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

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

1 Introduction

The Arctic is warming at ~~twice~~ about three times the rate of the global average (IPCC, ~~2014~~2021), impacting tundra vegetation and the carbon cycle. Vegetation influences the carbon stored in the tundra ecosystem through the exchange of carbon dioxide (CO_2) and methane (CH_4) from the soil into the atmosphere via respiration or by CO_2 uptake through photosynthesis. One of the largest natural reservoirs of organic carbon in the world is stored within Arctic soils, containing approximately 1,300 Pg of soil organic carbon (Hugelius et al., 2014). Once soils thaw, microbes can convert stored carbon into greenhouse gases that enter the atmosphere, contributing to global warming (McGuire et al., 2009; Schuur et al., 2008). This positive feedback could have dramatic effects on warming rates, and these effects are why most carbon cycle research in tundra systems focuses on abiotic controls on carbon fluxes (Kwon et al., 2019; Oechel et al., 2014; Sturtevant et al., 2012; Zona et al., 2010). Most of the studies investigating the patterns and controls on the carbon balance from Arctic ecosystems focused on the environmental controls on CO_2 and CH_4, while overlooking the role of herbivory. Since herbivores remove photosynthetic tissues of vegetation, herbivory should substantially decrease the ability of vegetation to photosynthesize and sequester CO_2 ~~should decrease substantially with herbivory~~ (Metcalfe and Olofsson, 2015). The decrease in vascular plant cover should also decrease CH_4 emissions, given that aerenchyma

in sedges (*Carex aquatilis* is the dominant vascular plant and sedge in our study site~~,~~; Davidson et al., 2016) facilitate the escape of CH_4 from deeper anoxic soil layers into the atmosphere (Dias et al., 2010; McEwing et al., 2015~~; Dias et al., 2010, ~~Ström et al., 2003; Whiting and Chanton, 1993). ~~I~~Moreover, in addition to transport, vascular plants ~~which only facilitate CH_4 transport from deeper anoxic soil layers into the atmosphere, but~~ also affect~~s~~ the release of labile carbon from photosynthetic tissues, which in turn stimulates CH_4 emission (Bhullar et al., 2014; McEwing et al., 2015; Ström et al., 2003; Tan et al., 2015~~; Whiting and Chanton, 1993~~). Investigating the impacts of herbivory on Arctic vegetation and its recovery after herbivory ~~can~~ would contribute to a refined ~~refining the~~ understanding of the response of tundra ecosystems to climate change.

Small rodents, especially lemmings, in the Arctic tundra of Alaska are important herbivorous consumers of plants and prey species for larger animals (Le Vaillant et al., 2018). Throughout the Arctic, few rodent species persist, of which lemmings are by far the most abundant and widespread, and are consequently identified as keystone species in tundra environments (Krebs, 2011). As dominant year-round grazers in the tundra, lemmings may heavily impact plant productivity (Olofsson et al., 2014). The site of our research, Utqiaġvik, Alaska, was an ideal site for studying the impact of lemmings on vegetation, as it has been reported that brown lemmings (*Lemmus trimucronatus*) deplete 100 times more primary production than caribou, a much larger herbivorous mammal that migrates throughout the Alaskan Arctic (Batzli et al., 1980). Due to their life history characteristics and abundance, lemmings can have a significant influence on the surrounding environment. Lemmings experience cyclic population dynamics where their population density oscillates, changing community interactions (Soininen et al., 2017). Lemming grazing during population peaks can dramatically affect vegetation (Olofsson et al., 2012), and therefore greenhouse gas fluxes from Arctic tundra; given the amount of vegetation consumed by lemmings, their presence could have substantial impacts on the carbon balance of tundra ecosystems. However, despite the role of lemmings as keystone herbivores, the direct impact of their vegetation consumption on the carbon cycle of Arctic tundra in Alaska is still largely unknown, with few published studies evaluating the role of lemming herbivory on the Arctic carbon balance and vegetation (Lara et al., 2017; Lindén et al., 2021; Metcalfe and Olofsson, 2015; Min et al., 2021).

Most of the studies analyzing the effects of lemmings on vegetation focused on ecosystem functioning in the absence of lemmings (Lara et al., 2017; Lindén et al., 2021; Min et al., 2021), the impacts of lemming waste products and carcasses on nutrient cycling and vegetation (McKendrick et al., 1980; Roy et al., 2020), the disturbance to soil via turnover by burrowing and fecal production (McKendrick et al., 1980), and recruitment and loss of forest vegetation (Ericson, 1977). This leaves a crucial gap in our understanding of how one of the main herbivores in a rapidly changing ecosystem, such as the Arctic, may affect carbon cycling. Since population cycles vary by species and region (Reid et al., 1995), qualitative predictions on how brown lemmings would alter Arctic vegetation and carbon cycling are uncertain.

In this study, we used enclosures to directly quantify impacts of lemming herbivory on tundra carbon cycling, both immediately after disturbance and during the growing season following the disturbance to examine vegetation recovery after one year. Thus far, very few studies (Johnson et al., 2011; Lara et al., 2017; Lindén et al., 2021; long-term exclosures) have investigated the effect of lemming herbivory on the tundra carbon cycle, including the timing of recovery of vegetation after lemming disturbance. By using enclosures to manipulate the number of lemmings per plot and observe a direct impact of lemming presence during peak annual activity, our study quantified the short-term effects of vegetation removal from lemming herbivory on carbon fluxes and the timing of vegetation recovery in the Alaskan Arctic.

The short-term effects of brown lemmings' herbivory on Arctic vegetation and carbon fluxes and their longer-term recovery are critical to understand how lemmings might influence tundra environments. For this purpose, we measured the impact of brown

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

79 summer 2019, we measured ~~control and treatment~~the plots again to evaluate vegetation recovery from lemmings' grazing. The

80 goal of this experiment was to understand: (1) how brown lemmings affect vegetation through herbivory and disturbance, and

81 therefore how they could impact the Arctic tundra carbon cycle and photosynthetic capacity of vegetation, and (2) the rate of

82 vegetation recovery after brown lemming herbivory.

83 We hypothesized that lemmings, given their high rate of vegetation consumption, would have a negative impact on

84 net CO_2 sequestration by vegetation, but due to the rapid regrowth of the annual vascular plants they preferentially

85 consume, the vegetation would fully recover in terms of biomass and CO_2 sequestration the growing season following

86 grazing. We expected CH_4 emission to decrease in response to herbivory, given the reduction in the

87 biomass   of   vascular   plants.

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90 these   herbivores   impacts CO_2 and CH_4 fluxes   and   the   photosynthetic   capacity   of   plants   in   the   Alaskan

91 Arctic environment, which we hope will further public interest in the understanding of complex interactions in the Arctic and

92 relationships that may exist between climate change, herbivory, and predator-prey interactions.

93 **2 Materials and methods**

94 **2.1 Study location**

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

96 comprised of polygonal ground (flat-, low-, and high-center ice-wedge polygons) that cover roughly 65 % of the land cover

97 (Billings and Peterson, 1980). The major vegetation type at this site is graminoid-dominated wetlands, consisting of mosses,

98 lichens, graminoids (grasses), and wet sedges (Davidson et al., 2016).

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

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

101 (71°19′21.10″   N: 156°36′33.04″   W).   This   site   was   near   a   pre-established   remote   flux   and

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

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

104
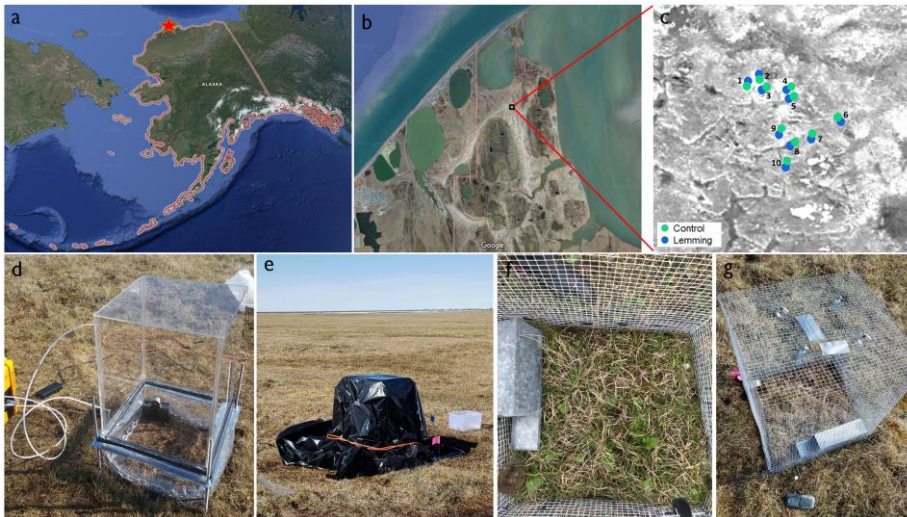
Figure 1. (a) The location of the study site, Utqiaġvik (Barrow), in Alaska (© Google Maps 2018, imagery from TerraMetrics) represented by a red star, (**b**) location of the sampling site (© Google Maps 2018, imagery from TerraMetrics), (**c**) distribution of the sampling plots on an image created using the coordinates of the plots in R (Worldview-3 panchromatic imagery taken 24 July 2016, Maxar Technologies), (**d**) chamber used for the greenhouse gas flux measurements, (**e**) chamber covered by light-blocking material, and (**f, g**) enclosures installed at each of the plots during the manipulation experiment.

2.2 Brown lemmings as a study species

Within the Arctic ecosystem of Alaska there are two species of lemmings: brown lemmings (*L. trimucronatus*) and northern collared lemmings (*Dicrostonyx groenlandicus*). Brown lemmings tend to be distributed among lower and middle Arctic tundra subzones (Stenseth, 1999). Although both brown and collared lemmings are found in Utqiaġvik, brown lemmings are more abundant in this region due to their preference for wetter habitats with relatively high-quality vegetation from lowlands (Batzli et al., 1983). Northern collared lemmings occupy drier habitats, and as a result are not as profuse and influential on vegetation in wet regions of the Alaskan Arctic such as Utqiaġvik (Batzli et al., 1983; Krebs et al., 2011; Morris et al., 2000).

2.2.1 Brown lemming consumption

Brown lemmings mostly consume graminoids in the summer and mosses in the winter (Batzli and Jung, 1980) . Brown lemmings can consume much more than predicted by general trends of terrestrial vertebrates (EPPO, 1994), consuming up to eight times their body weight each day (Stenseth and Ims, 1993). Thus, their extreme capacity for consumption, of vegetation (combined with their elevated population densitycyclic elevated population densities in the region,)Daily food intake of terrestrial vertebrates

128 ~~ranges from 10% of body weight for heavier species, such as caribou, to 30% for species under 100 grams, such as lemmings~~
129 ~~(EPPO, 1994). However, brown lemmings can eat much more than predicted from these general trends and can consume up to~~
130 ~~eight times their body weight each day (Stenseth and Ims, 1993). Thus, even though lemmings weigh less than 100 grams (Huck~~
131 ~~and Banks, 1982), their extreme capacity for consumption and elevated population density~~ can result in high vegetation removal.
132 Additionally, during winter lemmings destroy or uproot up to 90-100 % of surrounding aboveground biomass within their foraging
133 range (Stenseth and Ims, 1993). Arctic vegetation consumed by lemmings is generally nutrient-poor (Batzli et al., 1980). Brown
134 lemming digestive efficiency tends to be low, digesting only about 30 ~~percent~~ % of ingested food (Batzli et al., 1980). Due to
135 consistent year-round activity and their small body size, lemmings also have a high metabolic rate. Low nutrient content, low
136 digestive efficiency, and a high metabolic rate result in lemmings requiring a high rate of food intake for survival.

137 To reduce the risk of detection by predators (snowy owl, parasitic jaeger/arctic skua, arctic fox, and ermine), lemmings forage
138 on small areas near their burrows and maximize their foraging in these areas until their primary food source is depleted, at which
139 point they move to a new area of vegetation near a burrow or runway (Erlinge et al., 2011). This behavior shapes their foraging
140 habits and leads to a higher concentration of grazing on vegetation close to burrows and runways (Erlinge et al., 2011). As a result,
141 approximately 95-100 % of graminoid shoots are repeatedly clipped by lemmings occupying burrows and visiting runways in the
142 immediate vicinity of the vegetation, and as the distance from the burrows and runways increases, clipping becomes patchier and
143 the intensity of clipping on vegetation decreases (Batzli et al., 1980).

144 **2.2.2 Brown lemming population**

145 Populations of brown lemmings tend to reach peak densities every three to five years and then steeply decline (Stenseth, 1999).
146 Interactions between lemming populations as fast-growing consumers and plant populations as slowly recovering resources
147 represents a bitrophic system (Ims and Fuglei, 2005). In this system, vegetation could be heavily damaged by overgrazing during
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152 peak years of lemming abundance~~s~~.

153 A report on the monitoring of lemming abundance and distribution (Ott and Currier, 2012) estimated brown lemming density
154 near Utqiaġvik in 2012 to range from five to 65 lemmings per hectare. However, basic population density estimates may
155 underestimate the impact lemmings have on some vegetation due to an increased concentration in grazing very close to burrows
156 and runways (Erlinge et al., 2011). Ott and Currier (2012) also used baited Sherman traps to estimate abundance, a live-trapping
157 technique that may lead to an underestimate of the actual population density for this species, as brown lemmings are not readily
158 recaptured using baited Sherman traps; we found manual capture techniques to be much more effective than baited traps.

159 **2.3 Sampling plan and experimental design**

160 ~~This experiment was~~We performed this experiment over two summer growing seasons. During the first season (summer 2018),
161 we used enclosures to ensure even lemming herbivory pressure in each of our experimental plots. We manually captured the
162 lemmings used in this first season shortly after peak growing season (3-10 August), coinciding with accelerated lemming
163 reproduction and peak population density. We captured the lemmings in close proximity to our sampling sites while conducting
164 visual encounter surveys, and secured them ~~, but we only captured lemmings during the first summer field season (4-10 August~~
165 ~~2018), shortly after peak growing season. This period coincides with accelerated lemming reproduction and peak population~~

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166 ~~only. We captured lemmings manually at points of sampling while conducting our herbivory study and used them in Sherman traps with moist standing vegetation (grass and sedges). Our samples included both juveniles and adults.~~

167 We released or avoided capturing any sick, very slow, or noticeably pregnant lemmings. After capture, we relocated lemmings to

168 the study site and included them in the experimental plots. Like voles (close relatives of lemmings), lemmings have distinct

169 preferences for habitats containing their preferred food items (Batzli and Henttonen, 1990), which ~~this study~~we specifically selected for

170 when designing the location of the experimental plots ~~in this study in order~~ to be ~~as~~ representative ~~of realistic effects of lemming herbivory in areas of tundra near their burrows and runways~~.

171   We established 10 plot sets for this experiment. Each of the 10 plot sets included a lemming plot paired to a control (no-

172 lemming) plot nearby (20 plots in 10 sets total) (Fig. 1c). Each plot contained the different vegetation types, mosses, lichens,

173 graminoids, and wet sedges, and was selected to be as similar to the other plot within the same set as possible in order to minimize

174 biases due to spatial heterogeneity in vegetation and other landscape characteristics influencing vegetation and carbon fluxes (a

175 more in-depth analysis of these vegetation types was completed by Davidson et al. in 2016). We placed plot sets approximately 3

176 m apart from each other. Control plots were located within 1 m of lemming plots in the same set to keep environmental factors as

177 similar as possible. Plots were 50 x 50 cm in size; in each plot we dug a galvanized hardware cloth with a ½ inch grid down through

178 the thawed soil to the permafrost and up to 60 cm above the surface (Fig. 1f and g). We selected the size of these plots to be

179 consistent with a similar lemming exclosure experiment by Eskelinen and Virtanen (2005) in Finland. This size is also similar, yet

180 a bit larger than the experimental plots in the study by Lara et al. (2017) near Utqiaġvik, Alaska which used 30 x 30 cm chamber

181 bases within their exclosures. Control plots not only excluded lemmings for the duration of the experiment, but also served as a

182 control for the soil and vegetation disturbance resulting from digging galvanized hardware cloth into the soil. Plots that included

183 lemmings also included a top portion of hardware cloth that prevented lemmings from escaping via climbing and prevented

184 predators from removing the lemmings during the experiment. Inside each enclosure with a lemming was a locked-open Sherman

185 trap with cotton nestlets for protection from environmental elements.

186   Because rodents may experience physiological stress after being captured (Fauteux et al., 2018a), prior to the experiment we

187 kept the lemmings in small individual cages made of hardware cloth with a locked-open Sherman trap for shelter, cotton nestlets

188 for warmth, and vegetation for nutrition for at least an hour to help them acclimate. After this acclimation period, we placed the

189 lemmings in their individual plots for 16 hours. We based the duration of the experiment on field trials we carried out for several

190 weeks before the start of the experiment. These trials showed that 16 hours was enough time to observe an average impact on the

191 vegetation, visually similar to the effect lemmings have on areas near their burrows, but was not too long as to result in complete

192 vegetation consumption, unrepresentative of most areas where lemmings forage. Our field trials revealed that keeping lemmings

193 inside the enclosure for longer than 16 hours (which varied with lemming size) led to a complete vegetation removal, an extreme

194 scenario only observed in the very close proximity of the burrows, and not representative of most of their foraging areas. We

195 released the lemmings at the end of all these experiments in proximity to the locations where they were captured.

196   The subsequent season (summer 2019), we re-visited the sample plots to measure the impact of

197 lemmings one year after their grazing (24 June-7 August). During this season, we did not capture any

198 lemmings, nor did we perform any additional manipulation. To be able to assess longer-term impacts of the

199 manipulations carried out the previous summer, we collected measurements

200 throughout the following summer (Table 1) to represent pre-, early, and peak growing season (hereafter

201 defined as "rounds"). Sampling was carried out to monitor the timing of regrowth of photosynthetic tissue and recovery of the

202 plants at different times of the season in 2019: 24-29 June (round one: pre-growing season), 9-19

203 July (round two: early growing season), and 29 July-7 August (round three: peak

204 growing season).

205

	Data Collected	Frequency of Measurement
Summer 2018	CO_2 fluxes (NEE) and CH_4 fluxes, NDVI, air temperature, soil temperature, soil moisture, thaw depth, motion camera footage	Before (pre-herbivory) and after (post-herbivory) lemming treatment (N=10 before and N=10 after for each treatment, for a total of N=40 per NEE, CH_4 fluxes, NDVI; N=40 for air temperature; N=40 for soil temperature; N=100 for soil moisture; N=20 for thaw depth)
Summer 2019	CO_2 fluxes (NEE, ER, GPP) and CH_4 fluxes, NDVI, air temperature, soil temperature, soil moisture, thaw depth	Different times of the season (pre-, early, peak growing season) (N=10 for each round and treatment, for a total of N=60 per NEE, ER, GPP, CH_4 fluxes, NDVI; N=60 for air temperature; N=300 for soil temperature; N=240 for soil moisture; N=240 for thaw depth)

Table 1. Types of data collected and when they were measured during summer 2018 and summer 2019. All data were collected while lemmings were not in thepresent inside the experimental plots, except for the motion camera footage. NEE is defined as net ecosystem exchange, ER as ecosystem respiration, GPP as gross primary production..., and ER as…and NDVI as the normalized difference vegetation index.is the Normalized….

There could have been other sources of herbivory (such as caribou), but these sourcesy are not as frequent in these northernmost areas of the Arctic Coastal Plain. Additional sources of disturbance to vegetation could originate from a drastic change in environmental conditions, such as extreme temperatures, extremely dry conditions, etc.; however, these would not selectively remove the vascular plants while not affecting the moss layer, which is what we observed in this experiment.

2.4 Greenhouse gas fluxes and environmental conditions variables measurements

We used a Los Gatos Research (LGR) Ultraportable Greenhouse Gas Analyzer (UGGA Model 915-0011) to measure CO_2 and CH_4 concentrations (currently, global mean atmospheric concentrations for CO_2 and CH_4 are approximately 417 ppm and 1909 ppb, respectively; NOAA GML, 2022) and air temperature over time in all plots during both summer seasons (2018 and 2019). We measured CO_2 and CH_4 concentrations one day after lemming removal from the plots in summer 2018 (exact time varied based on weather conditions and when plots were measured in temporal relation to other plots) and during the different rounds of the growing season in summer 2019. To collect measurements, we built a clear plexiglass acrylic chamber (Davidson et al., 2016; McEwing et al., 2015) to enclose the plots once the aboveground portion of the caging had been detached and the lemming had been removed (Fig. 1d). This chamber was placed on a metal frame positioned in the ground outside of the plots and had clear polyvinyl material weighed down by heavy metal chains to produce a seal inside the chamber. These measurements were performed in a closed loop, where tubes connected the chamber to the gas analyzer and then air was circulated back to the chamber. We positioned a small fan inside the chamber to enassure appropriate air mixing. The We collected greenhouse gas concentrations were collected in the absence of lemmings.

We used the rate of concentration change to calculate carbon fluxes using the chamber volume and area covered by vegetation (i.e. responsible for the carbon emission or uptake) as a function of time, as described in McEwing et al. (2015). The CO_2 concentration change allowed us to calculate the net balance between the carbon uptake from photosynthesis and the carbon loss from respiration, also defined as the net ecosystem exchange (NEE), before and after manipulations as previously described (summer 2018) and to track the seasonal development of NEE during the following summer (2019). In the subsequent summer (2019), we used a light-blocking material to cover the chamber (Fig. 1e) for determining CO_2 ecosystem respiration (ER) and gross primary production (GPP) from NEE, calculated following Eq. (1):

$$GPP = NEE - ER ,$$

(1)

and using the sign convention suggested by Chapin et al. (2006). Since plant growth and photosynthetic uptake is restricted to the summer months in these Arctic ecosystems, we used GPP to indicate "the total amount of CO_2 'fixed' by land plants per unit time

238 through the photosynthetic reduction of CO_2 into organic compounds" (Gough, 2011) during the time of measurements, rather than
239 as an annual measurement.

240 We also measured a variety of environmental variables before and after each portion of the experiment (summer 2018) and
241 during each round (summer 2019). These environmental variables included air temperature recorded by the LGR gas analyzer, soil
242 temperature measured with a Thomas Scientific Traceable Kangaroo thermometer, soil water content recorded by a FieldScout
243 Soil Moisture Meter, and thaw depth using a metal probe marked every 5 cm. We examined these variables as controls that may
244 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
245 abiotic conditions. This assured potential differences in carbon fluxes were due to our manipulation, and not different
246 environmental conditions of various plots.

2.5 Camera footage and hyperspectral measurements

248 We quantified the impact of lemming herbivory and burrowing on vegetation using a Spectra Vista Corporation (SVC)
249 Spectroradiometer HR-512i, which measures spectral reflectance and records a picture of the vegetation being scanned. The
250 spectrometer yielded hyperspectral measurements for vegetation in the 338.9-1075.1 nm spectral range with 512 bands and a
251 bandwidth of ≤ 1.5 nm. We used the internal global positioning system (GPS) of the spectroradiometer to record geographic
252 coordinates   (latitude   and   longitude)   for   all   plots   to   an   accuracy   of   2.5   m.   We
253 collected hyperspectral measurements in the absence of lemmings.

254 We measured total reflected spectral exitance from a blank white reference panel right before sampling each plot set
255 (approximately every 20-30 scans, or 10-15 minutes) to estimate spectral irradiance based on reflectance calibration information
256 provided for the reference panel. We recorded spectral surface reflectance before and after each experimental treatment (summer
257 2018) and at different times during the season in the following summer (2019) and used it to calculate narrow-band normalized
258 difference vegetation index (NDVI) to compare the photosynthetic capacity of vegetation in the plots. NDVI is calculated as the
259 normalized difference between reflectance in the near infrared wavelengths (800.5 nm) and red wavelengths (680.2 nm). Lower
260 values of NDVI indicate no living vegetation and higher values indicate more green biomass.

261 We recorded a time-lapse of various parts of the experiment using a Brinno MAC200DN Outdoor Camera
262 to   collect   motion-sensor   video   footage   of   lemming   activity.   The   camera   also   allowed   for
263 re-visitation and surface cover characterizations of the plots to classify and quantify vegetation types within each plot and assess
264 how grazing had affected vegetation. We did not systematically record all trials on video, but instead used this technology as a
265 qualitative tool to visually document the activity of the lemmings.

2.6 Statistical analyses

267 We used the statistical program R, version 3.5.1 (R Core Team, 2019), for our statistical analyses. For the 2018 data, wWWe tested
268 for normality using a Shapiro-Wilk normality test. in 2018The 2018 data to bewere normally distributed (NEE $P = 0.489$, NDVI
269 $P = 0.816$), except the CH_4 data ($P < 0.001$), which were right-skewed, so we log-transformed the CH_4 data to help normalize them
270 ($P = 0.284$). After this transformation, we used a linear mixed-effects models (with the package "nlme"; (Pinheiro et al., 2018) to
271 test for the significance in the differences between the different treatments. For the 2019 data, we used both a linear mixed-effects
272 models with the package "nlme" and non-parametric Kruskal–Wallis tests, statisticsbecause we could not make all the data normal
273 using the same transformation method (log transformation, square root transformation) for every round during the season. We also
274 tested for equal variance using an F-test and found there was no significant difference between the variances (treatments) in 2018

275 (NEE $P = 0.172$, CH_4 flux $P = 0.810$, NDVI $P = 0.100$) and 2019 (NEE $P = 0.441$, ER $P = 0.650$, GPP $P = 0.852$, CH_4 flux $P =$
276 0.346, NDVI $P = 0.951$).

277   We tested multiple variations of the linear mixed-effects models using the methods for model selection in ecology described
278 in Zuur et al. (2009). We then plotted the models to examine the residuals of the data and found them to not appear heteroscedastic.
279 For the 2018 models, we used treatment (control, lemming plots), time (before, after experiment), and their interaction as fixed
280 factors in the models; for the 2019 models, we used treatment (control, lemming plots), round (pre-, early, and peak growing
281 season), and their interaction as fixed factors in the models. In all analyses we used the plot identification (1C, 1E, 2C, 2E, etc.)
282 nested within the plot set (1-10) as random factors. Mixed models allow us to account for temporal and spatial pseudoreplication
283 and to test the significance of the interactions among factors. When fixed factors were significant, we conducted a pairwise analysis
284 via a Tukey post-hoc test (with the package "emmeans"; Lenth et al., 2019) to investigate the interacting effects in the model.

285   To identify the effect of the manipulation on carbon fluxes and NDVI, we applied the linear
286 mixed-effects models and tested for differences in each environmental variable before and after lemming exposure in summer
287 2018. We then used the statistical analyses to help us explore if the post-lemming experimental plots showed a
288 significant change in carbon fluxes and NDVI when compared to pre-lemming experimental plots (2018),
289 and if the carbon fluxes and NDVI varied between treatments the following growing season (2019). Our analysis
290 of the NDVI from spectral indexes provided us with information on changes in plant biomass before and after each
291 manipulation in summer 2018 and vegetation regrowth in summer 2019.

3 Results

3.1 Environmental variables

294 Environmental controls on CO_2 and CH_4 fluxes such as air temperature, soil temperature, thaw depth, and soil moisture were
295 similar between the control and experimental plots in 2018 (Fig. A1a-h) and 2019 (Fig. A1i-p). During summer 2018, air
296 temperature ($P = 0.542$), soil temperature ($P = 0.960$), thaw depth ($P = 0.683$), and soil moisture ($P = 0.619$) were not significantly
297 different between control plots and lemming plots. During summer 2019, measurements of the control and lemming plots were not
298 significantly different for air temperature ($P = 0.887$), soil temperature ($P = 0.060$), thaw depth ($P = 0.512$), and soil moisture (P
299 $= 0.387$).

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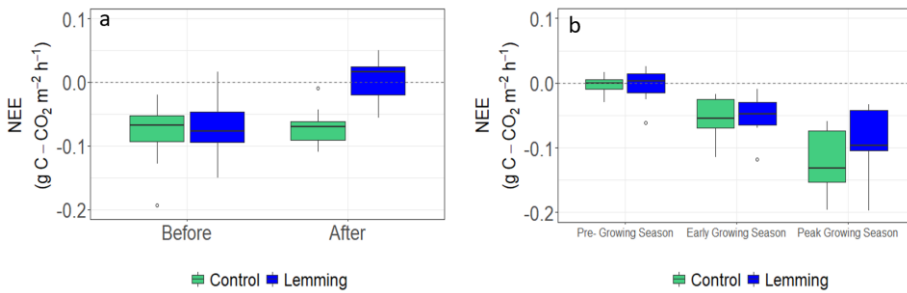
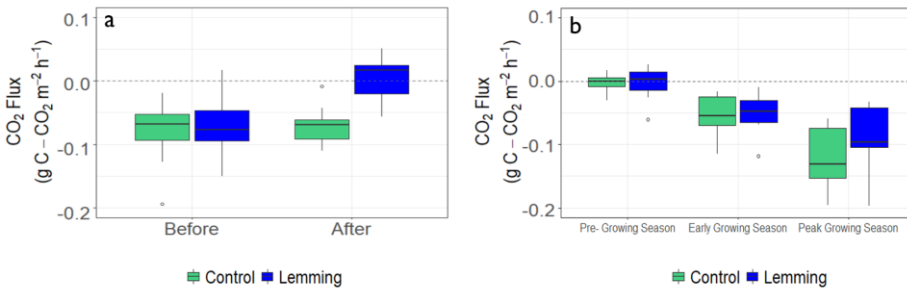
302 **3.2 Carbon fluxes**

303 **3.2 Carbon fluxes** ~~in the treatment plots~~

304 The presence of lemmings significantly impacted CO_2 fluxes (i.e. NEE) during summer 2018 when the
305 lemming enclosure treatment was implemented. Before the treatment, calculated NEE (Fig. 2a) and CH_4 fluxes (Fig. 3a)
306 for the control and lemming plots were similar. After we removed lemmings from experimental plots, net
307 CO_2 uptake decreased significantly (P < 0.001, Fig. 2a)
308 . In this context, net CO_2 uptake by vegetation, or carbon dioxide
309 sequestration, is the removal of CO_2 from the atmosphere and its storage in the above- and belowground biomass through
310 photosynthesis after accounting for the carbon loss through respiration. Therefore, when lemmings consume the
311 photosynthetic tissues of the vegetation (aboveground biomass), the vegetation is no longer able to
312 uptake CO_2 from the atmosphere, and NEE (the net ecosystem exchange equivalent to the net CO_2 fluxes) approaches either zero
313 or becomes less negative (a negative sign implies more carbon removal from the atmosphere).
314 By
315 the end of summer 2018, the effect of brown lemmings' herbivory changed the mean NEE for lemming plots from -0.074
316 ± 0.012 gC-CO_2m^{-2}h^{-1} (i.e. net CO_2 sequestration) to 0.003 ± 0.012 gC-CO_2m^{-2}h^{-1} (i.e. net CO_2 fluxes were around zero
317). Contrary to what we expected, CH_4 flux values did not significantly differ between control plots and plots subjected
318 to lemmings' herbivory ($P = 0.989$, Fig. 3a).

319   In summer 2019, we measured NEE and CH$_4$ fluxes again, and additionally calculated ER and GPP. During this second summer
320   of measurements, results of the linear mixed-effects models for NEE, ER, GPP, and CH$_4$ fluxes were all not significantly different
321   between control and lemming plots (NEE $P = 0.834$, Fig. 2b; ER $P = 0.742$, Fig. 4a; GPP $P = 0.716$, Fig. 4b; CH$_4$ flux $P = 0.869$,
322   Fig. 3b). These results were consistent with those of the Kruskal–Wallis test, which found there was no significant difference
323   between the treatments in 2019, either by testing the data set all together (NEE $P = 0.769$, ER $P = 0.221$, GPP $P = 0.513$, CH$_4$ flux
324    $P = 0.824$) or separating it for different times of the season (rounds) and testing each time separately (pre-growing season: NEE P
325    $= 0.245$, ER $P = 0.672$, GPP $P = 0.296$, CH$_4$ flux $P = 0.728$; early growing season: NEE $P = 0.853$, ER $P = 0.600$, GPP $P = 0.558$,
326   CH$_4$ flux $P = 0.638$; peak growing season: NEE $P = 0.293$, ER $P = 0.366$, GPP $P = 0.212$, CH$_4$ flux $P = 0.970$).

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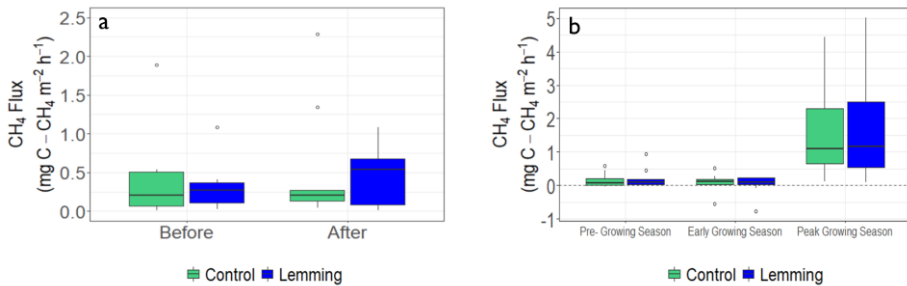
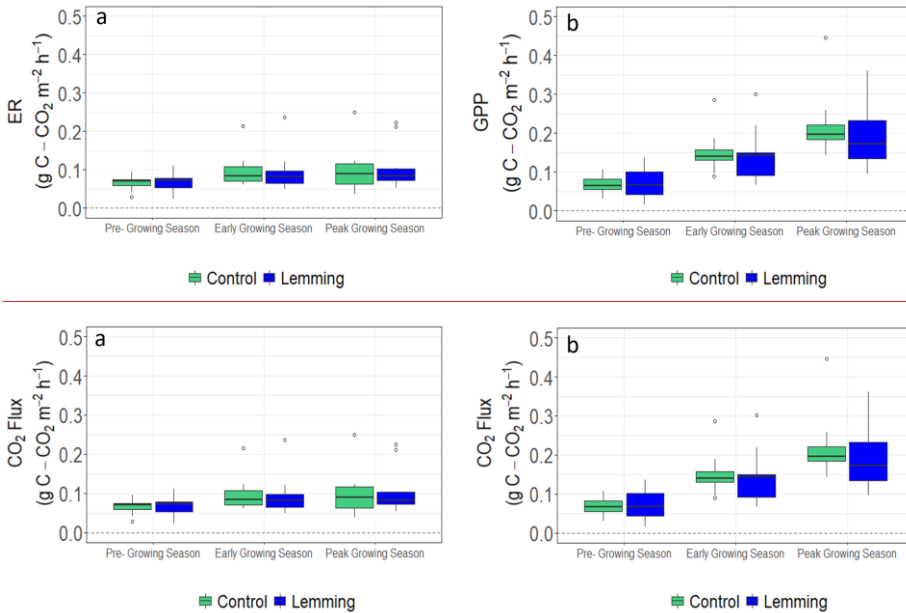
329   **Figure 2.** Box and whisker plots of 2018 and 2019 NEE for the control and lemming plots. Negative flux
330   values indicate carbon sequestration/uptake from the atmosphere by vegetation though photosynthesis and positive flux values indicate carbon
331   emission/loss into the atmosphere. (**a**) Median NEE for plots before and after the experiment in summer 2018 ($T = 4.62$, $P < 0.001$), and
332   (**b**) median NEE for plots during the three rounds of measurements in summer 2019 ($T = 0.21$, $P = 0.834$).

333

334 **Figure 3.** Box and whisker plots of 2018 and 2019 CH$_4$ fluxes for control and lemming plots. Negative flux values indicate uptake from the
335 atmosphere and positive flux values indicate emission to the atmosphere. (**a**) Median CH$_4$ flux for plots before and after the experiment in summer
336 2018 ($T = 0.01$, $P = 0.989$), and (**b**) median CH$_4$ flux for plots during the three rounds of measurements in summer 2019 ($T = -0.17$, $P = 0.869$).

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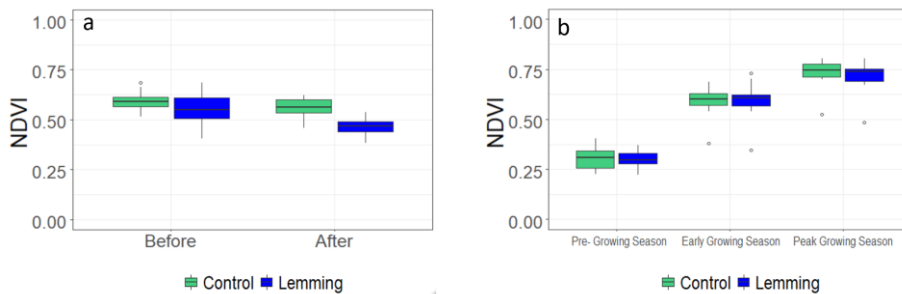
339 **Figure 4.** Box and whisker plots of ER and GPP for control and lemming plots
340 during the three rounds of data collection in summer 2019. Positive flux values indicate a positive respiration (carbon loss into the atmosphere)
341 and a positive carbon uptake by vegetation through photosynthesis. (**a**) Median ER ($T = -0.34$, $P = 0.742$), and
342 (**b**) median GPP ($T = -0.37$, $P = 0.716$). The signs of ER and GPP are always positive, but if ER is more than
343 GPP, then the ecosystem is a carbon source into the atmosphere (with a positive sign of NEE).

3.3 Hyperspectral surface reflectance and NDVI

345 Spectral reflectance derived from spectroradiometric radiances generally increased across visible and near infrared wavelengths
346 after lemmings' vegetation removal (Supplementary Fig. S1). Before placing lemmings in enclosures, control and lemming plots
347 exhibited similar surface reflectance values, while reflectance curves showed more substantial separation after lemming removal
348 (Supplementary Fig. S1). Analyzing the surface reflectance of the same control and lemming plots re-visited in summer 2019
349 revealed that the reflectance values for these different treatments were alike in each plot set, similar to what was observed before
350 the beginning of the manipulation experiment (Supplementary Fig. S2b).
351 To better quantify the changes in reflectance, we calculated the NDVI in all the control and treatment plots in both summer
352 2018 and 2019. Following lemming removal in the first summer, lemming plots had significantly lower NDVI than the control
353 plots ($P = 0.015$, Fig. 5a), consistent with the decrease in green biomass observed in the photographs collected before and after
354 placing the lemmings in the treatments' enclosure (Supplementary Fig. S1), and with the decreases in net CO$_2$ uptake (see NEE
355 close to zero after lemming vegetation consumption; Fig. 2a). The effect of brown lemmings' herbivory changed the mean NDVI
356 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

357 (Fig. 6̶5b). ~~Results of the linear mixed-effects model reveals that d~~During this time, there was no significant difference in NDVI when
358 comparing control plots to lemming plots ($P = 0.692$), which is consistent with the results of the Kruskal–Wallis test that found
359 there was no significant difference between the treatments in 2019 either by testing the data set all together ($P = 0.694$) or separating
360 it for different times of the season (rounds) and testing each time separately (pre-growing season: $P = 0.260$, early growing season:
361 $P = 0.418$, peak growing season: $P = 0.283$). ~~T~~but there was a significant difference ~~between rounds ($P < 0.001$). The significant difference~~ in NDVI across the rounds ($P < 0.001$), which
362 ~~is consistent~~coincides with the increased green biomass observed in collected photographs from pre- to early to peak growing season
363 (Supplementar~~y1~~y Fig. S2a).

365 **Figure 5.** Box and whisker plots of 2018 and 2019 NDVI values for control and lemming plots. (**a**) Median NDVI for plots before and after the
366 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
367 $= 0.41$, $P = 0.692$). Higher vascular plant green biomass in the pre-lemming treatment plots presented NDVI values in the 0.6 to 0.7 range,
368 whereas post-lemming treatment plots in 2018 exhibit NDVI values around 0.5.

369 **4 Discussion**

370 We found, within a short-term enclosure experiment, that brown lemmings' herbivory significantly decreased net CO_2 uptake
371 immediately after consumption of vegetation, while surprisingly not affecting CH_4 fluxes. Consumption of photosynthetically
372 active plant tissue by lemmings impacted the ability of the vegetation to sequester CO_2, nullifying CO_2 uptake by tundra vegetation.
373 The lack of significant difference in the evaluated environmental variables (air temperature, soil temperature, soil moisture, thaw
374 depth) between the control and lemming treatment plots suggests that these factors did not play a significant role in the difference
375 in net CO_2 fluxes before and after the treatments during the first summer~~, but that the decline in CO_2 flux values was due to~~
376 ~~vegetation removal by lemmings~~. Unfortunately, the design of this experiment, mostly focusing on the aboveground measurements
377 (except for the soil temperature, soil moisture, and thaw depth), did not allow for identifying the contribution of belowground
378 increased decomposition from the aboveground vegetation removal. However, as we did not notice an increase in CH_4 emission
379 with vegetation removal (which could have increased ~~with an increase~~ as an indirect effect of an increase in sugars related to
380 increased soil microbial respiration), we could assume that the direct effect of the removal of photosynthetic plant tissue was the
381 main mechanism~~s~~ explaining the decrease in the ability of the ecosystem to sequester carbon. Therefore, we believe ~~the main~~
382 ~~source of disturbance that would result in~~ that the removal of vascular plants ~~in these wet tundra ecosystems is~~ from lemming
383 herbivory was the main driver explaining the decrease in the ability of these ecosystems to uptake carbon. ~~There could be other~~
384 ~~sources of herbivory (such as caribou), but they are not as frequent in these northern areas of the Arctic Coastal Plain and would~~
385 ~~not have been able to access the vegetation within the galvanized hardware cloth enclosures. Additional sources of disturbance to~~
386 ~~vegetation could originate from a drastic change in environmental conditions, such as extreme temperatures, extremely dry~~

387 conditions, etc.; however, these would not selectively remove the vascular plants while not affecting the moss layer, which is what we observed in this experiment.

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

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

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

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

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

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

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

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

396 by the roots (McEwing et al., 2015; Ström et al., 2003; Zona et al., 2009). Labile carbon fuels methanogenesis, aiding in CH_4

397 production in the Arctic (Tan et al., 2015). However, labile carbon as a result of root exudation depends on photosynthetic activity

398 of vegetation to be a controlling mechanism of CH_4 emission (Bhullar et al., 2014; Ström et al., 2003). Thus, given the

399 photosynthetic activity of vegetation decreasing resulting from lemming consumption, it is likely that soil labile carbon did not

400 have a crucial impact on CH_4 emission in this study. The lack of response of CH_4 emissions to vegetation removal could be

401 explained by the large soil carbon stored in these permafrost soils (Hugelius et al., 2014). A decrease in labile carbon exudation

402 due to vegetation removal from herbivory may have not been limiting CH_4 emissions, consistent with a lack of response in

403 CH_4 emissions with a labile carbon addition in these sites (von Fischer et al., 2007).

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406 Moreover, when measured shortly after the lemming treatment, the CH_4 emission in the plots may have been inhibited by

407 Moreover, when measured shortly after the lemming treatment, the CH_4 emission in the plots may have been inhibited by lemming

408 Moreover, when measured shortly after the lemming treatment, the CH_4 emission in the plots

409 may have been inhibited by lemming urine. Ammonium from urine has been linked to an increase in CH_4 production (Lin

410 et al., 2009); however, it has been found that CH_4 fluxes can initially result in a mean negative flux shortly after the addition of

411 urine to the system (Boon et al., 2014). The timing in which we measured the greenhouse gases after the lemming treatments falls

412 within the initial window of time found by Boon et al. (2014) to have this effect; thus, urine produced by the lemmings in the plots

413 may have nullified the positive CH_4 emissions via the aerenchyma. Without further investigation into the soil chemistry, it is

414 difficult to determine which mechanisms of herbivore-plant interactions resulted in the lack of significance in CH_4 emission.

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

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

417 to lemming consumption. Since lemmings mostly consume vascular plants, such as graminoids and sedges, in the summer and

418 avoid non-vascular and slower growth vegetation, such as mosses and lichens (Batzli et al., 1980), the preferential consumption

419 of annual grasses and sedges likely led to the rapid recovery of the photosynthetic capacity of vegetation we observed in just one

420 year. From analysis of the motion-sensor video footage, we observed lemming foraging within the plots was representative of these

421 vegetation preferences. An in-depth analysis of the vegetation types found in our plots was completed in a previous study by our

422 team (Davidson et al., 2016).

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

424 (Supplementary Fig. S1). The control and experimental plots before the lemming treatment had relatively high and similar mean

425 NDVI values (Supplementary Fig. S1), suggesting their biomass had similar values (Goswami et al., 2015). Vegetation removal

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

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

While our experiment showed a potentially substantial impact of lemming herbivory on the CO_2 fluxes from these tundra ecosystems, we did not address the impact of varying degrees of intensity of herbivory and population cycling of brown lemmings on carbon fluxes and photosynthetic capacity of different vegetation communities. Roy et al. (2020) found that herbivore presence can alter communities of vegetation differently, as herbivores play a role in regulating a variety of plant species. These herbivores can lead to significant changes in the abundance of vegetation types, allowing for the potential of the tundra during the peak growing season to switch between a carbon source to sink in the absence of herbivory (Min et al., 2021). Since brown lemmings rely on a high rate of food intake to sustain growth and reproduction (Batzli et al., 1980) and experience population cycles with distinct seasonal and multiannual density fluctuations (Reid et al., 1995; Stenseth, 1999), rapid consumption of plant matter by lemmings as sustenance during population peaks may significantly contribute to shifts in plant communities and, thus, carbon cycle changes.

Since lemming population densities vary in response to multiple environmental factors (Fauteux et al., 2015; Soininen et al., 2017), predicting a 'normal' level of herbivory for this species is very challenging. Reports on estimated brown lemming density have found their local density to range from five to 65 lemmings per hectare (Ott and Currier, 2012; Alaskan Arctic) and about zero to nine lemmings per hectare (Fauteux et al., 2015; Canadian Arctic), which is variable and may be an underestimate due to the use of live-trapping, as mentioned previously. Moreover, in addition to space, it is important to consider time: we only kept lemmings inside the plots for 16 hours and there was no effect of lemming herbivory for the remainder of the experiment. The most relevant comparison we could find to define the degree of herbivory observed was the effect on vegetation near lemming burrows and runways in a similar ecosystem (Erlinge et al., 2011; Siberian tundra). Given the sparsity of available literature and data from these understudied Arctic ecosystems, it is difficult to categorize our lemming treatment as having some sort of 'normal' or 'heavy' impact on vegetation, which would be required to explore legacy effects of lemming herbivory.

Lemming populations may also vary in response to regulation by predators (Fauteux et al., 2018b). Given the substantial impact of lemming herbivory on the tundra carbon balance, indirect cues indicating predatory risk could

Given the substantial impact of lemming herbivory on the tundra carbon balance, indirect cues indicating predatory risk could change lemming foraging behavior, and in turn alter their effect on vegetation. The influence of predator-prey interactions on herbivory, and how they further impact vegetation and carbon fluxes in the Arctic tundra should be quantified by future studies to better understand multifaceted interactions in the Arctic (see supplementary materials).

5 Conclusions

We show that there is an immediate effect of lemmings on plant biomass and net CO_2 uptake by Arctic vegetation, but not on CH_4 flux in areas where lemmings forage. However, impacts on vegetation are temporary, and plant biomass and net CO_2

465 uptakevegetation can recover to its previous conditions by the end of the subsequent growing season. To further our understanding

466 of the complex interactions in the Arctic, it is vital to also explore the longer-term feedbacks that may exist between climate change,

467 herbivory, and predator-prey interactions. The effects of warming on snow cover and plant growth, as crucial environmental

468 resources to lemmings, could lead to drastic population changes for lemmings, and the longer-term effect of lemmings' herbivory

469 on vegetation might not be captured by a short-term manipulation. It is also critical to link the long-term lemming population

470 fluctuations to potential shifts in vegetation and climate change. Additionally, climate change is likely to also alter the abundance,

471 behavior, or even occurrence of predators of lemmings, which may in turn impact lemming abundance and foraging behaviors. For

472 these purposes, longer-term and broader scale ecological data would be particularly valuable to build on the short-term effect

473 highlighted in this study.

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

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

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

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

478 vegetation communities, as various plant species might be affected differently. Thus, it is relevant to examine the effects

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

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

481 Arctic tundra ecosystem, which might explain some of the substantial interannual variability in the tundra CO_2 fluxes not

482 explained by environmental variables alone.

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

484 author upon the journal's request.

485 *Data availability.* Data on carbon fluxes, hyperspectral surface reflectance, and environmental variables analyzed during this study will be

486 archived to the ORNL DAAC repository by the corresponding author upon the journal's request. All relevant data are included as figures in the

487 paper, and raw data may be made available upon request.

488 *Author contribution.* Study conception and design were carried out by Jessica Plein, Rulon Clark, Walter Oechel, and Donatella Zona. Material

489 preparation, data collection, and data processing were completed by Jessica Plein. Data scripts and codes were written by Jessica Plein, Kyle

490 Arndt, and Donatella Zona. Data analysis was performed by Jessica Plein and Donatella Zona. The drafts of the manuscript were written

491 by Jessica Plein and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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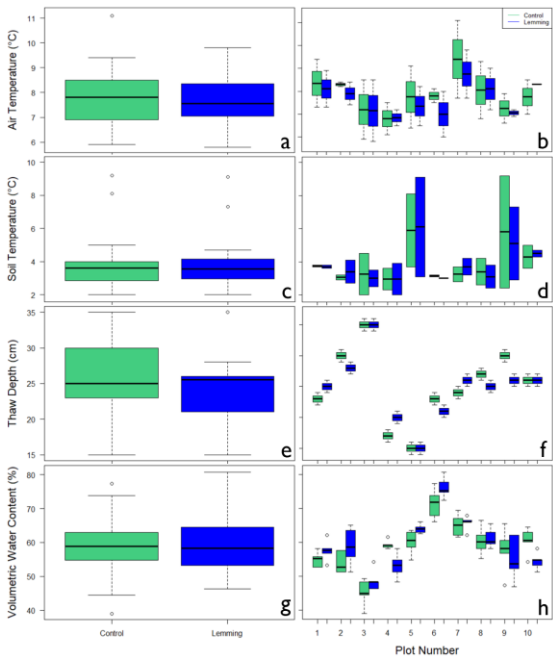
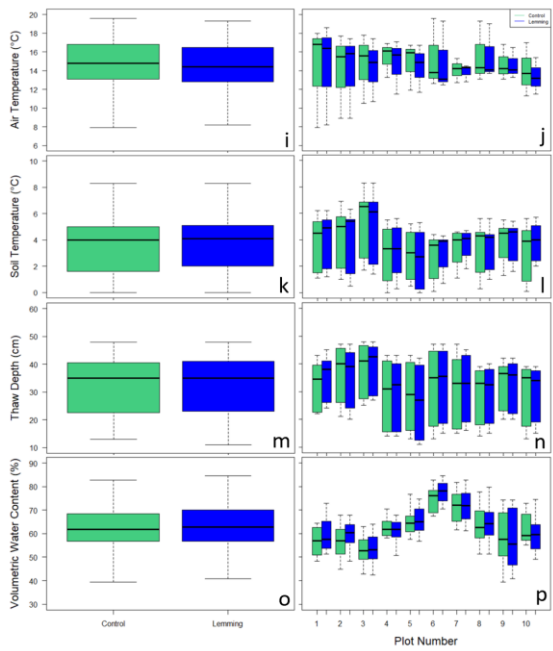
660 **Appendix A**

661

662

663 **Figure A1.** Box and whisker plots of environmental variables across treatment plots during (**a-h**) summer 2018 and (**i-p**) summer
664 2019. Environmental variables include (**a, i**) air temperature for the entire dataset, (**b, j**) air temperature by plot, (**c, k**) soil temperature for the
665 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
666 dataset, and (**h, p**) soil moisture by plot.
667