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Paul Stoy
Associate Editor
Biogeosciences
European Geosciences Union

Dear Editor,

Please find attached our revised manuscript entitled **"Response of vegetation and carbon fluxes to brown lemming herbivory in Northern Alaska"** *for possible publication in your journal.*

We would like to thank you and the referees for the helpful suggestions which substantially improved the manuscript. We include below point-by-point responses to the referees' comments, and detailed descriptions of the modifications we made to the manuscript (with line numbers for the manuscript with track-changes off). We hope that with these changes you will find our revised manuscript appropriate for publication in your journal.

Best Regards,
Jessica Plein

Department of Biology
San Diego State University

Referee Comment #1:

Plein and others explore the response of greenhouse gas fluxes to lemming herbivory on the North Slope of Alaska. Lemmings reduced NDVI and CO2 uptake that recovered the following year due to vegetation regrowth but had little impact on CH4 fluxes.

I found the study to be relevant and interesting to the readership of Biogeosciences; studies of the importance of herbivores on GHG fluxes are too infrequent and careful analyses like this help us appreciate the role of biology in the earth system. At the same time I was surprised at the idea that herbivory would decrease CH4 fluxes. Is there a wounding response in the aerenchyma that blocks their role as a CH4 conduit? All else being equal I would assume that herbivory might slightly increase CH4 fluxes that would be very difficult to see from a signal-to-noise perspective because the path that CH4 has to take to the atmosphere has been decreased slightly (by shorter aerenchyma, this won't be much of an effect) or possibly increased if herbivory was enough to reduce transpiration to the point that it impacts groundwater levels. It's hard to see how lemming herbivory would be sufficient to do this outside of massive lemming herbivory of which I am unaware, but if sedges simply regrow after herbivory there shouldn't be much of a methane impact, which was found. The idea that it escapes from the stem bases may hold if the stems help create preferential flow pathways in the soil, but this probably wouldn't compensate for any changes to the aerenchyma. Basically there should be no observable effect on CH4 which is what was found. Interesting to study nonetheless. I had few other concerns and feel that the manuscript is publishable with minor revisions after finding more literature basis for the impacts of herbivory on aerenchyma and subsequent expectations for CH4 flux.

We thank the referee for the useful comments, which we attempted to address in the revised manuscript. We modified the wording of the hypothesis at the end of the Introduction section and included more references. We more thoroughly explained how the removal of vegetation could affect CH_4 emissions, given that vegetation contributes not only to CH_4 transport from the soil to the atmosphere, but also the release of labile carbon in the soil, which stimulates CH_4 emission (lines 35-40). In the Discussion section, we elaborate on why the CH_4 results may not be what we expected due to how lemming herbivory affected the vegetation through the location of clipping and photosynthetic activity interacting with labile carbon (lines 343-358). Additionally, we discuss how lemming urine may counter the impact of changes to the aerenchyma on CH_4 emission, as ammonium from urine has been linked to an increase in CH_4 production, but may also result in a mean negative flux shortly after the addition of urine to the system (lines 359-365).

Referee Comment #2:

I have included in-line notes I took while reading through the manuscript for the first time, and some concluding notes (at the bottom of the final page) on my interpretation of the entire manuscript. As noted there, while I am suggesting major revisions I am excited by the experimental design and data of this paper and would gladly look at it again.

We thank the referee for the positive evaluation of our study and for the useful comments, which we incorporated in the revised manuscript. Below, we included answers to the comments listed in the referee's concluding notes.

<u>Here are the concluding notes at the bottom of the final page:</u>

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.

This is a very important point which we tried to address as best as we could with the data available in the literature. In the Discussion section (lines 390-399), we discuss that 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). However, as mentioned in the Materials and Methods section of the revised manuscript (lines 134-136), the use of live-trapping as a technique to estimate density for this species may underestimate the actual population density. 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 scientific literature on lemming herbivory is extremely sparse, and 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). We agree that separating the effect of normal and heavy legacy effects is very important, but 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.

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)

We added a table listing the data collected and frequency of measurement during both field seasons in the Materials and Methods section (see Table 1 in the revised manuscript), with the terms in the caption of Table 1 (lines 179-182). We also added more precise dates of data collection (lines 140, 177-178).

what are you referring to when you refer to carbon uptake? I suspect it will be important to define it for reader.

We included more details of the different terms we used in the Materials and Methods section. Specifically, we mentioned that the net ecosystem exchange (NEE) used in equation 1 (and shown in Fig. 2) was the net balance between the carbon uptake from photosynthesis and the carbon loss from respiration (lines 202-205). In the Results section, we further elaborated on the definition of carbon uptake in the context of this study (lines 274-275). We also specified in lines 301-302 of the revised manuscript (caption of Fig. 4) the meaning of carbon uptake and explained the meaning of the signs for NEE, GPP, and ER in Fig. 2 and Fig. 4 captions.

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?

This is a very important point that should be investigated in future studies. Unfortunately, the design of this experiment, mostly focusing on the aboveground measurements (except for the soil temperature, soil moisture, and thaw depth), did not allow for identifying the contribution of belowground increased decomposition from the aboveground vegetation removal. However, as we did not notice an increase in CH_4 emission with vegetation removal (which could have increased as an indirect effect of an increase in sugars related to increased soil microbial respiration), we could assume that the direct effect of the removal of photosynthetic plant tissue was the main mechanism explaining the decrease in the ability of the ecosystem to sequester carbon. We included this in the Discussion section (lines 335-342).

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?)

We included this detail in the Materials and Methods section (lines 192-194). The fluxes were measured one day after the removal of the lemming from each plot in summer 2018 (when we performed a manipulative experiment).

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).

We included these details in lines 64-70 of the Introduction section, and also added Table 1, which includes a full list of all the data collected during each of the field seasons and the frequency of these measurements (2018: before and after lemming treatment; 2019: pre-, early, and peak growing season).

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

We identified the predators of lemmings in the Materials and Methods section (line 119) of the revised manuscript.

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'.

We added more details of the potential relevance and larger implications of our study in lines 81-84 of the Introduction section. We feel that this study may help increase our understanding of how herbivores impact carbon fluxes and the photosynthetic capacity of plants in the Alaskan Arctic environment, and hope to further interest in complex interactions in the Arctic.

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

We thank the referee for the suggestions and hope the revisions are found to have strengthened the manuscript.

Referee Comment #3:

The manuscript, entitled "Response of vegetation and carbon fluxes to brown lemming herbivory in Northern Alaska" by Jessica Plein and coauthors (bg-2021-286) proposes in a research paper to study how brown lemming impacted the short-term response and the recovery of vegetation carbon uptake, NDVI and CO2 and CH4 emission to atmosphere. The study shows that the NDVI and carbon uptake by vegetation was immediately impacted by lemming placed in the enclosure, while there was no impact during the next-year recovery for every variables of the tundra functioning.

This manuscript is written with a perfect English and the experimentation has been conducted thoroughly. While only a few studies focus on small herbivore impact on C fluxes in Arctic, I found that the study is not extensive / comprehensive enough to be proposed in a large audience journal like Biogeoscience. Fundamentally, the study focuses on vegetation disturbance, which is due to the introduction of lemming enclosure but it could be any other source of disturbance and the response would have been the same. As such, the response shows nothing specific to lemming. Plant community is totally lacking at the study and the interpretation. This is essential as lemming is quite specific in its plant species diet and CH4 efflux can be promoted by species characterised by aerenchyma. As such, this could be a way to show the specificity of lemming herbivory. Of secondary importance, there are several parts I found too long and misplaced. Below I present more precisely the different parts that could be improved:

We thank the referee for their detailed recommendations, which we incorporated into our revised manuscript. We included in our revisions that we believe the main source of disturbance resulting in removal of vascular plants in these wet tundra ecosystems to be from lemming herbivory. There could be other sources of herbivory (such as caribou), but they 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 (lines 184-187). We measured a wide range of environmental variables in both control and experimental plots, as we described in lines 264-265, which showed no difference. Moreover, we described the vegetation community in the Materials and Methods section (lines 89-90), and added the vegetation types (mosses, lichens, graminoids, and wet sedges) into the sampling plan and experimental design subsection to emphasize the vegetation in our plots (lines 148-149). When designing our experiment (lines 144-146), we took into consideration the preferential diet of lemmings in summer (lines 110, 368-371). In the Discussion section, we mentioned that we used motion-sensor camera footage to observe that lemming foraging within the plots was representative of their vegetation preferences, and that those were the types of vegetation removed by the lemmings (lines 371-372). We also noted in the Materials and Methods and Discussion sections (lines 150-151, 372-373) that an in-depth analysis of the vegetation types found in our plots was completed in a previous study by our team (Davidson et al., 2016).

L10 and L25: This is a repetition and I propose to remove the one of the abstract

We removed this statistic from the Abstract section of the revised manuscript.

L182: GPP is the annual flux, while only three instantaneous measurements were recorded. It would be more accurate to use a name that better describes the variable.

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 through the photosynthetic reduction of CO_2 into organic compounds" (Gough, 2011) during the time of measurements, rather than as an annual measurement. We clarified this when introducing GPP in the Materials and Methods section (lines 209-212).

L208ff: Can you give details on the distribution of data and the one used in the regression?

We included this information on the data distribution in the Materials and Methods section of the revised manuscript (lines 239-247). We tested for normality using a Shapiro-Wilk normality test. The 2018 data were normally distributed (NEE $P = 0.489$, NDVI $P = 0.816$), except the CH_4 data ($P < 0.001$), which were right-skewed, so we log-transformed the CH_4 data to help normalize them ($P = 0.284$). After this transformation, we used linear mixed-effects models to test for the significance between the different treatments. For the 2019 data, we used linear mixed-effects models (like we did in 2018) and non-parametric Kruskal–Wallis tests because we could not make all the data normal using the same transformation method (log transformation, square root transformation) for every round during the season. Results of the Kruskal–Wallis tests were consistent with those of the linear mixed-effects models (see Results section; lines 282-289, 317-321). We also tested for equal variance using an F-test and found there was no significant difference between the variances (treatments) in 2018 (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 $P = 0.346$, NDVI $P = 0.951$). We plotted the models to examine the residuals of the data and found them to not appear heteroscedastic.

Figure 2 should be placed in the appendix or a more concise presentation should be drawn.

We moved this figure (now Fig. A1) to the Appendix A section in the revised manuscript.

L239: It would be important to give the atmospheric concentration of CH4.

We included the global mean atmospheric concentrations of both CO_2 and CH_4 when mentioning greenhouse gas concentrations in the Materials and Methods section (lines 190-191).

Figure 3 shows primary productivity with negative values, which is totally comprehensive. However, figure 5 shows the same variable with positive value, which is both not comprehensive and standardised with Fig. 3.

We more clearly explained the signs of the flux values in the captions of the figures in the revised manuscript. We mentioned that figure 3 (now Fig. 2) shows the net ecosystem exchange of 2018 and 2019, with negative values indicating the removal of CO_2 from the atmosphere by vegetation through photosynthesis, and positive values indicating the carbon loss into the atmosphere (lines 291-293). We also mentioned that figure 5 (now Fig. 4) shows the ecosystem respiration (4a) and gross primary production (4b), but in this case the positive sign is indicating a positive respiration (carbon loss into the atmosphere) and a positive carbon uptake by vegetation through photosynthesis (lines 301-302). We included that the signs of ER and GPP are always positive, but if ER is more than GPP, then the ecosystem is a carbon source into the atmosphere (with a positive sign of NEE) (lines 302-303). In the Materials and Methods section, we noted our usage of the equation GPP = NEE – ER and the sign convention suggested by Chapin et al. (2006) (lines 208-209).

L324ff: This paragraph seems to belong to introduction or material and method but not to the discussion.

We moved most of this paragraph to the Materials and Methods section, where the information is more relevant (lines 119-125). We saved part of the paragraph in the Discussion section for suggested areas of future research (lines 400-402).

I read your paper with great interest and I belief it is relevant to arctic ecology readership, providing the consideration of the issues presented here, especially the inclusion of vegetation species and traits. The long-term impact will be very much interesting and I encourage the authors to continue this much valuable and important work.

We thank the referee for their useful suggestions and hope they find our revised manuscript appropriate for the Biogeosciences audience.