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Herbivore absence can shift dry heath tundra from carbon source to sink during peak growing season

Elizabeth Min[1], **Megan E Wilcots**[2,3], **Shahid Naeem**[2], **Laura Gough**[4], **Jennie R McLaren**[5], **Rebecca J Rowe**[6], **Edward B Rastetter**[7], **Natalie T Boelman**[8] and **Kevin L Griffin**[1,2,8]

[1] Department of Earth and Environmental Science, Columbia University, New York City, NY, United States of America
[2] Department of Ecology, Evolution and Environmental Biology, Columbia University, New York City, NY, United States of America
[3] Department of Ecology, Evolution, and Behavior, University of Minnesota, Saint Paul, MN, United States of America
[4] Department of Biological Sciences, Towson University, Towson, MD, United States of America
[5] Department of Biological Sciences, The University of Texas at El Paso, El Paso, TX, United States of America
[6] Department of Natural Resources and the Environment, University of New Hampshire, Durham, NH, United States of America
[7] The Ecosystems Center, Marine Biological Laboratory, Woods Hole, MA, United States of America
[8] Lamont-Doherty Earth Observatory, Columbia University, Palisades, NY, United States of America

E-mail: ekm2130@columbia.edu

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Abstract

In arctic tundra, large and small mammalian herbivores have substantial impacts on the vegetation community and consequently can affect the magnitude of carbon cycling. However, herbivores are often absent from modern carbon cycle models, partly because relatively few field studies focus on herbivore impacts on carbon cycling. Our objectives were to quantify the impact of 21 years of large herbivore and large and small herbivore exclusion on carbon cycling during peak growing season in a dry heath tundra community. When herbivores were excluded, we observed a significantly greater leaf area index as well as greater vascular plant abundance. While we did not observe significant differences in deciduous dwarf shrub abundance across treatments, evergreen dwarf shrub abundance was greater where large and small herbivores were excluded. Both foliose and fruticose lichen abundance were higher in the large herbivore, but not the small and large herbivore exclosures. Net ecosystem exchange (NEE) likewise indicated the highest carbon uptake in the exclosure treatments and lowest uptake in the control (CT), suggesting that herbivory decreased the capacity of dry heath tundra to take up carbon. Moreover, our calculated NEE for average light and temperature conditions for July 2017, when our measurements were taken, indicated that the tundra was a carbon source in CT, but was a carbon sink in both exclosure treatments, indicating removal of grazing pressure can change the carbon balance of dry heath tundra. Collectively, these findings suggest that herbivore absence can lead to changes in plant community structure of dry heath tundra that in turn can increase its capacity to take up carbon.

1. Introduction

Historically a carbon sink [1], the arctic tundra is estimated to contain approximately a third of the world's soil carbon [2], the result of the long-term imbalance of plant productivity and decomposition rates [3]. This large carbon reservoir has drawn concern because it might be particularly vulnerable to climate change—as temperatures rise, the tundra could become a major carbon source if decomposition and respiration exceed carbon capture [4]. Therefore, to develop a predictive understanding of carbon cycling across scales, from local to global, it is crucial that the processes and feedbacks that drive the tundra carbon cycle are well understood. Modern carbon cycle models account for plant and microbe driven biogeochemical processes such as photosynthesis, and autotrophic and heterotrophic respiration [5–7]. Herbivores can also have strong impacts on carbon flux, particularly through their impacts on vegetation [8–10] but are usually not incorporated in these models. Here, we empirically assess the role of herbivory in Alaskan dry heath tundra and consider how modern carbon cycle models can include herbivory to improve their predictive capabilities.

Herbivores impact vegetation form and function as well as the plants' physical environment. Grazing by herbivores removes photosynthetic biomass, directly affecting photosynthetic capacity [8, 11]. Selective grazing can also change vegetation community composition and potentially alter community productivity [8, 11, 12]. Herbivores can also physically modify the environment through activities like trampling and burrowing, disturbing vegetation [13, 14] and affecting soil structure (e.g. soil compaction), which can affect ecosystem respiration rates [15]. Herbivores also redistribute nutrients though waste products, changing soil nutrient profiles [12, 16], as well as site biogeochemistry, which can also affect microbial respiration rates [9, 12, 17]. In arctic tundra, studies have also reported a variety of herbivore impacts depending on the tundra type and herbivore(s) in question. In shrub and graminoid tundra, exclusion of caribou and muskoxen over an 8 year period increased net carbon uptake by almost threefold [18]. In wet meadow, moist and mesic tundra, plots that were not subject to early season goose grubbing had a higher capacity to store carbon [19]. Long term lemming exclusion in seasonally flooded graminoid tundra and wet graminoid tundra caused the environment to shift from being a carbon sink to a carbon source to the atmosphere [20]. These varied responses emphasize the need for more studies on how arctic tundra carbon exchange is impacted in different tundra types and by different assemblages of herbivores to incorporate their effects in climate models.

Our experiment focused on the dry heath ecosystem because it is a major tundra ecotype, is likely to have ecotype-specific responses (because of the high dominance of lichen and low stature of the vascular plants) and is significantly understudied. Furthermore, high variability in carbon fluxes have been demonstrated among land cover types [21] highlighting the importance of studying carbon fluxes in less studied tundra types in order to develop a more accurate and complete understanding of the arctic carbon cycle. Our study focuses on two groups of mammalian herbivores common in dry heath tundra: large ungulates (e.g. caribou) and microtine rodents (i.e. voles and lemmings). In various tundra plant communities, both herbivore guilds have been shown to have profound influence on their abiotic and biotic environment, particularly in terms of vegetation cover type and abundance [22–24]. Long term caribou activity can cause major vegetation changes in tundra environments, shifting vegetation from moss and shrub dominated ecosystems to sedge dominated ecosystems [22]. Caribou trampling potentially causes substantial losses of lichen particularly if lichen mats are dry [25]. Peak years of lemming and vole populations have been associated with a 12%–24% decrease in plant biomass estimated using the normalized difference vegetation index (NDVI) derived from satellite imagery the following year [23]. As both herbivore types have demonstrably significant impacts on vegetation, they can potentially exert significant influence on the ecosystem's carbon flux.

We quantified the impact of long-term exclusion of large herbivores (EX_L) and the exclusion of large and small herbivores (EX_{L+S}), on leaf area index (LAI), vegetation abundance, and carbon dioxide (CO_2) exchange in a dry heath tundra community located on the North Slope of the Brooks Range near Toolik Lake, AK. By removing grazing pressure and trampling by herbivores, we expected to find an increase in overall vegetation abundance in both exclusion treatments. We predicted higher lichen abundance with the exclusion of caribou (in both EX_L and EX_{L+S} treatments), which are major consumers of lichen. Higher vegetation abundance and LAI would suggest higher light absorption by plants and increased photosynthesis. Consequently, we expected to find higher gross primary productivity (GPP) and peak season NEE with herbivore exclusion.

2. Methods

2.1. Study site and experiment setup

We conducted measurements at the Arctic Long Term Ecological Research (LTER) site at Toolik Lake, Alaska (68.2° N, 149.6° W, 760 m a.s.l.). Mean annual rainfall is 256.7 mm [26]. The plant community is largely comprised of dwarf deciduous and evergreen shrubs and lichen. Both large mammal herbivores, specifically caribou (*Rangifer tarandus*), and small mammal herbivores, mostly singing voles (*Microtus miurus*) and collared lemmings (*Dicrostonyx groenlandicus*), have been observed in the area [27, 28]. Toolik lies within the range of the central arctic caribou herd [29].

Three replicate blocks of multiple 5 m by 20 m plots were established. In 1996 an herbivory experiment was established on a previously undisturbed plot within each block. Within each block, one plot had a 5 × 10 m unfenced portion (CT), and a fenced portion (5 × 10 m). The fenced area was surrounded by a large-mesh fence (15.2 × 15.2 cm mesh) to exclude caribou. Within that fence, a smaller-mesh fence (1.3 × 1.3 cm mesh) was constructed that was 5 × 5 m in size to further exclude small mammals (EX_{L+S}). Thus EX_L treatment was also 5 × 5 m in size [30]. All measurements took place between 14 July and 28 July 2017 during peak growing season at peak leaf out [31, 32]. We made all measurements at least 0.5 m away from the fences to avoid artifacts due to differences in snow accumulation immediately next to the fences. Within each treatment within a plot, we selected three subplots arbitrarily and measured each for vegetation abundance, LAI (via NDVI) and carbon flux.

2.2. LAI

NDVI, a measure of greenness obtained from spectral reflectance measurements, can be used as a proxy for tundra LAI [33]. We collected reflectance data from each of our subplots using a field portable spectrometer (Unispec, PP Systems, Haverhill, MA, USA) calibrated with a measurement on a 99% reflectance standard (Spectralon, Lab Sphere, North Sutton, NH, USA) before each measurement. Data were taken at shoulder height (approximately 1.4 m above the ground) for a sample area of 0.18 m^2 and five repeat measurements were taken and averaged for each subplot. We calculated NDVI from the red and near infrared reflectance values as shown in equation (1) [34]:

$$\mathrm{NDVI} = \frac{R_{800} - R_{660}}{R_{800} + R_{660}} \quad . \tag{1}$$

All data were taken within a week of species abundance data to accurately compare vegetation abundance and reflectance. NDVI was then used to calculate LAI ($m^2{}_{\mathrm{leaf}}\ m^{-2}{}_{\mathrm{ground}}$) for each subplot according to the model described by Shaver *et al* [33] and Street *et al* [35]:

$$\mathrm{LAI} = 0.0026\mathrm{e}^{8.0783 \times \mathrm{NDVI}} \quad . \tag{2}$$

2.3. Vegetation abundance

We used a circular point frame [36] with a 40 cm radius and a grid with marked points 10 cm apart (total of 62 points) to measure vegetation and species abundance. At each point, a long pin was dropped perpendicular to the ground, and all vegetation touching the pin was recorded by species name. If the pin did not touch any vegetation, bare ground was recorded. We separated plant species into growth forms, vascular and non-vascular. Vascular plants were further subdivided into deciduous shrubs, evergreen shrubs and graminoids. No mosses or forbs were present. We recorded lichens by growth form-crustose, foliose and fruticose—as two of these lichen types (foliose and fruticose) are particularly important to winter diets of caribou [37].

2.4. Carbon flux measurements

Carbon flux measurements were taken from 10 am to 4 pm over five discontinuous days. We measured CO_2 exchange using a Li-6400XT (IRGA, Li-Cor, Lincoln, NE, USA) infrared gas analyzer operating in closed mode and connected to a clear, polycarbonate, cylindrical chamber with a clear lid (height = 31 cm, diameter = 75.5 cm). We placed the chamber over each subplot to measure changes to CO_2 concentration, water vapor, photosynthetically active radiation (PAR), and air temperature over an interval of 40 s following the establishment of stable environmental conditions. To minimize air leakage between the chamber and the ground, we attached a thick plastic skirt tightly to the bottom of the chamber and weighed down by a heavy chain. Gas flux measurements for each subplot were made at five different light levels ranging from full sun to complete darkness. Light levels were changed by covering the chamber with shade cloths of different thicknesses (for intermediate light levels), a blackout cloth for dark measurements, and leaving the chamber exposed to full sun. We made a minimum of three measurements for each light level. Only measurements made under stable environmental variables for the duration of the measurement interval, particularly the light level, were used for further analysis. Measurements with obvious leaks (e.g. negative NEE during dark measurements) were discarded.

We calculated net ecosystem exchange (NEE) (μmol m^{-2} s^{-2}) for each subplot using equation (3) [33, 35]:

$$\mathrm{NEE} = \frac{\rho \times V \times \frac{\mathrm{d}C}{\mathrm{d}t}}{A} \quad . \tag{3}$$

Air density, ρ, is equal to $P/(RT)$ where P is pressure, R is the universal gas constant and T is temperature in K. V is the volume of the flux chamber, A is the surface area the chamber covers and $\mathrm{d}C/\mathrm{d}t$ is the change in CO_2 concentration adjusted for water vapor. A negative NEE value indicates a carbon flux from the atmosphere to the environment.

2.5. Modeled NEE

To compare NEE among treatments, we applied our data to the PLIRTLE model, which has previously been used to calculate CO_2 fluxes in the tundra [33, 38].

$$\mathrm{NEE} = \mathrm{RE} - \mathrm{GPP} \quad . \tag{4}$$

Parameters for modeled ecosystem respiration (RE) were estimated according to the model described by equation (6) in Shaver *et al* (2007) (equation (5)). Because measurement temperature varied among treatments, we applied all dark NEE measurements for a given treatment to equation (5) to estimate the respiration parameters R_0, R_{x}, and β.

$$\mathrm{RE} = (R_0 \times \mathrm{LAI} + R_{\mathrm{x}})\mathrm{e}^{\beta \times T} \tag{5}$$

where R_0 (μmol $\mathrm{m}^{-2}{}_{\mathrm{leaf}}$ s^{-1}), R_{x} (μmol $\mathrm{m}^{-2}{}_{\mathrm{ground}}$ s^{-1}), and β ($^\circ\mathrm{C}^{-1}$) are empirically derived parameters, and T is air temperature inside the chamber ($^\circ$C). R_0, R_{x} and β values were restricted to values $\geqslant 0$.

Light response curves were built by fitting the NEE values measured at different light levels for a given treatment to equation (6), which was adapted from the earlier NEE model [33]. At low LAI values, such as those observed in dry heath tundra, equation (7) from Shaver *et al* [33] converges with equation (6) (supp 1 (available online at stacks.iop.org/ERL/16/024027/mmedia)):

$$\mathrm{NEE} = \mathrm{RE} - \frac{P_{\mathrm{maxL}} \times \mathrm{LAI} \times E_0 \times \mathrm{PAR}}{P_{\mathrm{maxL}} + E_0 \times \mathrm{PAR}} \qquad (6)$$

where P_{maxL} is the theoretical light saturated photosynthesis rate (μmol m^{-2} leaf s^{-1}), E_0 is the light use efficiency or the initial slope of the light response curve (μmol CO_2 $\mu\mathrm{mol}^{-1}$ photons) and PAR is the photosynthetically active radiation at the top of the canopy (μmol photons m^{-2} ground s^{-1}). We modeled NEE for each treatment using values of RE that were calculated from equation (5) with the parameters estimated for each treatment. The model parameters (equations (5) and (6)), for each treatment were then used to model NEE (equation (4)) over the range of ambient light and temperatures recorded during our measurements. Note we substituted the dry heath parameters reported by Shaver *et al* [33] for the CT treatment because of the limited number of high temperature dark measurements from these plots. Model performance for each treatment was assessed using root-mean-square error (RMSE) and R^2. The fitted NEE and RE parameters for each treatment were then used to estimate NEE, GPP, and RE for corresponding subplots, using subplot specific LAI, for two sets of light and temperature conditions: 600 PAR and mean noontime temperature (14.46 °C) (NEE_{600}, GPP_{600} and RE_{600}, respectively), and average PAR (355.3 μmol photons m^{-2} ground s^{-1} PAR) and average temperature (12.56 °C) of July 2017 ($\mathrm{NEE}_{\mathrm{AVE}}$, $\mathrm{GPP}_{\mathrm{AVE}}$, and $\mathrm{RE}_{\mathrm{AVE}}$). The weather data for July 2017 were collected at Toolik Field Station [26].

2.6. Statistical analysis

We analyzed data using a (generalized) linear mixed-effects model with treatment as a fixed effect and block as a random effect. For both linear mixed effect models and generalized linear mixed effect models, *p*-values for treatment significance were obtained from the likelihood ratio test. For linear mixed effect models, *p*-values for differences among treatment were obtained via Satterthwaite's degrees of freedom method from the lmerTest R package [39]. For generalized linear mixed effects models, *p*-value differences among treatments were obtained using maximum likelihood estimation. In the case of overdispersed data, an observation level random factor was added. In the cases where this additional random effect resulted in a singular fit, the results from the original model were reported (vascular plant counts and bare ground counts). For cases where the model resulted in a singular fit, the effect of block was checked for significance using a likelihood ratio test, then the block random effect was excluded from the original model (we did not have any cases where the likelihood ratio test indicated a significant block effect). Normality and heteroscedasticity were checked using Shapiro–Wilk tests and Levene's tests respectively. A *p*-value of <0.05 was considered significant. All analyses were completed in R v 3.5.1 [40] using the packages lme4 [41], lmerTest [39], car [42], and lsmeans [43].

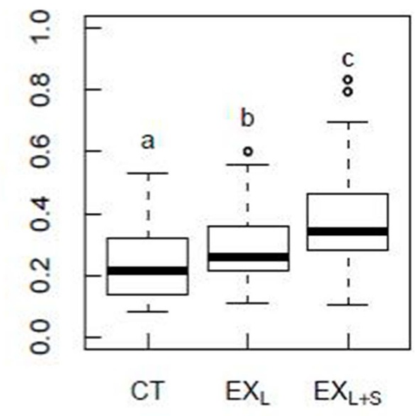

Figure 1. LAI per treatment. CT, $\mathrm{EX_L}$, and $\mathrm{EX_{L+S}}$ indicate treatments (control, large mammal exclusion and small and large mammal exclusion, respectively). Letters indicate significant differences between treatments. The dark bar, lower edge and upper edge of the box represent the median, first and third quartile respectively. Whisker edges represent the maximum and minimum values as defined as 1.5 times the interquartile range less than the first quartile or more than the third quartile. Open circles indicate outlier points that fall beyond the whiskers. $N = 27$.

3. Results

3.1. LAI and vegetation abundance

Herbivore exclusion significantly increased LAI and vegetation abundance. Mean LAI increased by 22.9% in $\mathrm{EX_L}$ ($M = 0.30 \pm 0.02$) and by 65.4% in $\mathrm{EX_{L+S}}$ ($M = 0.38 \pm 0.03$) compared to CT ($M = 0.24 \pm 0.02$) (figure 1). We also observed significantly greater vegetation abundance with herbivore exclusion. Lichens were significantly greater in $\mathrm{EX_L}$ treatment by almost 40% ($M = 91.2 \pm 5.52$), but not in $\mathrm{EX_{L+S}}$ ($M = 62.3 \pm 4.05$) compared to CT ($M = 65.5 \pm 4.21$) (figure 2(a)). Vascular plants abundance was significantly greater with herbivore exclusion compared to CT (61.0 ± 2.70), however there was no significant difference between $\mathrm{EX_L}$ ($M = 75.7 \pm 3.03$) and $\mathrm{EX_{L+S}}$ ($M = 83.2 \pm 3.19$) treatments (figure 2(b)). Pin hits recording bare ground were significantly lower in both $\mathrm{EX_L}$ ($M = 0.44 \pm 0.22$) and $\mathrm{EX_{L+S}}$ ($M = 1 \pm 0.34$) compared to CT ($M = 3 \pm 0.59$) (figure 2(c)).

We also observed shifts in plant growth form abundances in response to herbivore exclusion. Vascular plants were classified as dwarf deciduous shrubs (*Betula nana, Vaccinium uliginosum,* and *Arctostaphylos* alpina), dwarf evergreen shrubs (*Rhododendron tomentosum, Loiseleuria procumbens,*

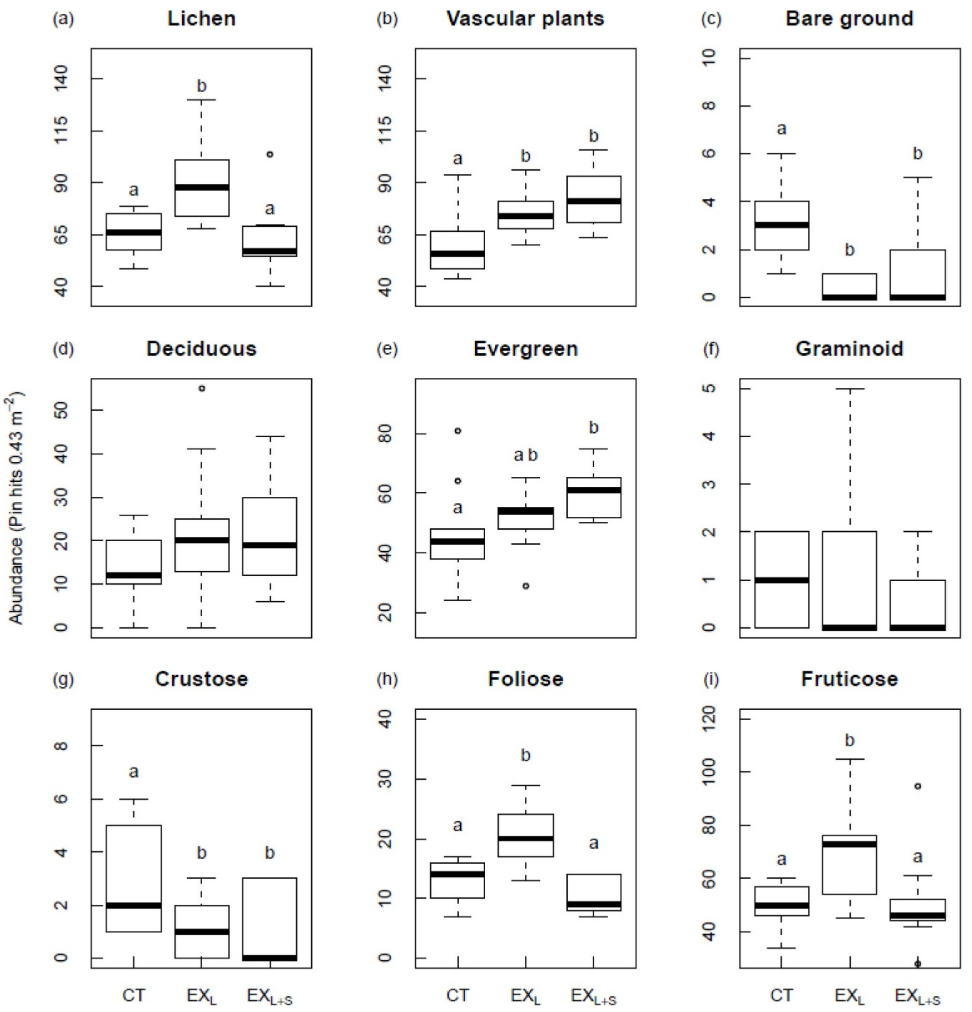

Figure 2. Graphs (a)–(c) show vascular plant, lichen and bare ground counts per treatment. Vascular plants abundances subdivided by growth forms per treatment are given in graphs (d)–(f). Lichen growth form abundances per treatment are given in (g)–(i). Letters indicate significant differences between treatments. Treatment, median, first and third quartiles, whiskers and outliers are defined as in figure 1.

Vaccinium vitis-idaea and *Empetrum nigrum*) and graminoids (*Carex* spp.). While we observed greater mean pin hits for dwarf deciduous shrubs by approximately 80% in both EX$_{\mathrm{L}}$ and EX$_{\mathrm{L+S}}$ treatments compared to CT, these differences were not significant because of the large variability and low replication (CT $M = 12.1 \pm 2.7$, EX$_{\mathrm{L}}$ $M = 21.7 \pm 4.6$, EX$_{\mathrm{L+S}}$ $M = 21.8 \pm 4.7$) (figure 2(d)). However, dwarf evergreen shrub abundance was significantly greater by 28% in EX$_{\mathrm{L+S}}$ compared to CT (CT $M = 46.0 \pm 3.6$, EX$_{\mathrm{L}}$ $M = 50.6 \pm 3.9$, EX$_{\mathrm{L+S}}$ $= 59.0 \pm 4.4$) (figure 2(e)). Graminoid species were rare and no differences among treatments were observed (CT $M = 1 \pm 0.3$, EX$_{\mathrm{L}}$ $M = 1.3 \pm 0.4$, EX$_{\mathrm{L+S}}$ $M = 0.6 \pm 0.2$) (figure 2(f)).

Lichen was subdivided into three functional types, crustose (*Lepraria neglecta*), foliose (*Masonhalea* richardsonii, Thamnolia tomentosum, and *Cladonia carneola*) and fruticose (*Cladonia* spp., *Alectoria ochroleuca,* and *Stereocaulon tomentosum*). Crustose lichen were much rarer than the other lichen functional types and had the highest abundance in CT (CT $M = 3.19 \pm 0.66$, EX$_{\mathrm{L}}$ $M = 1.1 \pm 0.36$, EX$_{\mathrm{L+S}}$ $M = 1.1 \pm 0.36$) (figure 2(g)).The abundance of both foliose and fruticose lichens were significantly higher in EX$_{\mathrm{L}}$ treatment than in CT or EX$_{\mathrm{L+S}}$. Mean foliose abundance was greater by approximately 61% in EX$_{\mathrm{L}}$ than in CT (CT $M = 12.9 \pm 1.20$, EX$_{\mathrm{L}}$ $M = 20.8 \pm 1.52$, EX$_{\mathrm{L+S}}$ $M = 10.2 \pm 1.07$) (figure 2(h)), while mean fruticose abundance was greater by more than 38% in EX$_{\mathrm{L}}$ than in CT (CT $M = 49.0 \pm 4.45$, EX$_{\mathrm{L}}$ $M = 68.0 \pm 5.94$, EX$_{\mathrm{L+S}}$ $M= 49.5 \pm 4.50$) (figure 2(i)).

3.2. Modeled carbon flux

Our modeled carbon flux results show a higher carbon uptake by the environment with herbivore exclusion (table 2). Herbivore exclusion significantly affected both NEE_{600} and NEE_{AVE} as both EX_L and EX_{L+S} had lower NEE and thus greater carbon uptake than CT. Treatment did not have a significant effect on either GPP_{600} or GPP_{AVE}, although mean values for both GPP fluxes were lower in the exclosures compared to CT. We observed a significant difference in both RE_{600} and RE_{AVE}, specifically that EX_L had lower respiration than both EX_{L+S} and CT (table 2). $P_{\mathrm{maxL}} \times$ LAI was highest in EX_{L+S} and lowest in CT (table 1 has parameter estimates only).

4. Discussion

Herbivores can have a major impact on vegetation through both selective (grazing) and nonselective (trampling) activities and consequently can impact carbon cycling [9, 12]. Our study shows that the long-term exclusion of large and small mammalian herbivores in dry heath tundra led to significantly greater LAI and abundance of some plant growth forms and lichens, and that these changes have the potential to change dry heath tundra from a carbon source to sink during the peak growing season. Our modeled carbon flux suggests that under average light and temperature conditions, dry heath tundra is a carbon source, which is in agreement with previously published literature [44]. Herbivore exclusion treatments significantly affected modeled carbon flux, as indicated by the more negative values of NEE_{600} and NEE_{AVE} for both EX_L and EX_{L+S} compared to CT (table 2). Our results underscore the key role herbivores play in regulating the carbon balance in dry heath tundra.

4.1. LAI and vegetation abundance

As anticipated, we observed significantly greater LAI and lower bare ground with herbivore exclusion, while vascular plant abundance was higher, indicating herbivore activity reduced plant abundance. Roy *et al* [45] reported that herbivore exclusion had no significant effect on relative abundance of individual plant growth forms in the same experimental plots. Point frame measurements incorporate structural complexity that can be missed with percent cover measurements, which may partially explain differences in our results. The difference in spatial scale of our measurements (Roy *et al* surveyed 8 m^2 $plot^{-1}$) in combination with the heterogeneity of dry heath tundra might have also contributed to the differences in our findings. Herbivore exclusion resulted in greater evergreen plant abundance, in agreement with a 10 year herbivore exclusion study in dry heath tundra [46]. We observed no difference in deciduous shrub abundance, which was unexpected, but might be explained by the unpalatability of resinous *B. nana* [47], which comprised a major portion of deciduous shrubs in our plots. Evergreen shrubs species have lower leaf level photosynthetic rates compared to deciduous shrubs, potentially resulting in a lower carbon uptake for a given light level and LAI if they become the more dominant species [48]. There was a larger mean difference in the abundance of deciduous plants between EX_L and CT than in EX_{L+S} to CT, with EX_L having a slightly greater abundance than EX_{L+S}. Evergreen plants on the other hand were more abundant in EX_{L+S} than in EX_L. The high abundance of evergreen plants in EX_{L+S} might therefore also partially explain this treatment's lower P_{maxL} despite its higher LAI relative to EX_L.

We observed that fruticose and foliose lichen abundances were higher in EX_L compared to CT; this result was expected as caribou are major consumers of these lichen [49] and is in agreement with other studies that report higher lichen biomass and cover with reduced caribou grazing pressure in heath tundra [22, 28, 50]. Crustose lichens, which only rarely occurred in our plots and unlike foliose and fruticose lichens are not preferentially foraged by caribou [51], had lower abundances in the exclosures than in CT. We did not observe a similarly greater lichen abundance in EX_{L+S}, which was surprising as caribou are also excluded in this treatment. Exclusion of both size classes of herbivores have been reported to both increase [28] and decrease [52] lichen cover, suggesting that decreased grazing by caribou is not the only determinant of lichen abundance. Lichen abundance also varies in caribou-only exclusion experiments depending on the ecosystem [50]. It is possible that small mammal herbivory in EX_L provided lichen with a competitive edge against vascular plants, because small mammals preferentially graze on vascular plants [27]; that competitive edge was not present in the EX_{L+S}. The exact composition of the vegetation community may also affect relative abundances of lichen and vascular plants as it has also been reported that lichen can both reduce and enhance vascular plant seedling establishment depending on the types of vegetation present [53].

4.2. Modeled carbon flux

Dry heath tundra has been reported to be a net carbon source [44, 54–56] even during the growing season [44]. Our results agree with these previous studies, as NEE_{ave} is positive, indicating carbon release, in CT during peak growing season. R^2 values for the NEE models ranged from 0.50 to 0.68 were lower than those reported for dry heath type tundra in Shaver *et al* [33], which may be partially explained by our lower sample size, but RMSE values, which ranged from 0.670 to 1.117, were in line with previous reported values. Herbivore absence in tundra ecosystems has been linked to increases in carbon uptake [18, 57, 58], with exceptions [20]. We anticipated that there would be higher carbon uptake in the

Table 1. Estimated parameters and statistics for the three treatments. Parameters were fit using a non-linear least squares. NEE values were calculated using Monte Carlo simulation. Italicized values indicate parameters taken from Shaver *et al* [33] or otherwise have no calculated standard error.

	P_{maxL} (μmol m^{-2} leaf s^{-1})	E_0 (μmol CO$_2$ μmol^{-1} photons)	R_0 (μmol m$^{-2}{}_{\text{leaf}}$ s^{-1})	R_x (μmol m$^{-2}{}_{\text{ground}}$ s^{-1})	β (°C^{-1})	R^2	RMSE	NEE$_{600}$ (μmol m^{-2} s^{-1})	NEE$_{\text{July}}$ (mol m^{-2} s^{-1})
CT	*15.07*	*0.03*	*1.62*	*0.69*	*0.03*	0.66	0.67	*−0.34*	1.22 ± 0.0
EX$_L$	19.21 ± 3.84	0.03 ± 0.01	0 ± 1.15	0.62 ± 0.63	0.05 ± 0.03	0.50	1.02	−0.97 ± 2.17	−0.45 ± 0.0
EX$_{L+S}$	15.67 ± 2.23	0.02 ± 0.00	0.55 ± 0.65	0.57 ± 0.36	0.05 ± 0.02	0.67	1.12	−0.71 ± 1.25	0.37 ± 0.0

Table 2. Mean NEE, GPP and RE values were calculated for each treatment using the appropriate model parameters and subplot specific LAI. Superscript letters indicate statistical significance.

	NEE$_{600}$ (μmol m^{-2} s^{-1})	GPP$_{600}$ (μmol m^{-2} s^{-1})	RE$_{600}$ (μmol m^{-2} s^{-1})	NEE$_{\text{AVE}}$ (μmol m^{-2} s^{-1})	GPP$_{\text{AVE}}$ (μmol m^{-2} s^{-1})	RE$_{\text{AVE}}$ (μmol m^{-2} s^{-1})
CT	-0.19 ± 0.20^{a}	−1.80 ± 0.25	1.61 ± 0.05^{a}	0.15 ± 0.14^{a}	−1.37 ± 0.18	1.53 ± 0.05^{a}
EX$_L$	-0.99 ± 0.20^{b}	−2.36 ± 0.25	1.37 ± 0.05^{b}	-0.48 ± 0.14^{b}	−1.71 ± 0.18	1.23 ± 0.05^{b}
EX$_{L+S}$	-0.78 ± 0.20^{b}	−2.40 ± 0.25	1.62 ± 0.05^{a}	-0.24 ± 0.14^{b}	−1.72 ± 0.18	1.47 ± 0.05^{a}

exclosures, concurrent with the increase in vascular plants we observed, which our modeled NEE$_{600}$ and NEE$_{\text{ave}}$ support. Furthermore, under average temperature and light conditions for July 2017, herbivore exclusion switched the dry heath tundra from carbon source to sink. On average, we observed lower GPP (greater photosynthetic carbon uptake) in the exclosures than in CT, but differences between treatments were not significant, contrary to LAI and vascular abundance, which were both higher in the exclosures. This is possibly because the higher LAI and vascular plant abundances were driven by less productive species (i.e. evergreen dwarf shrubs) [48]. However, the higher vascular abundance and LAI in the exclosures were reflected in NEE, which indicated significantly higher carbon uptake. Carbon uptake in drier tundra types (such as our study site) have been reported to be higher with herbivore exclusion [57] in agreement with our findings, though not always significantly [20]. Stronger responses appear to be related to shifts in vegetation composition, specifically increases in vascular plants [57], which likely have a more direct impact on carbon flux than lichen.

Higher lichen cover in EX$_L$ is a possible explanation for the lower RE observed in that treatment compared to EX$_{L+S}$ and CT as it can insulate soils and lower the temperature experienced by the microbial community underneath [59, 60]. There was no distinction between the exclusion of large and small herbivores and large herbivores only on growing season NEE despite the difference in diets between the two herbivore assemblages, similar to what was found in European heath tundra [57]. However, the unexpectedly lower RE in EX$_L$ indicates that these treatments may have subtle differences that are not apparent under weather conditions experienced in our study. Microbial activity in more insulated soils can have different temperature sensitivity than in less insulated soils [61], raising the possibility that the treatments might have differing responses to warming.

Studies suggest climate change will have negative impacts on many arctic animal species, including caribou [62, 63] and small mammals [64–67]. Many caribou herd populations have been declining, including those in northern Canada [68] though the Porcupine Herd in northeast Alaska has recently seen record highs [69]. Climate change can potentially have a dampening effect on boom and bust cycles of small mammals like voles and lemmings [70–72]. These future projections underscore the importance of understanding herbivore and carbon cycling interactions in the arctic tundra.

5. Conclusion

We have shown that herbivore absence correlates with increases in vegetation abundance and LAI in arctic dry heath tundra, which in turn is associated with increased carbon uptake. Moreover, our modeled NEE predicts herbivore absence has the potential to change dry heath tundra from a carbon source to sink during peak growing season. As climate change causes rapid changes to the arctic tundra ecosystems, incorporating the relationship between herbivores and ecosystem productivity in carbon cycling models is crucial to accurately predicting tundra carbon balance.

Data availability statement

The data that support the findings of this study are openly available at the following DOIs: https://doi.org/10.6073/pasta/3319313d52f5da852316567b2a5c0cad [73] and https://doi.org/10.6073/pasta/4b75019636e6f95760fcd49de4c99579 [74].

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Conflict of interest

The authors declare no conflict of interest.

ORCID iDs

Elizabeth Min https://orcid.org/0000-0001-7889-6693
Megan E Wilcots https://orcid.org/0000-0002-0383-4065
Shahid Naeem https://orcid.org/0000-0002-6569-2648
Laura Gough https://orcid.org/0000-0002-9312-7910
Jennie R McLaren https://orcid.org/0000-0003-2004-4783
Rebecca J Rowe https://orcid.org/0000-0002-0492-568X
Edward B Rastetter https://orcid.org/0000-0002-8620-5431
Natalie T Boelman https://orcid.org/0000-0003-3716-2372
Kevin L Griffin https://orcid.org/0000-0003-4124-3757

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