



# 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 Utqiagvik, 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<sub>2</sub>) and methane (CH<sub>4</sub>) 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<sub>2</sub> uptake, while not significantly impacting CH<sub>4</sub>  
19 emissions. Methane emissions were likely not significantly affected due to CH<sub>4</sub> 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<sub>2</sub> 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<sub>2</sub> 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<sub>2</sub>) and methane (CH<sub>4</sub>)  
27 from the soil into the atmosphere via respiration or by CO<sub>2</sub> 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<sub>2</sub> and CH<sub>4</sub>, while overlooking the role of  
34 herbivory. Since herbivores remove photosynthetic tissues of vegetation, the ability of vegetation to photosynthesize and sequester  
35 CO<sub>2</sub> should decrease substantially with herbivory (Metcalf and Olofsson, 2015). The decrease in vascular plant cover should also  
36 decrease CH<sub>4</sub> emissions, given that aerenchyma in sedges facilitate the escape of CH<sub>4</sub> into the atmosphere (McEwing et al., 2015).

phrasing is awkward in lines 34/35

exp = ADDING  
herbivory to a  
no-herbivory  
plot? or are  
lemmings  
seasonal/  
migratory?

might be  
useful to  
expound on  
how e.g.  
"microbes  
consume  
stored carbon  
and thus  
convert it into  
greenhouse  
gases via  
respiration  
and other  
processes"



37 Investigating the impacts of herbivory on Arctic vegetation and its recovery after herbivory <sup>would</sup> **can** contribute to refining <sup>our</sup> **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, Utqiagvik, 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). <sup>but see</sup>

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 enclosures) 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<sub>4</sub>  
<sup>soil ^</sup>

compared to other ecosystems where? other non-tundra systems in the Arctic, or elsewhere globally where lemmings exist?

What is the crucial gap that you're taking on here? I think there needs to be a sentence between the last two in this paragraph that spells it out explicitly for those of your readers who aren't Arctic experts (like myself!).

enclosure s? are you manipulating population density? etc! that'd be

short pulses of? I'm not totally clear on how enclosures show you herbivory if lemmings are already present, and I think it'd be good to emphasize this.

awkward phrasing 41/42; also redundant with 40

why?

sequestration in soil or in veg?



77 emission to decrease with decrease in biomass of vascular plants, given their role in the CH<sub>4</sub> 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<sub>2</sub>) and methane (CH<sub>4</sub>) fluxes and the photosynthetic capacity of plants in the Alaskan Arctic  
80 environment.

I think I'd more clearly delineate your hypotheses at the conclusion of your intro. (e.g. "We hypothesized that lemming presence would do X to soil storage...we also hypothesized that lemming presence would reduce both CH<sub>4</sub> and CO<sub>2</sub> fluxes because of XYZ...lastly, we hypothesized that a year of recovery from lemming herbivory and disturbance would result in XYZ." Right now they blend in with your other text and don't pop out for easy reading of your goals and predictions!

## 81 2 Materials and methods

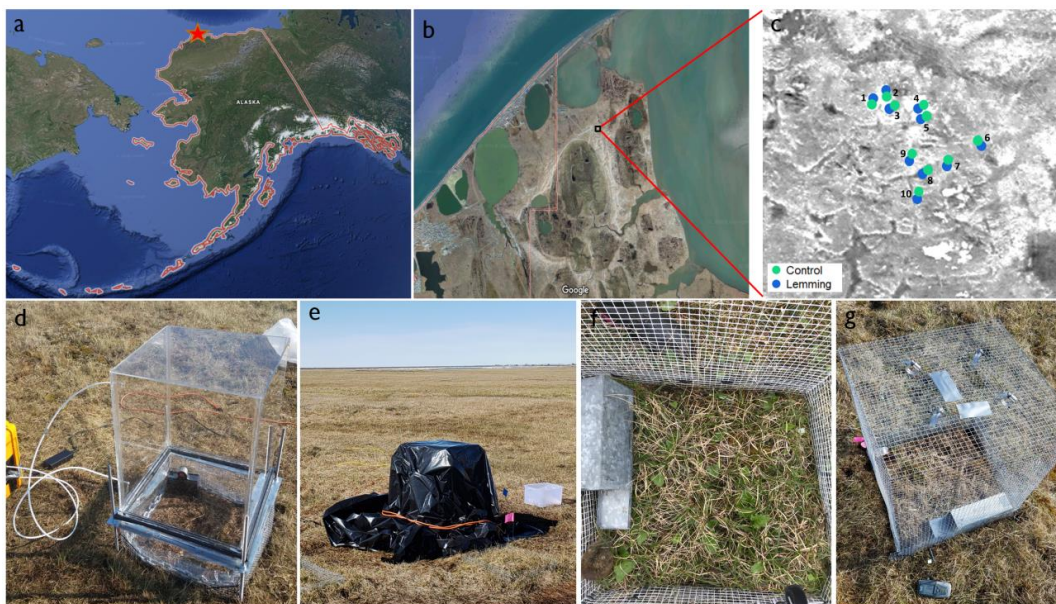
### 82 2.1 Study location

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

this is a little jargon-y for a biogeochemical audience, and more so for an herbivory audience I suspect! wonderful descriptors but i might suggest simplifying the language. (line 84)

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).

cool!!!



92  
93 **Figure 1.** (a) The location of the study site, Utqiagvik (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.

would suggest saving this (line 95) for the supplement, or methods if it's important! e.g. "all sampling sites located on preexisting maps from Worldview-3 using R Studio software" or similar.

### 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 Utqiagvik, 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 Utqiagvik (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 Utqiagvik 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.

### 111 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. I would move this second paragraph first, considering you reference the 'elevated population' in what is now the first paragraph.

### 126 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.

I think I'd suggest reframing your sampling plan into sentences; right now, with "but we only", it sets your reader up for some kind of disappointment! When in reality you just had two different sampling plans for the two years, and it isn't lacking anything. Perhaps: "We sampled vegetation at our sites over two summer growing seasons. During the first season (summer 2018), we used enclosures to ensure even lemming herbivory pressure in each of our experimental plots. We marginally captured the lemmings used in this first season shortly after peak growing season (4-10 August), coinciding with accelerated lemming reproduction and peak population density, in close proximity to our sampling sites while conducting visual encounter surveys. We secured them..." etc. Then go and explain how you set up your 2018 season. I also think you could potentially make the description of the experiment a little more efficient/save some room!

then go ahead and describe season #2 in 2019 :)

I would rephrase these intro sentences to be more focused on lemming physiology; seems unnecessary to include the information on the other herbivores in a general global sense. Perhaps instead: "Brown lemmings mostly consume graminoids in the summer and mosses in winter, and can consume up to 8x their body weight each day. Thus, their extreme capacity for consumption of vegetation (combined with their elevated population density in the region)..."





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 enclosure 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 Utqiagvik, Alaska which used 30 x 30 cm chamber bases within their enclosures. 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).

right now, the way your last paragraph is set up here (to describe 2019) it sounds like you did not make any flux measurements in 2018, but the next section makes it clear you did. I would perhaps cut out any description of what measurements you took in 2019; just make it clear that you are looking at legacy effects of heavy herbivory from the previous summer so did not perform any herbivory manipulations on the plots.

#### 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<sub>2</sub> and  
169 CH<sub>4</sub> 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<sub>2</sub>  
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<sub>2</sub> ecosystem respiration (ER) and gross  
181 primary production (GPP) from NEE, calculated following Eq. (1):

$$182 \quad GPP = NEE - ER .$$

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<sub>2</sub> and CH<sub>4</sub> 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  $\leq 1.5$  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.

small comment: you mostly use first-person active tense here (which I love!) but a few times switch to passive voice.

## 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<sub>2</sub> and CH<sub>4</sub> fluxes, and  
211 on NDVI. We tested multiple variations of these models using the model selection for mixed effects models in ecology described

would clarify whether  
flux measurements in  
2018 were collected  
before or after the  
lemming herbivory  
experiment

i think a table describing ‘portion’ (e.g. ‘pre-herbivory’ and ‘post-herbivory’, and ‘round’ (e.g. ‘pre, early, peak growing season) would be really helpful as a visual assist here, in your statistical analysis section, and in your results. Just was reading results and realized I wasn’t totally clear that you’d measured fluxes etc. in 2018 both before and after so came up here to check.



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.

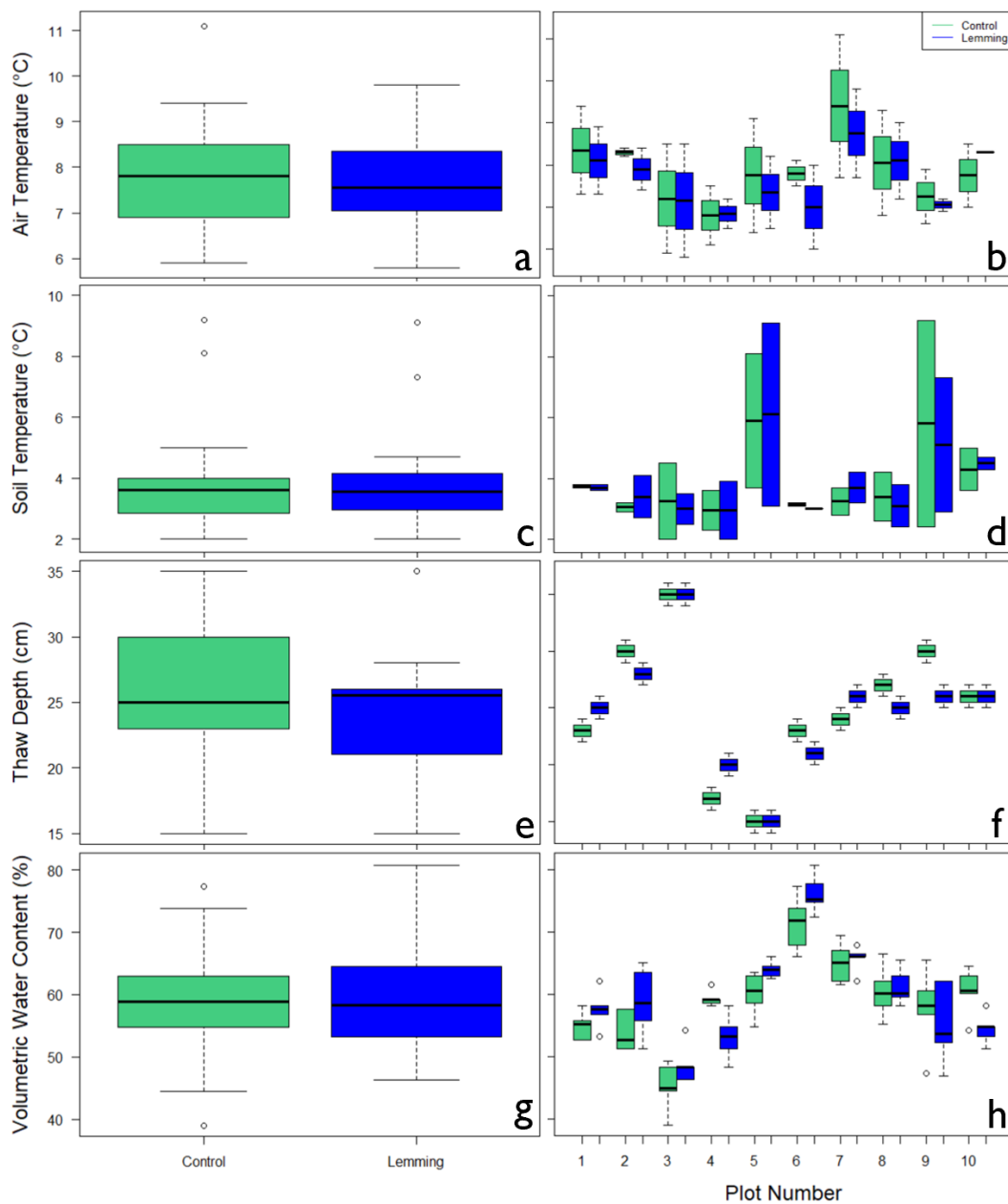
219 To identify the effect of the manipulation on the CO<sub>2</sub>, CH<sub>4</sub>, and spectral indexes, we applied the linear mixed-effects models  
220 to test differences in each environmental variable before and after lemming exposure in summer 2018. The statistical analyses also  
221 helped 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.

this second paragraph is a bit awkward and perhaps re-hashes some of what you've already done a great job describing in the previous paragraph. I would suggest re-phrasing/paring it down a little bit! Perhaps would help to switch back to first-person active voice here.

## 225 **3 Results**

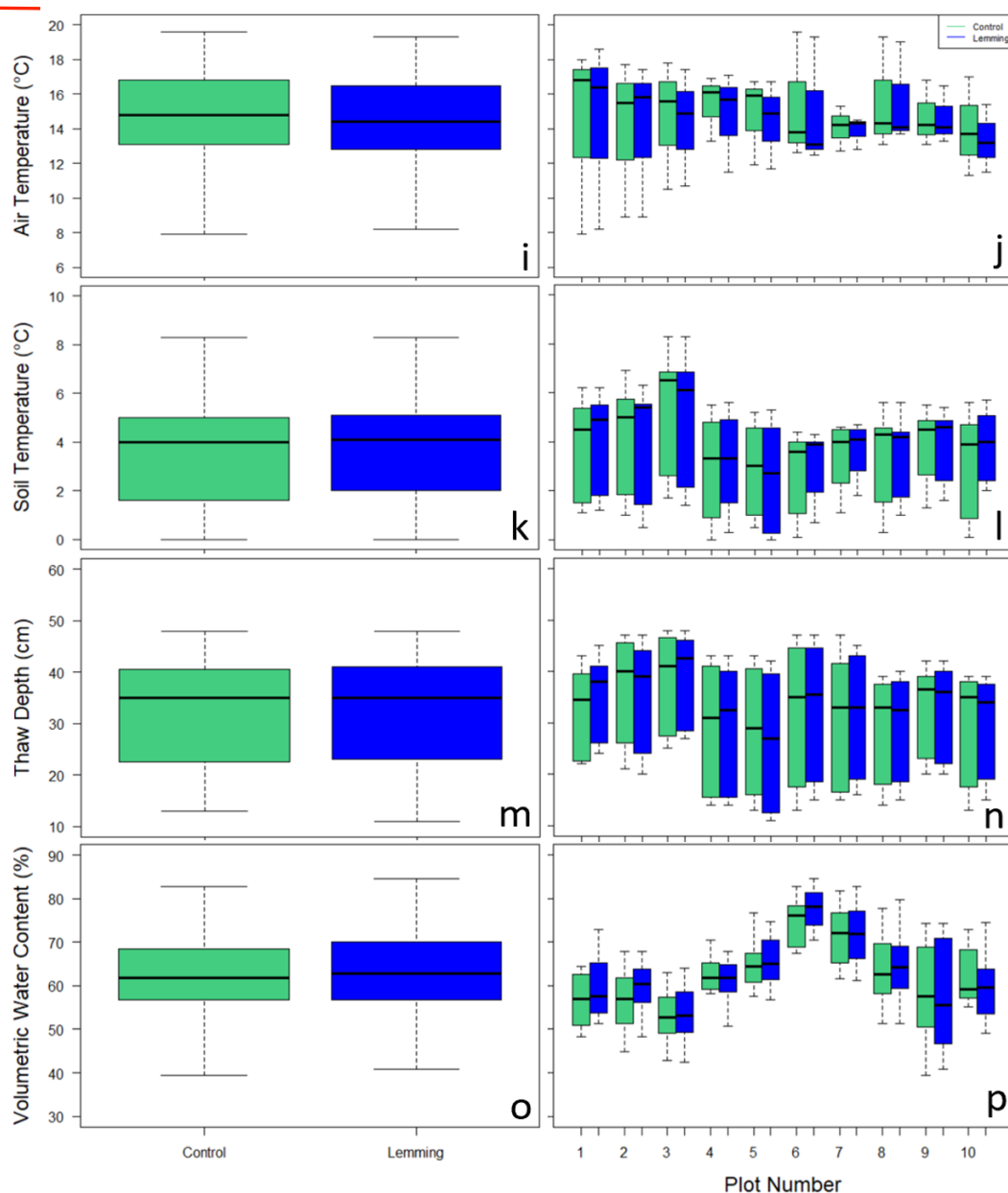
### 226 **3.1 Environmental variables within the plots**

227 Environmental controls on CO<sub>2</sub> and CH<sub>4</sub> 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





234

235 **Figure 2.** Box and whisker plots of environmental conditions across treatment plots during (a-h) summer 2018 and (i-p) summer 2019.

236 Environmental variables include (a, i) air temperature for the entire dataset, (b, j) air temperature by plot, (c, k) soil temperature for the entire

237 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,

238 and (h, p) soil moisture by plot.

### 239 3.2 Carbon fluxes in the treatment plots

“...during summer 2018 when the lemming enclosures treatment was implemented”

240 The presence of lemmings significantly impacted CO<sub>2</sub> fluxes (i.e. NEE) during the first summer of measurements. Before the

241 treatment, calculated CO<sub>2</sub> (Fig. 3a) and CH<sub>4</sub> (Fig. 4a) fluxes for the control and lemming plots were similar. After we placed and



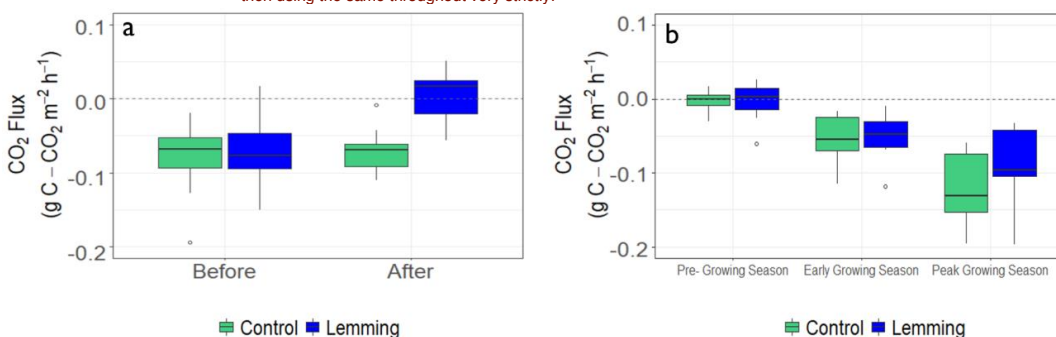
decreased

242 ~~then~~ removed lemmings from experimental plots, CO<sub>2</sub> uptake ~~was~~ significantly ( $P < 0.001$ ) ~~lower~~ (i.e. CO<sub>2</sub> fluxes were around  
243 zero); less CO<sub>2</sub> was taken up by the system in experimental plots than in control plots (Fig. 3a). Contrary to what we expected,  
244 CH<sub>4</sub> 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<sub>2</sub> flux for lemming plots from  $-0.074$   
246  $\pm 0.012$  gC-CO<sub>2</sub>m<sup>-2</sup>h<sup>-1</sup> (i.e. CO<sub>2</sub> sequestration) to  $0.003 \pm 0.012$  gC-CO<sub>2</sub>m<sup>-2</sup>h<sup>-1</sup> (i.e. no different from zero).

247 In summer 2019, we measured CH<sub>4</sub> 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<sub>4</sub> 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<sub>4</sub>  
250 flux  $P = 0.869$ , Fig. 4b).

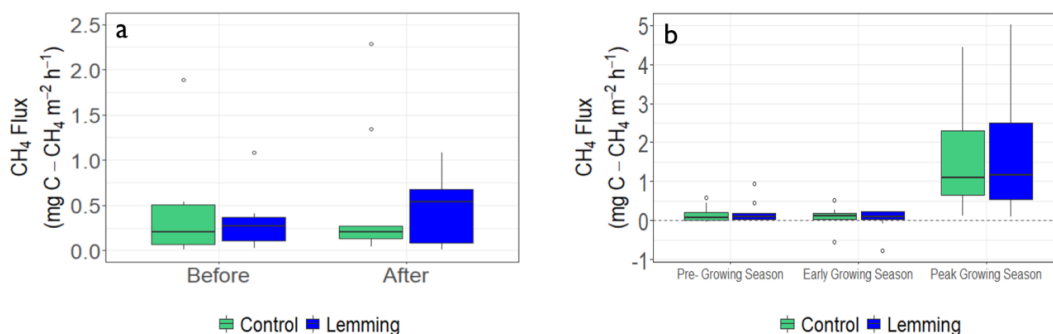
you might want to stick to a single defined reference for NEE/CO<sub>2</sub> flux; in 2018 results you use CO<sub>2</sub> flux, and here you use NEE. (e.g. does CO<sub>2</sub> flux include plants, or is the same as ER, etc.) Since these terms "can" be fuzzy, I'd suggest defining the variables as you plan to use them in the intro, and then using the same throughout very strictly!

move sentence on  
line 245-246 to after  
your reference to fig.  
3a; feels funky to go  
from CO<sub>2</sub> to CH<sub>4</sub>,  
back to CO<sub>2</sub>



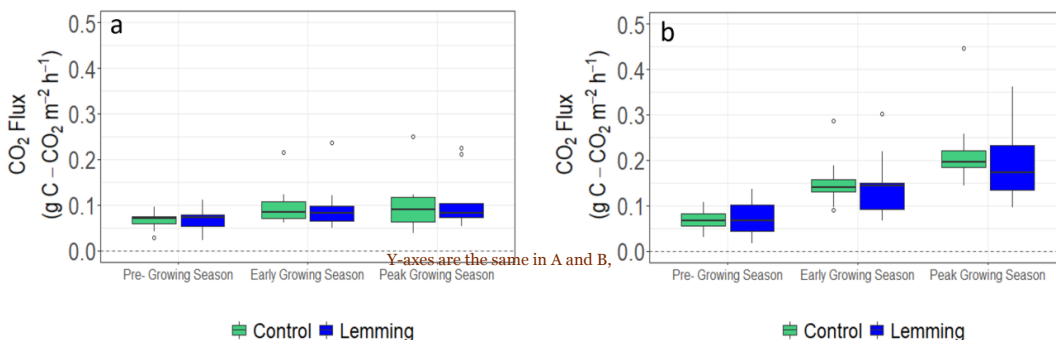
251

252 **Figure 3.** Box and whisker plots of 2018 and 2019 CO<sub>2</sub> net ecosystem exchange fluxes for the control and lemming plots. Negative flux values  
253 indicate carbon sequestration/uptake from the atmosphere and positive flux values indicate carbon emission/loss to the atmosphere. (a) Median  
254 CO<sub>2</sub> flux for plots before and after the experiment in summer 2018 ( $T = 4.62$ ,  $P < 0.001$ ), and (b) median CO<sub>2</sub> flux for plots during the three  
255 rounds of measurements in summer 2019 ( $T = 0.21$ ,  $P = 0.834$ ).



256

257 **Figure 4.** Box and whisker plots of 2018 and 2019 CH<sub>4</sub> fluxes for control and lemming plots. Negative flux values indicate uptake from the  
258 atmosphere and positive flux values indicate emission to the atmosphere. (a) Median CH<sub>4</sub> flux for plots before and after the experiment in summer  
259 2018 ( $T = 0.01$ ,  $P = 0.989$ ), and (b) median CH<sub>4</sub> flux for plots during the three rounds of measurements in summer 2019 ( $T = -0.17$ ,  $P = 0.869$ ).



260

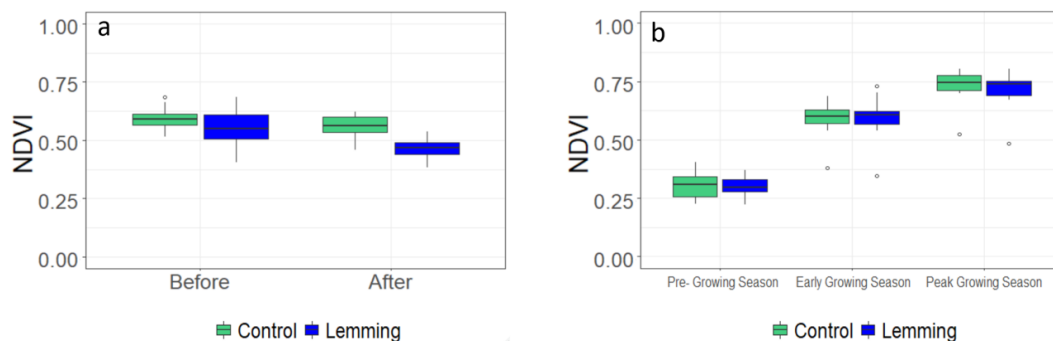
261 **Figure 5.** Box and whisker plots of CO<sub>2</sub> ecosystem respiration and gross primary production fluxes for control and lemming plots during the  
262 three rounds of data collection in summer 2019. (a) Median CO<sub>2</sub> ecosystem respiration flux ( $T = -0.34, P = 0.742$ ), and (b) median CO<sub>2</sub> gross  
263 primary production flux ( $T = -0.37, P = 0.716$ ).

not totally clear to me how these measurements are different from this plot; from my understanding of your methods, you calculated GPP in 2019? again would suggest a table or similar with terms/definitions as you use them here of all your chamber variables!

### 264 3.3 Hyperspectral surface reflectance and NDVI

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

271 To better quantify the changes in reflectance, we calculated the NDVI in all the control and treatment plots in both summer  
272 2018 and 2019. Following lemming removal in the first summer, lemming plots had significantly lower NDVI than the control  
273 plots ( $P = 0.015$ , Fig. 6a), consistent with the decrease in green biomass observed in the photographs collected before and after  
274 placing the lemmings in the treatments' enclosure (Supplemental Fig. 1), and with the decreases in CO<sub>2</sub> uptake (see NEE close to  
275 zero after lemming vegetation consumption; Fig. 3a). The effect of brown lemmings' herbivory changed the mean NDVI for  
276 lemming plots from  $0.551 \pm 0.021$  to  $0.465 \pm 0.021$ . During the second summer, median NDVI values of all plots were similar  
277 (Fig. 6b). During this time, there was no significant difference in NDVI when comparing control plots to lemming plots ( $P =$   
278  $0.692$ ), but there was a significant difference between rounds ( $P < 0.001$ ). The significant difference in NDVI across the rounds is  
279 consistent with the increased green biomass observed in collected photographs from early to peak season (Supplemental Fig. 2a).



280

281 **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  
282 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 ( $T$



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.

#### 285 4 Discussion

286 We found, within a short-term enclosure experiment, that brown lemmings' herbivory significantly decreased CO<sub>2</sub> uptake  
287 immediately after consumption of vegetation, while surprisingly not affecting CH<sub>4</sub> fluxes. Consumption of photosynthetically  
288 active plant tissue by lemmings impacted the ability of the vegetation to sequester CO<sub>2</sub>, nullifying CO<sub>2</sub> 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<sub>2</sub> fluxes before and after the treatments during the first summer, but that the decline in CO<sub>2</sub> flux values was due to vegetation  
292 removal by lemmings.

293 Notably, lemmings' herbivory did not affect CH<sub>4</sub> fluxes, even though plant transport of CH<sub>4</sub> is a critical pathway for emission  
294 in tundra ecosystems (Lai, 2009; McEwing et al., 2015); plants offer substrate for methanogenesis and increase CH<sub>4</sub> transport  
295 (Bridgham et al., 2013). The lack of a significant effect on CH<sub>4</sub> 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<sub>4</sub> emissions;  
297 belowground clipping at the root-shoot or porewater-root boundary is more likely to impact CH<sub>4</sub> emission, but aboveground  
298 clipping is less likely to affect CH<sub>4</sub> emission. This differential effect is likely related to the location of CH<sub>4</sub> escape through  
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<sub>4</sub> 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<sub>4</sub> 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<sub>2</sub> 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

here i think important to distinguish between sequestering in soil, versus plant biomass, and how that might impact flux? I can also see the vegetation being eaten as impacting soil respiration bc it's exposed to light, or similar? TL;DR – what are you referring to here with the word 'sequester'? are you talking about net carbon export by the lemmings (who may not have deposited all their waste after 16hrs), or some kind of soil-based issue with sequestration?

somewhat conflicts with an earlier intro statement that clarified seasonality in browsing habits by lemmings?





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.

^ these last two paragraphs, I feel, could be condensed into one that focuses on the spatial AND temporal variability in carbon uptake/emission in the tundra over a year, considering the spatial dependence (e.g. heavy herbivory near burrows) and temporal dependence (peak abundance season) of heavy lemming herbivory. then the rest of this section could be speculating how these variabilities in space and time add up to a net effect on the waterlogged tundra, which is what seems to me the most interesting possible application of this work (e.g. what if lemming population increased due to predator loss or some positive effect of climate change or something). As they stand, these paragraphs contain cool and interesting information but not as much synthesis / new interpretations. It shows up in the conclusions but i think should be introduced here (or else they seem like they come out of left field in conclusion section).

## 334 5 Conclusions

335 We show that there is an immediate effect of lemmings on plant biomass and CO<sub>2</sub> uptake by Arctic vegetation, but not on CH<sub>4</sub> 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<sub>2</sub> 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<sub>2</sub> 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<sub>2</sub> 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.

after 336-337 sentence, did 1yr post-treatment also impact fluxes or just vegetation?



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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370 indicated in Alaska Department of Fish and Game permits 18-167 and 19-131 and Institutional Animal Care and Use Committee (IACUC)  
371 Animal Protocol Form #16-08-014C.

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other more general notes:

I enjoyed reading this immensely, as I think it's a really cool experimental setup. My comments refer mostly to the framing of the write-up as I think the strength of the experimental design is not currently shining through as well as it could given how cool I personally took it to be! I would suggest that the authors re-frame the paper to exploring the LEGACY effects of heavy lemming herbivory, by quantifying what 'normal' herbivory is in the site and how much more herbivory the experimental enclosures experienced over 16 days (perhaps using the existing NDVI data) to demonstrate the difference. The interpretation and discussion could then probe the circumstances in which such heavy herbivory could occur (e.g. climate-change-induced lengthening of snow-free time; loss of predation; an eruption in lemming population size; etc.) and the resilience of the ecosystem in terms of its recovery after such an event.

important to define the variables you measured/refer, as well as the timeline of your experiment, to very specifically in a table or list (see in-line comments)

what are you referring to when you refer to carbon uptake? I suspect it will be important to define it for reader. and, when you conclude in discussion that lemming herbivory negatively impacted the sites' ability to sequester carbon, do you mean as aboveground biomass/belowground biomass/belowground deposition of sugars/increased soil microbial respiration/decomposition of root biomass after tops are eaten? Which of these factors is that that is increasing carbon flux, and why do you posit so?

REALLY need to say how soon after lemming removal you measured all your fluxes. that will change your proposed explanation for the change in flux. (see above) (maybe in the table describing sampling timeline that you proposed in the doc itself?)

important that you refer to what they're measuring carefully; as a first-time reader of this work, my impression was that they were measuring the short and longer-term legacy effects of heavy herbivory (bc lemmings are still present here, so they were not removing herbivory; they were imposing then removing heavier herbivory).

It is worth identifying the predators of lemmings since they end up coming up a few times in discussion/conclusion.

lastly: it is worth circling back to the intro/drive in discussion. It's likely going to feel more closed-loop if the intro brings up why knowing the near-term AND legacy impacts of heavy herbivory on carbon cycling in this system. (Changes to populations of predators? Climate change? etc.) E.g. the conclusions do it, but the intro does not hook the reader with 'why should I be excited that you did this experiment with heavy herbivory'.

in closing: really cool experimental design! While I am suggesting some fairly large revisions here (e.g. in framing of the paper and some more synthesis/interpretation), given the cool design and the very clear results, I am excited to see how it turns out and would gladly read another version.