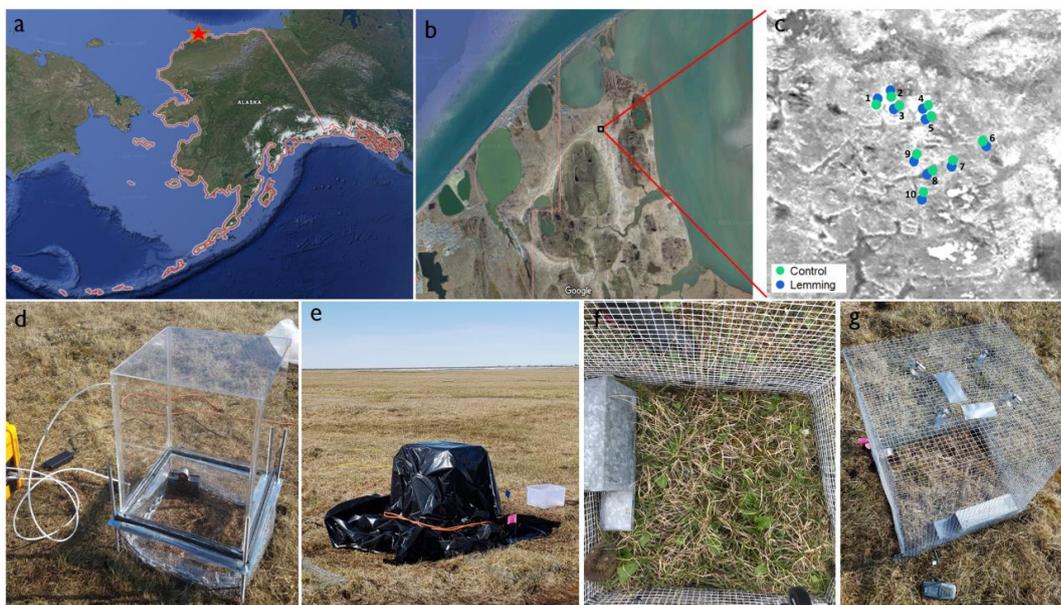
77 emission to decrease with decrease in biomass of vascular plants, given their role in the CH_4 transport from deeper anoxic soil

78 layers into the atmosphere. Our broader goals are to increase our understanding of how the foraging behaviors of these herbivores

79 impacts carbon dioxide (CO_2) and methane (CH_4) fluxes and the photosynthetic capacity of plants in the Alaskan Arctic

80 environment.

81 **2 Materials and methods**

82 **2.1 Study location**

83 This study was carried out in Utqiaġvik (formerly Barrow), Alaska (Fig. 1a). Located in the Arctic Coastal Plain, Utqiaġvik is

84 comprised of flat-, low-, and high-center ice-wedge polygons that cover roughly 65% of the land cover (Billings and Peterson,

85 1980). The major vegetation type at this site is graminoid-dominated wetlands, consisting of mosses, lichens, graminoids, and wet

86 sedges (Davidson et al., 2016).

87 The study area was located near the Barrow Atmospheric Baseline Observatory and an atmospheric monitoring site managed

88 by the National Oceanic and Atmospheric Administration (NOAA) (Fig. 1b), approximately 2 km south of the Arctic Ocean and

89 1 m elevation above sea level (71°19′21.10″ N: 156°36′33.04″ W). This site was near a pre-established remote flux and

90 meteorological tower monitored by the Global Change Research Group (Goodrich et al., 2016) and has substantial lemming

91 populations relative to other Arctic tundra areas in Alaska (Ott and Currier, 2012).

92

93 **Figure 1. (a)** The location of the study site, Utqiaġvik (Barrow), in Alaska (© Google Maps 2018, imagery from TerraMetrics) represented by a

94 red star, (**b**) location of the sampling site (© Google Maps 2018, imagery from TerraMetrics), (**c**) distribution of the sampling plots on an image

95 created using the coordinates of the plots in R (Worldview-3 panchromatic imagery taken 24 July 2016, Maxar Technologies), (**d**) chamber used

96 for the greenhouse gas flux measurements, (**e**) chamber covered by light-blocking material, and (**f, g**) enclosures installed at each of the plots

97 during the manipulation experiment.

98 **2.2 Brown lemmings as a study species**

99   Within the Arctic ecosystem of Alaska there are two species of lemmings: brown lemmings (*L. trimucronatus*) and northern
100   collared lemmings (*Dicrostonyx groenlandicus*). Brown lemmings tend to be distributed among lower and middle Arctic tundra
101   subzones (Stenseth, 1999). Although both brown and collared lemmings are found in Utqiaġvik, brown lemmings are more
102   abundant in this region due to their preference for wetter habitats with relatively high-quality vegetation from lowlands (Batzli et
103   al., 1983). Northern collared lemmings occupy drier habitats, and as a result are not as profuse and influential on vegetation in wet
104   regions of the Alaskan Arctic, such as Utqiaġvik (Batzli et al., 1983; Krebs et al., 2011; Morris et al., 2000). A report on the
105   monitoring of lemming abundance and distribution (Ott and Currier, 2012) estimated brown lemming density near Utqiaġvik in
106   2012 to range from five to 65 lemmings per hectare. However, basic population density estimates may underestimate the impact
107   lemmings have on some vegetation due to an increased concentration in grazing close to burrows and runways (Erlinge et al.,
108   2011). Ott and Currier (2012) also used baited Sherman traps to estimate abundance, a technique that may lead to an underestimate
109   for this species, as brown lemmings are not readily captured using baited Sherman traps; we found manual capture techniques to
110   be much more effective than baited traps.

2.2.1 Brown lemming consumption and population

112   Brown lemmings mostly consume graminoids in the summer and mosses in the winter (Batzli and Jung, 1980). Daily food intake
113   of terrestrial vertebrates ranges from 10% of body weight for heavier species, such as caribou, to 30% for species under 100 grams,
114   such as lemmings (EPPO, 1994). However, brown lemmings can eat much more than predicted from these general trends and can
115   consume up to eight times their body weight each day (Stenseth and Ims, 1993). Thus, even though lemmings weigh less than 100
116   grams (Huck and Banks, 1982), their extreme capacity for consumption and elevated population density can result in high
117   vegetation removal. Additionally, during winter lemmings destroy or uproot up to 90-100% of surrounding aboveground biomass
118   within their foraging range (Stenseth and Ims, 1993). Arctic vegetation consumed by lemmings is generally nutrient-poor (Batzli
119   et al., 1980). Brown lemming digestive efficiency tends to be low, digesting only about 30 percent of ingested food (Batzli et al.,
120   1980). Due to consistent year-round activity and their small body size, lemmings also have a high metabolic rate. Low nutrient
121   content, low digestive efficiency, and a high metabolic rate result in lemmings requiring a high rate of food intake for survival.
122   Populations of brown lemmings tend to reach peak densities every three to five years and then steeply decline (Stenseth, 1999).
123   Interactions between lemming populations as fast-growing consumers and plant populations as slowly recovering resources
124   represents a bitrophic system (Ims and Fuglei, 2005). In this system, vegetation could be heavily damaged by overgrazing during
125   peak years of lemmings.

2.3 Sampling plan and experimental design

127   This experiment was performed over two summer seasons, but we only captured lemmings during the first summer field season
128   (4–10 August 2018), shortly after peak growing season. This period coincides with accelerated lemming reproduction and peak
129   population density. We captured brown lemmings manually in proximity of our sampling sites while conducting visual encounter
130   surveys, and secured them in Sherman traps with cotton nestlets and vegetation (grasses and sedges). Our samples included both
131   juvenile and adult life stages. We released or avoided capturing any sick, very slow, or noticeably pregnant lemmings. After
132   capture, we relocated lemmings to the study site and included them in the experimental plots. Like voles (close relatives of
133   lemmings), lemmings have distinct preferences for habitats containing their preferred food items (Batzli and Henttonen, 1990),
134   which this study specifically selected for when designing the location of the experimental plots to be as representative of realistic
135   effects of lemming herbivory in areas of tundra near their burrows and runways.

136   We established 10 plot sets for this experiment. Each of the 10 plot sets included a lemming plot paired to a control (no-
137   lemming) plot nearby (20 plots in 10 sets total) (Fig. 1c). Each plot was selected to be as similar to the other plot within the same
138   set as possible in order to minimize biases due to spatial heterogeneity in vegetation and other landscape characteristics influencing
139   vegetation and carbon fluxes. We placed plot sets approximately 3 m apart from each other. Control plots were located within 1 m
140   of lemming plots in the same set to keep environmental factors as similar as possible. Plots were 50 x 50 cm in size; in each plot
141   we dug a galvanized hardware cloth with a ½ inch grid down through the thawed soil until the permafrost and up to 60 cm above
142   the surface (Fig. 1f and g). We selected the size of these plots to be consistent with a similar lemming exclosure experiment by
143   Eskelinen and Virtanen (2005) in Finland. This size is also similar, yet a bit larger than the experimental plots in the study by Lara
144   et al. (2017) near Utqiaġvik, Alaska which used 30 x 30 cm chamber bases within their exclosures. Control plots not only excluded
145   lemmings for the duration of the experiment, but also served as a control for the soil and vegetation disturbance resulting from
146   digging galvanized hardware cloth into the soil. Plots that included lemmings also included a top portion of hardware cloth that
147   prevented lemmings from escaping via climbing and prevented predators from removing the lemmings during the experiment.
148   Inside each enclosure with a lemming was a locked-open Sherman trap with cotton nestlets for protection from environmental
149   elements.

150   Because rodents may experience physiological stress after being captured (Fauteux et al., 2018a), prior to the experiment we
151   kept the lemmings in small individual cages made of hardware cloth with a locked-open Sherman trap for shelter, cotton nestlets
152   for warmth, and vegetation for nutrition for at least an hour to help them acclimate. After this acclimation period, we placed the
153   lemmings in their individual plots for 16 hours. We based the duration of the experiment on field trials we carried out for several
154   weeks before the start of the experiment. These trials showed that 16 hours was enough time to observe an average impact on the
155   vegetation, visually similar to the effect lemmings have on areas near their burrows, but was not too long as to result in complete
156   vegetation consumption, unrepresentative of most areas where lemmings forage. Our field trials revealed that keeping lemmings
157   inside the enclosure for longer than 16 hours (which varied with lemming size) led to a complete vegetation removal, an extreme
158   scenario only observed in the very close proximity of the burrows, and not representative of most of their foraging areas. We
159   released the lemmings at the end of all these experiments in proximity to the locations where they were captured.

160   The subsequent summer (24 June–9 August 2019) we re-visited the sample plots to measure the impact of lemmings one year
161   after their grazing. During the following summer (2019), we did not capture any lemmings, and did not perform any additional
162   manipulation. To be able to assess longer-term impacts of the manipulations carried out the previous summer, we collected
163   greenhouse gas fluxes, environmental variables, and hyperspectral reflectance throughout the summer to represent pre-, early, and
164   peak growing season (hereafter defined as "rounds"). Sampling was carried out to monitor the timing of regrowth of photosynthetic
165   tissue and recovery of the plants at different times of the season: in late June to early July of 2019 (round one: pre-growing season),
166   mid-July of 2019 (round two: early growing season), and late July to early August of 2019 (round three: peak growing season).

167   **2.4 Greenhouse gas flux and environmental conditions measurements**

168   We used a Los Gatos Research (LGR) Ultraportable Greenhouse Gas Analyzer (UGGA Model 915-0011) to measure CO_2 and
169   CH_4 concentrations and air temperature over time in all plots during both summer seasons (2018 and 2019). To collect
170   measurements, we built a clear plexiglass acrylic chamber (Davidson et al., 2016; McEwing et al., 2015) to enclose the plots once
171   the aboveground portion of the caging had been detached and the lemming had been removed (Fig. 1d). This chamber was placed
172   on a metal frame positioned in the ground outside of the plots and had clear polyvinyl material weighed down by heavy metal
173   chains to produce a seal inside the chamber. These measurements were performed in a closed loop, where tubes connected the

174 chamber to the gas analyzer and then air was circulated back to the chamber. We positioned a small fan inside the chamber to

175 assure appropriate air mixing. The greenhouse gas concentrations were collected in the absence of lemmings.

176 We used the rate of concentration change to calculate carbon fluxes using the chamber volume and area covered by vegetation

177 (i.e. responsible for the carbon emission or uptake) as a function of time, as described in McEwing et al. (2015). The CO_2

178 concentration change allowed us to calculate net ecosystem exchange (NEE) before and after manipulations as previously described

179 (summer 2018) and to track the seasonal development of NEE during the following summer (2019). In the subsequent summer

180 (2019), we used a light-blocking material to cover the chamber (Fig. 1e) for determining CO_2 ecosystem respiration (ER) and gross

181 primary production (GPP) from NEE, calculated following Eq. (1):

182 $GPP = NEE - ER$.   (1)

183 We also measured a variety of environmental variables before and after each portion of the experiment (summer 2018) and

184 during each round (summer 2019). These environmental variables included air temperature recorded by the LGR gas analyzer, soil

185 temperature measured with a Thomas Scientific Traceable Kangaroo thermometer, soil water content recorded by a FieldScout

186 Soil Moisture Meter, and thaw depth using a metal probe marked every 5 cm. We examined these variables as controls that may

187 explain shifts in CO_2 and CH_4 fluxes within the study area and to monitor if plots in each of the sets were experiencing similar

188 abiotic conditions. This assured potential differences in carbon fluxes were due to our manipulation, and not different

189 environmental conditions of various plots.

190 **2.5 Camera and hyperspectral measurements**

191 We quantified the impact of lemming herbivory and burrowing on vegetation using a Spectra Vista Corporation (SVC)

192 Spectroradiometer HR-512i, which measures spectral reflectance and records a picture of the vegetation being scanned. The

193 spectrometer yielded hyperspectral measurements for vegetation in the 338.9-1075.1 nm spectral range with 512 bands and a

194 bandwidth of ≤ 1.5 nm. The internal global positioning system (GPS) of the spectroradiometer recorded geographic coordinates

195 (latitude and longitude) for all plots to an accuracy of 2.5 m. The lemmings were removed from the plots before collecting

196 hyperspectral measurements.

197 We measured total reflected spectral exitance from a blank white reference panel right before sampling each plot set

198 (approximately every 20-30 scans, or 10-15 minutes) to estimate spectral irradiance based on reflectance calibration information

199 provided for the reference panel. We recorded spectral surface reflectance before and after each experimental treatment (summer

200 2018) and at different times during the season in the following summer (2019) and used it to calculate narrow-band normalized

201 difference vegetation index (NDVI) to compare the photosynthetic capacity of vegetation in the plots. NDVI is calculated as the

202 normalized difference between reflectance in the near infrared wavelengths (800.5 nm) and red wavelengths (680.2 nm). Lower

203 values of NDVI indicate no living vegetation and higher values indicate more green biomass.

204 A Brinno MAC200DN Outdoor Camera recorded a time-lapse of various parts of the experiment to collect motion-sensor video

205 footage of lemming activity. The camera also allowed for re-visitation and surface cover characterizations of the plots to classify

206 and quantify vegetation types within each plot and assess how grazing had affected vegetation. We did not systematically record

207 all trials on video, but instead used this technology as a qualitative tool to visually document the activity of the lemmings.

208 **2.6 Statistical analyses**

209 We used the statistical program R, version 3.5.1 (R Core Team, 2019), for our statistical analyses. We implemented linear mixed-

210 effects models with the package "nlme" (Pinheiro et al., 2018) to analyze the environmental controls on CO_2 and CH_4 fluxes, and

211 on NDVI. We tested multiple variations of these models using the model selection for mixed effects models in ecology described
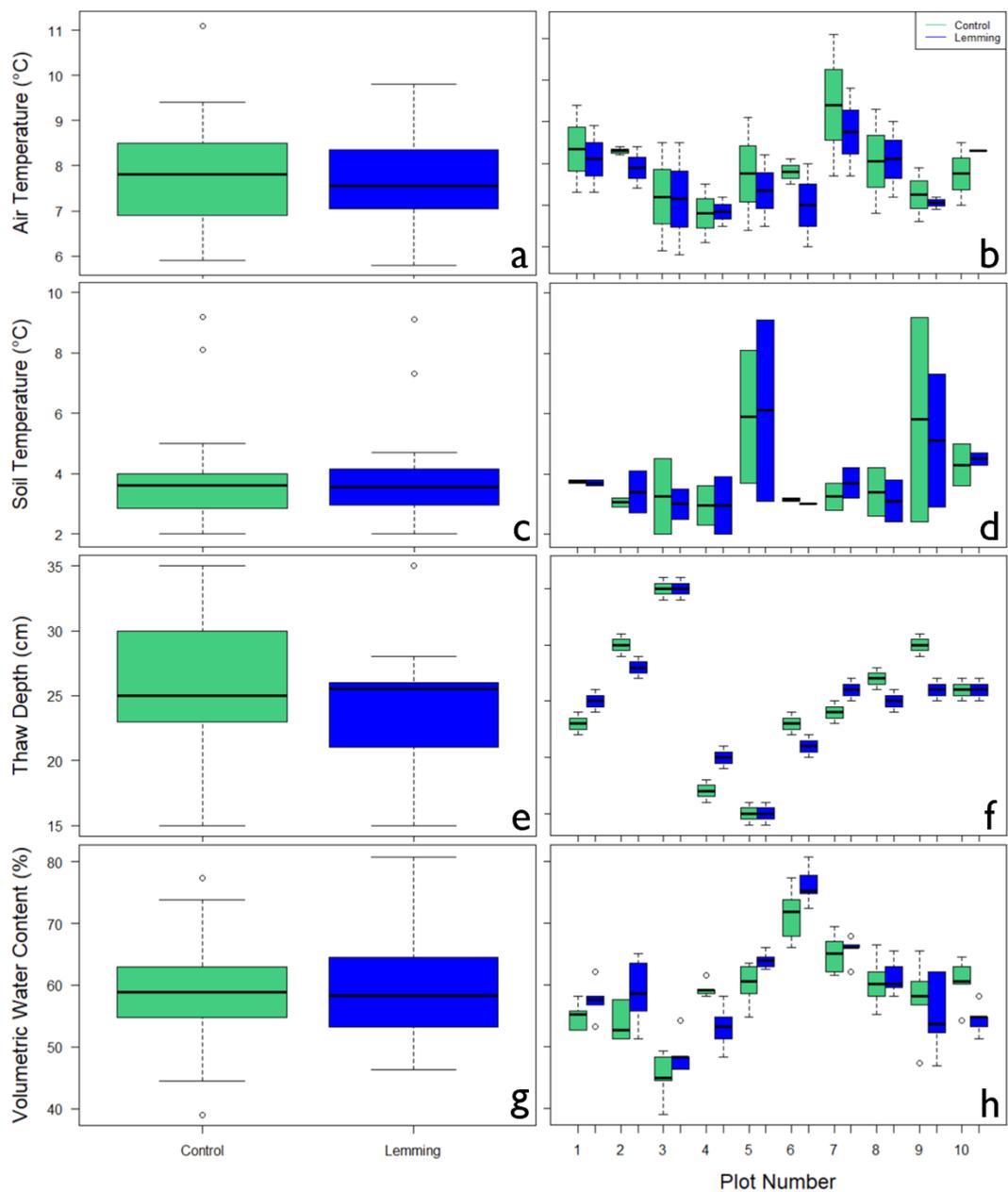
212   in Zuur et al. (2009). For the 2018 models, we used treatment (control, lemming plots), time (before, after experiment), and their

213   interaction as fixed factors in the models; for the 2019 models, we used treatment (control, lemming plots), round (pre-, early, and

214   peak growing season), and their interaction as fixed factors in the models. In all analyses we used the plot identification (1C, 1E,

215   2C, 2E, etc.) nested within the plot set (1-10) as random factors. Mixed models allow us to account for temporal and spatial

216   pseudoreplication and to test the significance of the interactions among factors. When fixed factors were significant, we used the

217   package "emmeans" (Lenth et al., 2019) to conduct a pairwise analysis via a Tukey post-hoc test that investigated the interacting

218   effects in the model.

219   To identify the effect of the manipulation on the CO_2, CH_4, and spectral indexes, we applied the linear mixed-effects models

220   to test differences in each environmental variable before and after lemming exposure in summer 2018. The statistical analyses also

221   helped us explore if the post-lemming experimental plots showed a significant change in greenhouse gas fluxes when compared to

222   pre-lemming experimental plots (2018) and if the greenhouse gas fluxes varied between treatments the following growing season

223   (2019). The NDVI analysis provided information on changes in plant biomass before and after each manipulation in summer 2018
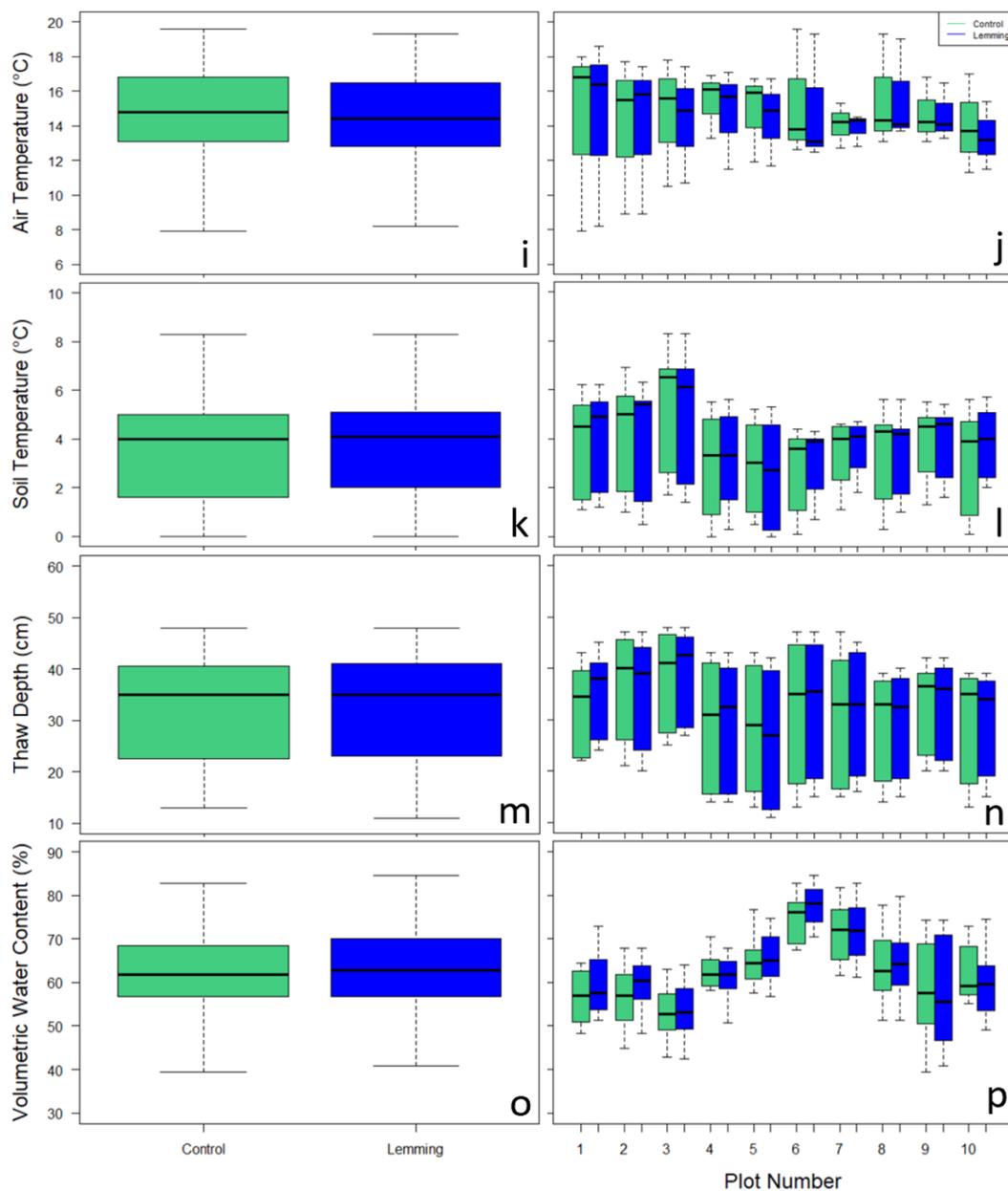
224   and vegetation regrowth in summer 2019.

3 Results

3.1 Environmental variables within the plots

227   Environmental controls on CO_2 and CH_4 fluxes such as air temperature, soil temperature, thaw depth, and soil moisture were

228   similar between the control and experimental plots in 2018 (Fig. 2a-h) and 2019 (Fig. 2i-p). During summer 2018, air temperature

229   ($P = 0.542$), soil temperature ($P = 0.960$), thaw depth ($P = 0.683$), and soil moisture ($P = 0.619$) were not significantly different

230   between control plots and lemming plots. During summer 2019, measurements of the control and lemming plots were not

231   significantly different for air temperature ($P = 0.887$), soil temperature ($P = 0.060$), thaw depth ($P = 0.512$), and soil moisture ($P

232   = 0.387$).

233

Figure 2. Box and whisker plots of environmental conditions across treatment plots during (**a-h**) summer 2018 and (**i-p**) summer 2019. Environmental variables include (**a, i**) air temperature for the entire dataset, (**b, j**) air temperature by plot, (**c, k**) soil temperature for the entire dataset, (**d, l**) soil temperature by plot, (**e, m**) thaw depth for the entire dataset, (**f, n**) thaw depth by plot, (**g, o**) soil moisture for the entire dataset, and (**h, p**) soil moisture by plot.

3.2 Carbon fluxes in the treatment plots

The presence of lemmings significantly impacted CO_2 fluxes (i.e. NEE) during the first summer of measurements. Before the treatment, calculated CO_2 (Fig. 3a) and CH_4 (Fig. 4a) fluxes for the control and lemming plots were similar. After we placed and
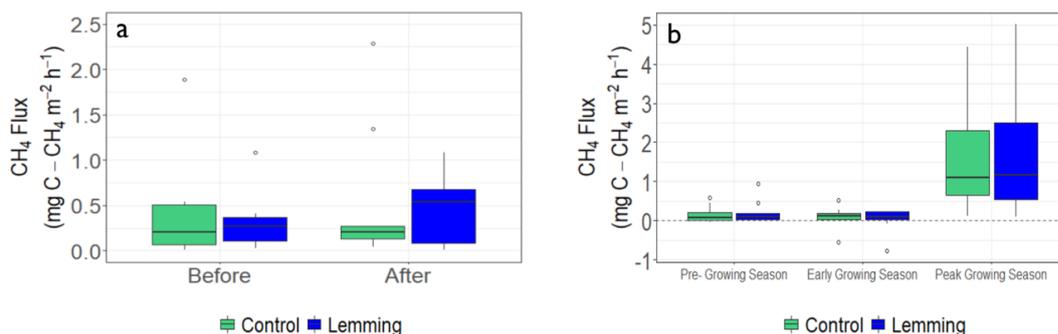
242 then removed lemmings from experimental plots, CO_2 uptake was significantly ($P < 0.001$) lower (i.e. CO_2 fluxes were around

243 zero); less CO_2 was taken up by the system in experimental plots than in control plots (Fig. 3a). Contrary to what we expected,

244 CH_4 flux values did not significantly differ between control plots and plots subjected to lemmings' herbivory ($P = 0.989$, Fig. 4a).

245 By the end of summer 2018, the effect of brown lemmings' herbivory changed the mean CO_2 flux for lemming plots from -0.074

246 ± 0.012 gC-CO_2m^{-2}h^{-1} (i.e. CO_2 sequestration) to 0.003 ± 0.012 gC-CO_2m^{-2}h^{-1} (i.e. no different from zero).

247 In summer 2019, we measured CH_4 fluxes and NEE again, and additionally calculated ecosystem respiration (ER) and gross

248 primary production (GPP). During this second summer of measurements, NEE, ER, GPP, and CH_4 flux were all not significantly

249 different between control and lemming plots (NEE $P = 0.834$, Fig. 3b; ER $P = 0.742$, Fig. 5a; GPP $P = 0.716$, Fig. 5b; and CH_4
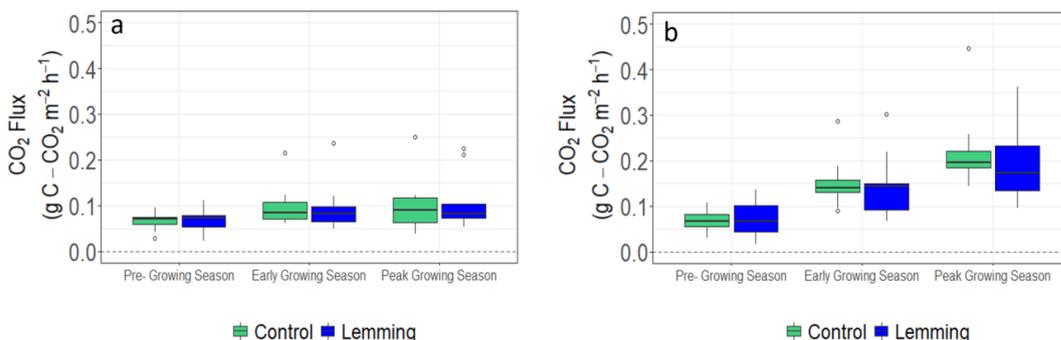
250 flux $P = 0.869$, Fig. 4b).

251

Figure 3. Box and whisker plots of 2018 and 2019 CO_2 net ecosystem exchange fluxes for the control and lemming plots. Negative flux values
indicate carbon sequestration/uptake from the atmosphere and positive flux values indicate carbon emission/loss to the atmosphere. (**a**) Median
CO_2 flux for plots before and after the experiment in summer 2018 ($T = 4.62$, $P < 0.001$), and (**b**) median CO_2 flux for plots during the three
rounds of measurements in summer 2019 ($T = 0.21$, $P = 0.834$).

256

Figure 4. Box and whisker plots of 2018 and 2019 CH_4 fluxes for control and lemming plots. Negative flux values indicate uptake from the
atmosphere and positive flux values indicate emission to the atmosphere. (**a**) Median CH_4 flux for plots before and after the experiment in summer
2018 ($T = 0.01$, $P = 0.989$), and (**b**) median CH_4 flux for plots during the three rounds of measurements in summer 2019 ($T = -0.17$, $P = 0.869$).
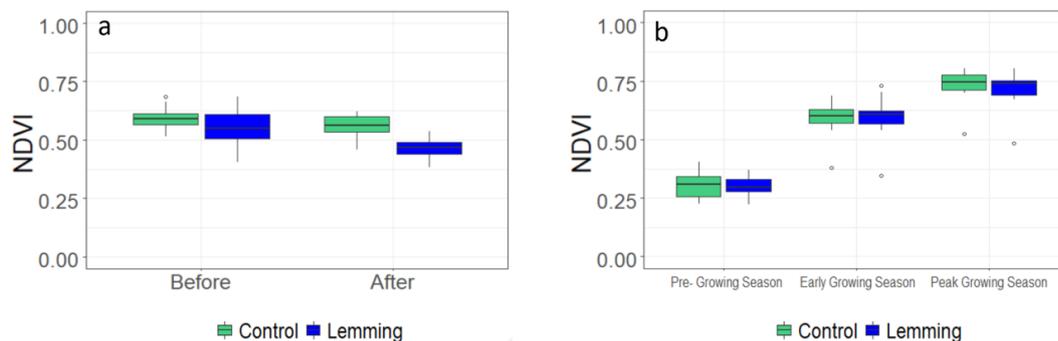
Figure 5. Box and whisker plots of CO_2 ecosystem respiration and gross primary production fluxes for control and lemming plots during the three rounds of data collection in summer 2019. (**a**) Median CO_2 ecosystem respiration flux ($T = -0.34$, $P = 0.742$), and (**b**) median CO_2 gross primary production flux ($T = -0.37$, $P = 0.716$).

3.3 Hyperspectral surface reflectance and NDVI

Spectral reflectance derived from spectroradiometric radiances generally increased across visible and near infrared wavelengths after lemmings' vegetation removal (Supplemental Fig. 1). Before placing lemmings in enclosures, control and lemming plots exhibited similar surface reflectance values, while reflectance curves showed more substantial separation after lemming removal (Supplemental Fig. 1). Analyzing the surface reflectance of the same control and lemming plots re-visited in summer 2019 revealed that the reflectance values for these different treatments were alike in each plot set, similar to what was observed before the beginning of the manipulation experiment (Supplemental Fig. 2b).

To better quantify the changes in reflectance, we calculated the NDVI in all the control and treatment plots in both summer 2018 and 2019. Following lemming removal in the first summer, lemming plots had significantly lower NDVI than the control plots ($P = 0.015$, Fig. 6a), consistent with the decrease in green biomass observed in the photographs collected before and after placing the lemmings in the treatments' enclosure (Supplemental Fig. 1), and with the decreases in CO_2 uptake (see NEE close to zero after lemming vegetation consumption; Fig. 3a). The effect of brown lemmings' herbivory changed the mean NDVI for lemming plots from 0.551 ± 0.021 to 0.465 ± 0.021. During the second summer, median NDVI values of all plots were similar (Fig. 6b). During this time, there was no significant difference in NDVI when comparing control plots to lemming plots ($P = 0.692$), but there was a significant difference between rounds ($P < 0.001$). The significant difference in NDVI across the rounds is consistent with the increased green biomass observed in collected photographs from early to peak season (Supplemental Fig. 2a).

Figure 6. Box and whisker plots of 2018 and 2019 NDVI values for control and lemming plots. (**a**) Median NDVI for plots before and after the experiment in summer 2018 ($T = -3.69$, $P = 0.015$), and (**b**) median NDVI for plots during the three rounds of measurements in summer 2019 (T

11

283   = 0.41, P = 0.692). Higher vascular plant green biomass in the pre-lemming treatment plots presented NDVI values in the 0.6 to 0.7 range,

284   whereas post-lemming treatment plots in 2018 exhibit NDVI values around 0.5.

4 Discussion

286   We found, within a short-term enclosure experiment, that brown lemmings' herbivory significantly decreased CO_2 uptake

287   immediately after consumption of vegetation, while surprisingly not affecting CH_4 fluxes. Consumption of photosynthetically

288   active plant tissue by lemmings impacted the ability of the vegetation to sequester CO_2, nullifying CO_2 uptake by tundra vegetation.

289   The lack of significant difference in the evaluated environmental variables (air temperature, soil temperature, soil moisture, thaw

290   depth) between the control and lemming treatment plots suggests that these factors did not play a significant role in the difference

291   in CO_2 fluxes before and after the treatments during the first summer, but that the decline in CO_2 flux values was due to vegetation

292   removal by lemmings.

293   Notably, lemmings' herbivory did not affect CH_4 fluxes, even though plant transport of CH_4 is a critical pathway for emission

294   in tundra ecosystems (Lai, 2009; McEwing et al., 2015); plants offer substrate for methanogenesis and increase CH_4 transport

295   (Bridgham et al., 2013). The lack of a significant effect on CH_4 fluxes may be due to the location of their vegetation removal on

296   consumed plants. Kelker and Chanton (1997) showed the location of the clipping of vegetation affects the CH_4 emissions;

297   belowground clipping at the root-shoot or porewater-root boundary is more likely to impact CH_4 emission, but aboveground

298   clipping is less likely to affect CH_4 emission. This differential effect is likely related to the location of CH_4 escape though

299   vegetation, which is just at the root-shoot or porewater-root boundary (Kelker and Chanton, 1997). Clipping has an effect not only

300   on gas transport, but also on substrate availability. Vegetation can have an impact on stimulating CH_4 through labile carbon exuded

301   by the roots (McEwing et al., 2015). However, given the short-term nature of this experiment and the large soil carbon storage in

302   these ecosystems, soil labile carbon was likely not limiting to CH_4 emissions (McEwing et al., 2015; Zona et al., 2010).

303   Measurements collected the summer following our herbivory experiment (2019), revealed that the vegetation recovery after

304   brown lemming disturbance was rapid. In 2019, vegetation quickly regrew to a condition comparable to that found in 2018, prior

305   to lemming consumption. Lemmings mostly consume vascular plants, such as graminoids, and avoid non-vascular and slower

306   growth vegetation, such as mosses and lichens (Batzli et al., 1980). The preferential consumption of annual grasses and sedges

307   likely led to the rapid recovery of the photosynthetic capacity of vegetation we observed in just one year.

308   As expected, the biomass of vegetation decreased during summer 2018 due to the impact of lemming consumption

309   (Supplemental Fig. 1). The control and experimental plots before the lemming treatment had relatively high and similar mean

310   NDVI values (Supplemental Fig. 1), suggesting their biomass had similar values (Goswami et al., 2015). Vegetation removal by

311   brown lemmings significantly lowered the mean NDVI of the plots subjected to lemming herbivory. By summer 2019, the mean

312   NDVI value of these same lemming plots indicated that the vegetation was fully recovered from the lemmings' impact the previous

313   summer.

314   While our experiment showed a potentially substantial impact of lemming herbivory on the CO_2 fluxes from these tundra

315   ecosystems, we did not address the impact of varying degrees of intensity of herbivory and population cycling of brown lemmings

316   on carbon fluxes and photosynthetic capacity of different vegetation communities. Roy et al. (2020) found that herbivore presence

317   can alter communities of vegetation differently, as herbivores play a role in regulating a variety of plant species. These herbivores

318   can lead to significant changes in the abundance of vegetation types, allowing for the potential of the tundra during the peak

319   growing season to switch between a carbon source to sink in the absence of herbivory (Min et al., 2021). Since brown lemmings

320   rely on a high rate of food intake to sustain growth and reproduction (Batzli et al., 1980) and experience population cycles with

321   distinct seasonal and multiannual density fluctuations (Reid et al., 1995; Stenseth, 1999), rapid consumption of plant matter by

322   lemmings as sustenance during population peaks may significantly contribute to shifts in plant communities and, thus, carbon cycle

323   changes.

324   Lemming populations may be regulated by predators, such as through typical density-dependent processes that affect

325   population dynamics (Fauteux et al., 2018b). To reduce the risk of detection by predators, lemmings forage on small areas nearby

326   their burrows and maximize their foraging in these areas until their primary food source is depleted, at which point they move to a

327   new area of vegetation near a burrow or runway (Erlinge et al., 2011). This behavior shapes their foraging habits and leads to a

328   higher concentration of grazing on vegetation closer to burrows and runways (Erlinge et al., 2011). As a result, approximately 95-

329   100% of graminoid shoots are repeatedly clipped by lemmings occupying burrows and visiting runways in the immediate vicinity

330   of the vegetation, and as the distance from the burrows and runways increases, clipping becomes patchier and the intensity of

331   clipping on vegetation decreases (Batzli et al., 1980). Given the substantial impact of lemming herbivory on the tundra carbon

332   balance, direct or strong, indirect cues indicating predatory risk could change lemming foraging behavior, and in turn alter their

333   effect on vegetation, and should be quantified by future studies.

334   **5 Conclusions**

335   We show that there is an immediate effect of lemmings on plant biomass and CO_2 uptake by Arctic vegetation, but not on CH_4 flux

336   in areas where lemmings forage. However, impacts on vegetation are temporary, and vegetation can recover to its previous

337   condition by the end of the subsequent growing season. To further our understanding of the complex interactions in the Arctic, it

338   is vital to also explore the longer-term feedbacks that may exist between climate change, herbivory, and predator-prey interactions.

339   The effects of warming on snow cover and plant growth, as crucial environmental resources to lemmings, could lead to drastic

340   population changes for lemmings, and the longer-term effect of lemmings' herbivory on vegetation might not be captured by a

341   short-term manipulation. It is also critical to link the long-term lemming population fluctuations to potential shifts in vegetation

342   and climate change. Additionally, climate change is likely to also alter the abundance, behavior, or even occurrence of predators

343   of lemmings, which may in turn impact lemming abundance and foraging behaviors. For these purposes, long-term and broader

344   scale ecological data would be particularly valuable to build on the short-term effect highlighted in this study.

345   Overall, our study suggests that brown lemmings have the ability to significantly alter vegetation by consuming photosynthetic

346   tissue, which hinders the sequestration by the vegetation and shifts CO_2 fluxes in the areas surrounding their burrows and runways.

347   We report that this effect is short-lived due to the preferential consumption by lemmings of plant species that quickly regrow and

348   recover by the next growing season. However, the duration of the impacts of lemming herbivory might change in different

349   vegetation communities, given that various plant species might be affected differently. Thus, it is relevant to examine the effects

350   of lemmings on a wide range of ecosystems to make regional estimates of their short-term influence on CO_2 fluxes and NDVI.

351   Future research should also more carefully quantify the interactions between lemmings, their predators, and carbon cycling in the

352   Arctic tundra ecosystem, as they might explain some of the substantial interannual variability in the tundra CO_2 fluxes, not

353   explained by environmental variables alone.

354   *Code availability.* R codes generated for data analysis during this study will be archived to the ORNL DAAC repository by the corresponding

355   author upon the journal's request.

356 *Data availability.* Data on carbon fluxes, hyperspectral surface reflectance, and environmental variables analyzed during this study will be
357 archived to the ORNL DAAC repository by the corresponding author upon the journal's request. All relevant data are included as figures in the
358 paper, and raw data may be made available upon request.

359 *Author contribution.* Study conception and design were carried out by Jessica Plein, Rulon Clark, Walter Oechel, and Donatella Zona. Material
360 preparation, data collection, and data processing were completed by Jessica Plein. Data scripts and codes were written by Jessica Plein and Kyle
361 Arndt. Data analysis was performed by Jessica Plein and Donatella Zona. The first draft of the manuscript was written by Jessica Plein and all
362 authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

363 *Competing interests.* The authors declare that they have no conflict of interest.

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