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Above- and belowground responses to long-term herbivore exclusion

Austin Roy ^a, Matthew Suchocki ^b, Laura Gough ^b, and Jennie R. McLaren ^a

^aDepartment of Biology, University of Texas at El Paso, El Paso, Texas, USA; ^bDepartment of Biological Sciences, Towson University, Towson, Maryland, USA

ABSTRACT

Herbivores can play an important role in determining arctic ecosystem function with effects determined in part by herbivore identity. We examined the impact of long-term (twenty-two years) small and large mammal herbivore exclusion in two arctic plant communities in northern Alaska: dry heath (DH) and moist acidic tundra (MAT). Our aims were to examine how herbivore exclusion influences (1) plant communities and (2) soil nutrient pools and microbial processes. Though herbivore absence increased moss and decreased evergreen shrub cover in MAT, there were few other significant effects on vegetation in either community. We also observed no influence of exclusion on most soil properties. However, in DH, phosphatase activity was greater in areas where small mammals alone were present, suggesting that they are altering phosphorus (P) availability, perhaps through herbivores' influence on the plant community and subsequently on competition for P with the microbial community. We conclude that herbivore impacts in the Arctic are dependent on both the plant community and herbivore identity (size). We show the importance of understanding the roles of herbivores in the Arctic and contribute to a growing number of herbivore studies in a biome likely to experience future changes in herbivore communities and ecosystem function.

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Introduction

Herbivores can have strong influences on ecosystem properties and processes, with their impact depending on the identity of the herbivores present. Communities of larger-bodied herbivores have been described as having larger impacts than communities of smaller-bodied herbivores (Cumming and Cumming 2003), although a number of studies have shown important effects of small herbivores on ecosystem properties (Howe and Brown 1999; Bakker et al. 2004; Johnson et al. 2011) and even effects of similar sized to those of large mammals on nitrogen (N) cycling (Clark et al. 2005). Additionally, herbivore identity as either a migrant or resident species may be an important control on the impacts of herbivores on ecosystems, especially in the Arctic. Migratory species such as caribou (*Rangifer tarandus*) may use areas at high densities for a short period of time; in contrast, resident species such as voles (*Microtus* spp.) and lemmings (*Lemmus* spp.) have relatively small home ranges and are present and active year-round. Some resident herbivore species may

also go through large population increases and crashes (Batzli et al. 1980; Ims, Yoccoz, and Killengreen 2011), with these species being more important at local scales during times of high abundance.

Arctic herbivores can influence ecosystems by altering plant communities and soil processes. Small and large arctic herbivores may influence vegetation abundance and cover (Johnson et al. 2011; Cahoon et al. 2012), plant biomass (Olofsson, Tommervik, and Callaghan 2012), light limitation (Borer et al. 2014), plant nutrient levels (Jefferies, Klein, and Shaver 1994; Tuomi et al. 2019), photosynthetic potential (Li et al. 2018), and productivity and plant senescence (Chew 1974; Batzli 1978; Mosbacher et al. 2018). In addition to influencing vegetation, herbivores can have both direct and indirect effects on soil processes. Arctic mammalian herbivores can redistribute soil (Tikhomirov 1959; McKendrick et al. 1980) and may influence carbon (C) and nutrient cycling by bringing material from lower soil layers to the soil surface (Ballova et al. 2019) where it can be accessed by microbes and plants. Herbivores can also influence soil

properties and nutrient cycling by producing feces and urine (Clark et al. 2005), influencing the composition of the litter pool (Wardle, Bonner, and Barker 2002), altering soil temperatures (van der Wal, van Lieshout, and Loonen 2001; Borer et al. 2014), and affecting soil pore space and soil moisture (van Klink et al. 2015). These interactions between herbivores and arctic ecosystem functions have the potential to influence this ecosystem over long time periods.

Long-term herbivore exclusions have provided insights into the chronic impact of herbivores on arctic ecosystems. For example, in one of the longest running exclusion experiments on the north coast of Alaska, data showed higher graminoid abundance and lower lichen abundance in control sites compared to herbivore exclusion sites after fifty years of lemming exclusion (Johnson et al. 2011), implying that there may be a positive relationship between herbivore activity and plant biomass. Though most research examining arctic herbivores has observed decreases in plant biomass due to herbivory (Moen and Oksanen 1998; Olofsson, Moen, and Oksanen 2002; Post and Pedersen 2008; Olofsson et al. 2009), other studies have shown increases (Johnson et al. 2011) or no difference (Olofsson, Moen, and Oksanen 2002) in plant biomass, suggesting that the effects of herbivores may vary by vegetation community. Differences in effects of herbivory may in part be due to differences in vegetation communities (Moen and Oksanen 1998) or the length of time the experiment has been running and possible transient effects of herbivory (Tilman 1988; Mallen-Cooper, Nakagawa, and Eldridge 2019). Long-term exclusions in the Arctic have also shown a relationship between herbivores and landscape level ecosystem functions such as albedo, methane (CH_4) flux, ecosystem respiration, net ecosystem exchange, and C storage (Cahoon et al. 2012; Vaisanen et al. 2014; Lara et al. 2016; Ylanne and Stark 2019). These exclusion experiments have been informative about herbivore–ecosystem interactions, but most experiments excluded either all herbivores or a specific size class of herbivores and did not examine the potential differential impacts between herbivore guilds (e.g., ungulates vs. rodents; although see Pastor and Naiman 1992; Grellmann 2002; Olofsson et al. 2009).

Herbivore exclusions constructed in the 1990s at the Arctic Long-Term Ecological Research (ARC-LTER) site near Toolik Lake, Alaska, provide an opportunity to examine the long-term impacts of herbivores and begin to understand how different herbivore guilds influence ecosystem structure. These exclusions have increased the understanding of the interaction between herbivores and vegetation communities (Gough, Ramsey, and Johnson 2007; Gough et al. 2008) and soil food webs (Gough et al.

2012). Though these exclusions were monitored for the past twenty years, the impact of herbivore exclusion on soil biogeochemical and physical processes remains unexamined. Furthermore, most studies have focused on the influence of herbivory on arctic vegetation and ecosystem-level processes, and fewer studies have assessed the long-term impacts of arctic herbivores on soil nutrient pools and microbial processes (although see Stark and Grellmann 2002; Olofsson, Stark, and Oksanen 2004; Sitters et al. 2017, 2019; Stark et al. 2019). This has led to the need to have a better understanding of the role of herbivores in systems with slow nutrient cycling. Our goal was to examine how the vegetation community and soil nutrient pools respond to long-term reduced herbivore activity in two arctic plant communities. The specific questions we aimed to answer were as follows:

- (1) What are the long-term impacts of reduced mammal activity on vegetation community structure and soil nutrient pools in two arctic plant communities?
- (2) How does the guild of mammalian herbivores (rodent vs. caribou) affect vegetation community and soil processes?

Materials and methods

Study site

We conducted this study in long-term herbivore exclusions located in moist acidic tundra (MAT) and dry heath (DH) tundra at the ARC-LTER site near Toolik Lake, Alaska, during the summer of 2017. The ARC-LTER is located north of the Brooks Range along the Dalton Highway (68° 37'40" N, 149°35'41" W). The MAT experimental site is located along the southern side of Toolik Lake at an elevation of 755 m, and the DH site is located along the northeastern side of the lake at an elevation of 720 m. Vegetation at the MAT site is equally represented by evergreen shrubs (*Rhododendron palustre*, *Vaccinium vitis-idaea*), deciduous shrubs (*Betula nana*, *Rubus chamaemorus*), and graminoids (*Eriophorum vaginatum*, *Carex bigelowii*) with abundant *Sphagnum* mosses (Gough, Ramsey, and Johnson 2007; Gough et al. 2012; McLaren, Buckeridge et al. 2017), while the DH site is dominated by evergreen shrubs (*Loiseleuria procumbens*, *Rhododendron palustre*, *Empetrum nigrum*, *V. vitis-idaea*) and lichens (Gough, Wookey, and Shaver 2002; Gough et al. 2012). For a complete list of plant species in both plant communities, please see our online data (data accessibility section). Both sites are underlain by continuous permafrost (Shaver et al. 2014). At Toolik Field Station (<1 km from either

experimental site), air temperatures range from -57.6 to 28.2°C (mean annual air temperature = -6.8), soil surface temperatures range from -25.7 to 33.0°C (mean annual soil temperature = -0.6), and yearly mean precipitation is 256.7 mm (Environmental Data Center Team 2017). Local mammalian dominant resident herbivores include singing voles (*Microtus miurus*) and tundra voles (*M. oeconomus*), with additional herbivores including collared lemmings (*Dicrostonyx groenlandicus*), red-backed voles (*Clethrionomys rutilus*), arctic ground squirrels (*Spermophilus parryii*), and migratory caribou (Batzli and Henttonen 1990; Gough et al. 2008). Plant species important for local small mammal herbivores include tussock cotton grass (*Eriophorum vaginatum*) for tundra voles and willows (*Salix* spp.) for singing voles (Batzli and Lesieutre 1991). Lichens, shrubs, and tussock cotton grass are important local forage species for caribou (Walsh et al. 1997; Walker et al. 2001; Joly, Jandt, and Klein 2009).

Experimental herbivore exclosures were established within each vegetation community in 1996 (Figure 1) within an existing experimental layout consisting of three (DH) or four (MAT) blocks of 5×20 m plots separated by 2-m walkways. At each block there is a fencing plot (5×20 m each), with a series of 5×5 m fences and control sites. Each block consists of a large herbivore exclosure (LF, 15.2×15.2 cm mesh), a large and small herbivore exclosure (SF, $1.3 \text{ cm} \times 1.3 \text{ cm}$ mesh), and a control (CT, no fencing) plot (Gough, Ramsey, and Johnson 2007). Each exclosure is approximately 2 m tall to prevent herbivores from feeding over the exclosures and has approximately 10 cm of the

exclosures buried into the soil to prevent small mammals from burrowing under the exclosures. Although all three treatments are present at both sites, the LF plots in the MAT were not sampled for this study.

Vegetation community

In late July 2017, we assessed the vegetation community within each experimental plot at the DH and MAT sites. We used 1×1 m quadrats to quantify the percentage cover of vascular and nonvascular plants, bare ground, and plant litter in eight contiguous replicates within each plot. Vascular plants were identified to species level and mosses and lichens were grouped across species. For analysis we determined proportional cover by summing the percentage cover of all plants and then calculating the relative abundance of each group to standardize across plots. Most analyses were conducted on plant growth forms (graminoids, evergreen shrubs, deciduous shrubs, forbs, lichens, mosses) rather than individual species.

Soil analysis

We collected soil samples from each treatment in the DH on 22 July 2017 and MAT on 24 July 2017. For the DH, we collected three randomly located samples per plot; using a serrated bread knife we collected 10×10 cm columns of the organic horizon to a depth of 5 cm. For the DH, the mineral layer was shallow (~ 5 cm depth), so we only sampled the upper organic layer of soil (top 5 cm of the organic layer). Additionally, because the mineral layer had numerous rocks and would thus require large volumes of soil sampled for analysis, in this community we did not sample this layer in order to minimize destructive impacts in these long-term exclosures. In the MAT, three 10×10 cm columns of soils were cut from each plot to a depth of approximately 30 cm or to the depth of the active layer (i.e., frozen soil was not sampled), whichever was less. We separated each column of MAT soil into the upper organic layer (top 5 cm, as above), the lower organic layer (the remaining depth of the organic column), and 5 cm of the mineral layer (when accessible) in the field. We separated the top 5 cm from the rest of the organic layer to enable comparison between the two ecosystem types and also to follow sampling protocols from other previously published studies at these sites (Mack et al. 2004; McLaren and Buckeridge 2019).

For each soil column and depth, we dried a subsample of each core (approximately 5 cm^3) at 50°C for 48 hours to assess bulk density and gravimetric water content. When volume could not be accurately assessed, only gravimetric water content

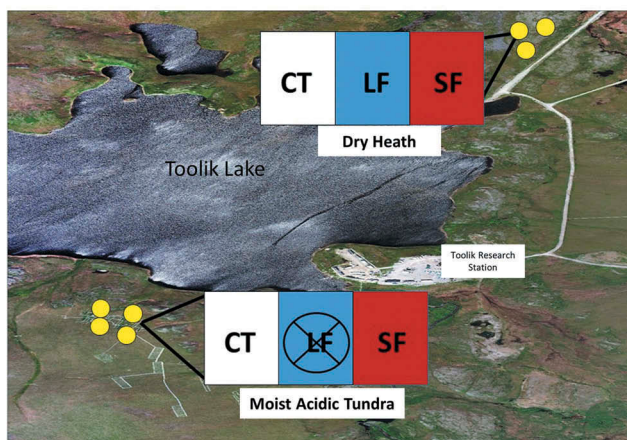


Figure 1. Overview of study area located in two types of arctic tundra near Toolik Lake, Alaska. Yellow dots represent locations of experimental herbivore exclosures, with three fencing blocks in DH and four in MAT. Each block included a CT (no herbivores excluded), an SF (large and small herbivores excluded), and an LF (large herbivores only excluded). The fencing block designs are inlayed.

measurements were taken. Subsequently, we individually homogenized each soil sample by hand, removing all large roots (>1 mm diameter), partitioned samples for analysis within two days of collection, and then froze samples before shipping to the University of Texas at El Paso, where they were stored at -20°C until analysis.

We analyzed soil samples for total percentage C (% C) and total percentage N (%N), inorganic nutrients (NH_4^+ , NO_3^- , PO_4^{3-}); organic nutrients (extractable organic C [EOC], extractable total N [ETN], extractable organic P [EOP]); microbial biomass C, N, P; and extracellular enzyme activity using the following methods.

We dried, ground, and processed soil subsamples for percentage C and percentage N contents using a dry combustion C and N analyzer (ElementarPyroCube). To determine soil inorganic nutrients, we thawed and extracted frozen subsamples (5 g) in 25 ml of 0.5 M K_2SO_4 for 2 hours, filtered through glass filter paper, and analyzed extractant using colorimetric microplate assays (BioTek Synergy HT microplate reader, BioTek Instruments Inc., Winooski, Vermont). $\text{NH}_4^+\text{-N}$ (NH_4^+) was determined using a modified Berlethot assay (Rhine et al. 1998), $\text{NO}_3^-\text{-N}$ (NO_3^-) using a modified Griess assay (Doane and Horwath 2003), and $\text{PO}_4^{3-}\text{-P}$ (PO_4^{3-}) using a malachite green assay (D'Angelo, Crutchfield, and Vandiviere 2001).

EOC was determined colorimetrically after an Mn(III) reduction assay (Bartlett and Ross 1988). ETN and EOP were determined using a modified alkaline persulfate digestion using a 1:1 ratio of oxidizing reagent to sample and autoclaved for 40 minutes at 121°C . (Lajtha et al. 1999) followed by analysis for NO_3^- and PO_4^{3-} respectively as above. To determine microbial biomass C, N, and P, we conducted the above assays on samples using a direct chloroform addition modification of the fumigation–extraction method (Brookes et al. 1985; Voroney, Brooks, and Beyaert 2006), where 5 g of thawed soil was incubated for 24 hours with 2 ml of ethanol-free chloroform, followed by extraction in 25 ml of 0.5 M K_2SO_4 . We calculated microbial biomass for C, N, and P (MBC, MBN, and MBP) by subtracting ETN, EOP, or EOC respectively of nonfumigated samples from that of fumigated samples. No correction factor was applied for incomplete CHCl_3 release or sorption of P because these values are not known for K_2SO_4 extraction for these two ecosystems.

Extracellular enzyme (exoenzyme) activity was assessed for ten exoenzymes involved in the microbial acquisition of C, N, and P: C-acquiring enzymes (β -glucosidase, β -cellobiosidase, β -xylosidase, α -glucosidase), N-acquiring

enzymes (*N*-acetyl-glucosaminidase, leucine amino peptidase) and P-acquiring enzymes (phosphatase, phosphodiesterase), as well as the oxidative enzymes phenol oxidase and peroxidase. One gram of soil was blended with a sodium acetate buffer to reflect natural soil conditions ($\text{pH} = 5$) and pipetted onto ninety-six-well plates with eight replicates per soil. Substrate tagged with fluorescing 4-methylumbelliferone (MUB) or 7-amido-4-methyl coumarin (MC; leucine amino peptidase only) was added to soil slurries. Samples were incubated at 20°C and enzyme activity (fluorescence) measured every 30 minutes for 3.5 hours following methods adapted from Saiya-Cork, Sinsabaugh, and Zak (2002) and McLaren, Buckeridge, et al. (2017). For each substrate, we measured the background fluorescence of soils and substrate and the quenching of MUB or MC by soils and used standard curves of MUB or MC to calculate the rate of substrate hydrolyzed. Fluorescence was measured at 365 nm excitation and 450 nm emission using a BioTek Synergy HT microplate reader (BioTek Instruments Inc.). Oxidative enzyme analysis was performed using an L-3,4-dihydroxyphenylalanine (L-DOPA) substrate for phenol oxidase and peroxidase. Color absorbance was measured at 460 nm using a reader after 24 hours of incubation.

Statistical methods

We performed statistical analyses with the program R (R Core Team 2018) with a cutoff of $p < .05$ for inferring statistical significance. In all analyses, sites were analyzed separately. In DH, there were three treatment blocks with three types of fencing treatments (CT, LF, SF), whereas in MAT there were four blocks and two fencing treatments (CT, SF). A block factor was included to reflect the field experimental design.

To assess changes in plant communities, we used the package *vegan* (Oksanen et al. 2019) to calculate Shannon diversity indices for each treatment at each site; Pielou's evenness was then calculated from the diversity values. Differences in diversity, evenness, and species richness between treatments in each vegetation community were examined using analysis of variance (ANOVA) or *t*-tests as appropriate. To determine whether there was an effect of exclosures on percentage cover, we used a blocked multivariate analysis of variance (MANOVA) with Pillai's trace test statistic and an experimental block as our blocking factor for each site. In the MANOVA, we used percentage cover of each plant growth form (graminoid, evergreen shrub, deciduous shrub, forb, lichen, moss, bare ground) as the dependent variable and exclosure treatment (CT, SF, LF) as the independent variable.

Differences in soil variables between treatments and soil depth were determined using ANOVA or *t*-tests as

appropriate, with nutrient concentrations, microbial biomass, and enzyme activity as response variables and enclosure type and soil depth as independent variables. When data could not be normalized, Kruskal-Wallis and Wilcoxon tests were used. For soil response variables, vegetation communities were analyzed separately, with soil depth only analyzed in MAT and guild identity (SF and LF treatments) only analyzed in DH.

Results

Vegetation

In DH tundra, we observed changes in the vegetation structure due to herbivory presence and the identity of the herbivore present in the system. Shannon diversity indices varied between the fencing treatments ($F_{2,6} = 5.19$, $p = .05$). Tukey's post hoc tests showed that diversity in the large herbivore only enclosure (LF) trended lower than controls (CT; $p = .08$) and all herbivore enclosures (SF; $p = .07$), though there was no difference in diversity between SF and CT ($p > .10$; Table 1). Similar to diversity, evenness values varied among treatments ($F_{2,6} = 9.98$, $p = .01$), with LF again being lower than CT ($p = .02$) and SF ($p = .02$; Table 1). There were no differences among treatments for species richness ($F_{2,6} = 2.68$, $p = .15$; Table 1). Although the mean abundance of some plant groups appeared to differ across fencing treatments, particularly lichens, which had lower abundance in CT than SF and LF (Figure 2), the MANOVA found no significant effect

of fencing on the plant community overall ($F_{2,6} = 0.97$, $p = .54$) or for any individual growth forms ($p > .05$).

In the MAT, in contrast with DH, we found no difference in Shannon diversity between the SF treatment and the CT ($t_{4,86} = 1.28$, $p = .18$). Furthermore, we found no differences in evenness ($t_{3,95} = -0.24$, $p = .82$) or richness ($t_{5,46} = 1.70$, $p = .15$) between treatments (Table 1). Again, we found no significant effect of fencing on plant community composition overall ($F_{1,6} = 0.97$, $p = .28$; Figure 2). However, when analyzing each growth form independently, we found that herbivore exclusion significantly increased moss cover ($F_{2,6} = 13.00$, $p = .01$) and reduced evergreen shrub cover ($F_{1,6} = 10.00$, $p = .01$). There was also a trend toward greater graminoid cover inside the SF treatment ($F_{1,6} = 2.70$, $p = .15$).

Soil nutrient pools

Generally, there were significant differences in soil variables between sites, with MAT having higher CNP pool concentrations and enzyme activities than DH (Supplemental Table 1). There were no significant responses to long-term herbivore exclusion for percentage C and N, inorganic N and P pools, extractable CNP pools, or microbial biomass CNP pools in either vegetation community (Table 2, Supplemental Table 2, Figure 3, and Supplemental Figures 1–3). Small mammal activity did not affect soil exoenzyme activity in the MAT (Supplemental Table 3, Supplemental Figure 5). In the MAT, most soil variables differed by depth

Table 1. Mean and standard error for species diversity, species richness, and evenness of plant communities in 2017 from an herbivore enclosure experiment in two different tundra types: DH and MAT.

Site	Treatment	Shannon diversity	SE of diversity	Species richness	SE of richness	Evenness	SE of evenness
DH	CT	1.53	0.01	6.08	0.26	0.66	0.09
	LF	1.52	0.04	6.79	0.19	0.64	0.15
	SF	1.55	0.01	6.04	0.24	0.67	0.16
MAT	CT	1.57	0.01	9.31	0.26	0.58	0.06
	SF	1.42	0.01	9.31	0.18	0.52	0.03

Note. All values were calculated at 1 m².

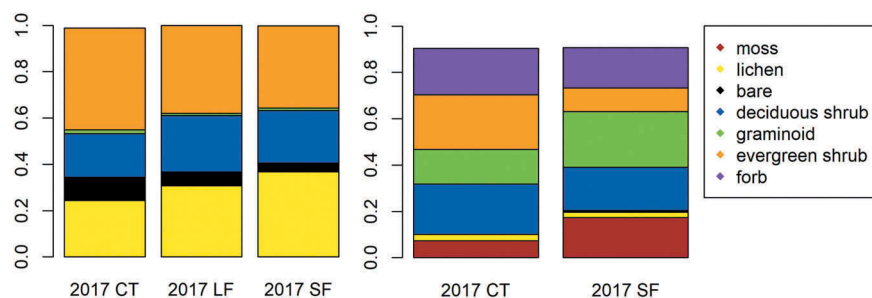


Figure 2. Relative abundance of vegetation growth forms from an herbivore enclosure experiment located in MAT ($n = 4$) and DH ($n = 3$) tundra at the ARC-LTER located at Toolik Lake, Alaska. Data were collected in July 2017.

Table 2. Impact of herbivores on soil variables after twenty years of exclusion. ANOVA and Kruskal-Wallis summary results from comparisons of soil variables between exclosures in DH and MAT.

	DH			MAT		
	Fence			Fence		
	Stat	<i>p</i>	df	Stat	<i>p</i>	df
% C	$F = 0.39$	.69	2,6	$W = 78$	.76	1
% N	$F = 0.36$	.71	2,6	$F = 0.68$	.42	1,6
C:N	$F = 0.20$	.82	2,6	$F = 0.25$	.62	1,6
NH ₄	$F = 0.16$	.86	2,6	$W = 75.5$	.86	1
NO ₃	$\chi^2 = 2.00$	.37	2	$W = 68$	.83	1
PO ₄	$\chi^2 = 0.80$	.67	2	$W = 85$	.47	1
EOC	$F = 0.53$	.61	2,6	$W = 89$	.35	1
ETN	$F = 0.36$	.71	2,6	$W = 69$	.89	1
EOP	$\chi^2 = 0.83$	.66	2	$W = 79$	.71	1
MBP	$\chi^2 = 0.62$	.73	2	$W = 64$	.30	1
MBN	$\chi^2 = 0.80$	.67	2	$W = 79$	.44	1
MBP	$\chi^2 = 0.36$	.84	2	$W = 66$	.75	1

($p < .01$; Supplementary Table 2, Supplemental Figures 6–7) but not by treatment ($p = .05$). In the DH, there were few effects of herbivore exclusion on exoenzyme activity (Supplemental Figure 4, Supplemental Table 3). We did observe that areas that were only accessed by small mammal herbivores (LF) had significantly higher phosphodiesterase activity ($F_{2,6} = 8.66$, $p = .02$) than areas that could be accessed by both large and small herbivores and herbivore-free exclosures (Figure 3).

Discussion

Overall, we found few effects of long-term reductions in herbivore activity on vegetation in two arctic plant communities. Although the effects were not large, herbivore presence did alter each plant community differently. In the MAT, mosses were more abundant and evergreen shrubs were less abundant in areas where herbivores were excluded compared to controls, similar to effects found after a shorter period of herbivore exclusion in these same plots (Gough, Ramsey, and Johnson 2007; Gough et al. 2012). Herbivore activity in MAT negatively affected graminoids; thus, when herbivores were removed, graminoid cover increased and evergreen shrubs may have experienced greater competition, resulting in a decline in evergreen relative abundance. Though Gough, Ramsey, and Johnson (2007) showed that herbivory became more important under fertilized conditions, our data show that even without fertilization, herbivory can play a role in regulating some forage species. The increase in mosses with reduced caribou and vole activity has also been seen in other studies (Rydgren et al. 2007) and is likely due to voles using mosses as winter forage (Batzli and Lesieutre 1991) and potentially disturbing the mosses through trampling (van der Wal, van Lieshout, and Loonen 2001) and creating runways. Such increases in moss cover may also negatively influence evergreen

shrub establishment and growth (Holmgren et al. 2015) and may additionally partially explain the reduced evergreen shrub cover we observed in the MAT. Even though we did not observe exclusion effects on soil properties in the MAT, changes in moss cover due to herbivory may influence system properties such as nutrient availability (Olofsson et al. 2009; Bueno et al. 2016) and soil temperatures (Gornall et al. 2011) in the future.

Our results from the DH sites show that the influence of herbivores on this plant community is different from that in the MAT, by decreasing plant diversity and evenness when caribou alone are excluded, and that interactions between types of herbivores may be important. Although there were no statistical differences in plant growth form abundance among treatments, likely due to low replication at the block level and therefore low statistical power, there was greater lichen cover in large mammal exclusion (LF) plots (37 ± 7 percent) compared to areas where all herbivores access (CT) plots (24 ± 3 percent) in the DH, which corresponds with increases in lichen cover with caribou exclusion found in other studies (Olofsson, Stark, and Oksanen 2004; Gough et al. 2008; Pajunen, Virtanen, and Roininen 2008). However, this observed increase was not present when small mammals were also excluded (SF plots, 30 ± 9 percent). Though this increase in lichen cover was not observed in a European heath community when herbivores were excluded (Grellmann 2002), it suggests that there may be an interaction between the activity of different herbivore guilds; lichen cover may increase due to the absence of caribou, but small mammal activity or foraging on vascular plants could also potentially alleviate competition pressure on lichens by reducing vascular plant abundance.

In addition to differing effects on the vegetation communities, we found that herbivore guilds may impact soils differently. In the DH site, we found higher phosphodiesterase activity in areas where large, but not small, mammals were excluded, compared to control sites (all herbivores present) and all herbivore exclusion. An increase in phosphatases suggests that microbes are experiencing P limitation, and the trend of increases in PO_4^{3-} in the large herbivore exclusion (LF) treatments (Supplemental Figure 2) further suggests that this increase in phosphatases may be increasing P availability in the soil. Thus, increases in phosphatases in the DH indicate that large mammals may be regulating P availability but only when small mammals are not present. In contrast to Sitters et al. (2019), which found that heavy reindeer grazing created more P-limited conditions, our results support the opposite trend—that reduced caribou activity creates

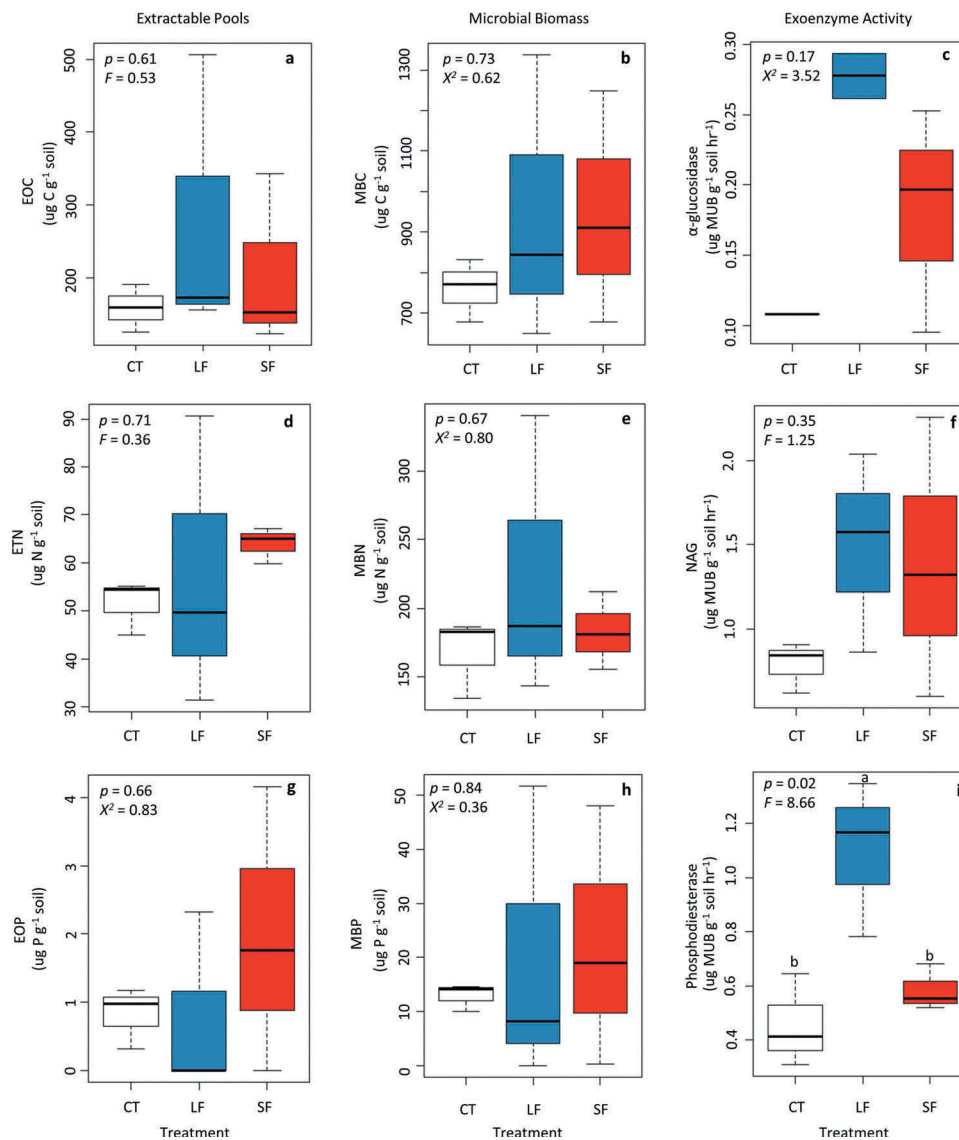


Figure 3. Box plots showing the impact of herbivores on (a), (d), (g) extractable organic nutrients, (b), (e), (h) microbial biomass, and (c), (f), (i) potential exoenzyme activity in soils collected in July 2017 from an herbivore exclosure experiment in DH ($n = 3$) tundra at the ARC-LTER located at Toolik, Alaska.

P-limited conditions. Our observed increase in lichens in the LF treatments may partially explain increased phosphatases. Because P can be limiting to lichens (Hurri, Makkonen, and Hyvärinen 2007) and lichens can produce their own phosphatases (Hogan et al. 2010), increases in lichen abundance may directly result in increases in phosphatase activity. Alternatively, changes in the vegetation community may alter competition for P in the microbial community and, in turn, influence phosphatase production.

Although the purpose of this article was to compare herbivore impacts between each plant community, and we thus focus on shallow soils, we did observe generally higher carbon and nutrient concentrations in the organic soils than mineral soils in the MAT (Supplemental Tables 2 and 3). The impacts of

herbivores (urine, feces, litter inputs) are likely concentrated in the upper portion of soil layers and then cycle between the organic layers. This is supported by the few differences we observed between the organic layers. Though the mineral layer differed from the organic layers, we found few responses in the mineral layer due to herbivore treatments, suggesting that the impacts of herbivores may be immediate and not persist over long time periods. Though we did not sample at depth in the DH, we expect that we would see similar deep soil responses to herbivores as in the MAT.

Our sampling is part of an ongoing effort examining how herbivores influence ecosystem dynamics in these long-term exclosures (Gough, Ramsey, and Johnson 2007; Gough et al. 2008, 2012). Our data show little change

from previous samplings, which also show relatively few changes over time (Gough and Johnson 2018), and provide valuable additional time points for this experiment and the examination of ecosystem functions in a changing arctic environment. Interestingly, in a study design similar to ours in another heath community but also including fertilization (Stark and Grellmann 2002), slower nutrient cycling under grazing after seven years of exclusion was reported. Their research found that excluding herbivores influenced MBC and microbial respiration, but MBN was only affected by exclusion plus fertilization (Stark and Grellmann 2002). The fact that we did not detect any changes in soil nutrient pools twenty-one years after treatment began (Supplemental Table 3) indicates that influences of herbivores may be transient. Many of the variables we examined (e.g., available nutrients) show strong variation seasonally (McLaren, Darrouzet-Nardi, et al. 2018) and between years (Edwards and Jefferies 2013), and with a single sampling it is possible that we missed transient effects that occurred during other parts of the growing season or during other years. Alternatively, studies have found that herbivore impacts may increase through time (Mallen-Cooper, Nakagawa, and Eldridge 2019) and, due to slow ecosystem processes in the Arctic, it may take greater than twenty years to see effects. Because the impacts of herbivores in the Arctic can persist for greater than 150 years (Egelkraut et al. 2018), their impacts are likely to change over time (Mallen-Cooper, Nakagawa, and Eldridge 2019), and more work is needed to track the legacy level effects of herbivory within arctic ecosystems.

The level and intensity of herbivore activity may also influence arctic ecosystem processes. Some studies have shown that heavy grazing can increase N cycling and primary productivity and moderate grazing may decrease these properties (Zamin and Grogan 2013), whereas others have shown the opposite (Pastor and Naiman 1992). Regardless, changes in herbivore density may have lasting effects on ecosystem functions and may be especially important with species with cyclic population densities such as voles. In the year of this study, and the years immediately preceding it, vole abundance was low (Maguire and Rowe 2017; Rowe and Steketee 2019, unpublished data), and vole densities inside the exclosures may have not differed greatly from that outside the exclosures. In addition to low densities of voles, the activities of these herbivores are particularly localized (e.g., latrine sites) and thus our randomized soil sampling may have missed sites where herbivore activities do affect soil nutrient cycling. Although we found few effects during a potential low phase of the local vole population cycle, the effect of voles on ecosystem functions during the high point in their population cycle has been documented in other

ecosystems (Olofsson, Tommervik, and Callaghan 2012), suggesting that the effects of voles in this ecosystem are density dependent. Potential suppression in arctic herbivore population cycles (Ims, Henden, and Killengreen 2008) may thus alter the role of herbivores in arctic systems in the future.

Here we described the influence of herbivores on vegetation and soil function in two arctic plant communities after twenty years of herbivore exclusion. We found that herbivory pressure altered moss cover and evergreen shrub abundance in the MAT and influenced P-acquiring enzyme activity in the DH. We provide evidence of differing impacts between different herbivore guilds for both vegetation and soil properties. Although other studies found stronger effects of herbivores under increased nutrient or warmed conditions, our data, collected under ambient conditions, may provide a baseline with which to examine the impacts of herbivores in a changing arctic environment. Future changes in arctic systems may alter herbivore populations and communities as well as their influences on ecosystem ecology. Though our replicate numbers were low, we believe that our results are representative of the potential impacts of herbivores in these two Alaskan arctic plant communities. However, the impacts of herbivores on these processes are likely to vary among the major regional vegetation types, and we recommend that further studies incorporate additional systems to better elucidate the impacts of herbivores in the Arctic as a whole. Future work should also examine how potential changes in herbivore population dynamics and species assemblages of herbivores may influence ecosystem functions.

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Data Accessibility

Data from this project are available on the Arctic Data Center. McLaren et al. (2019), Soil biogeochemical variables collected on the Arctic LTER experimental plots in moist acidic and dry heath tundra, Arctic LTER Toolik Field Station, Alaska, 2017 (<https://doi.10.6073/pasta/5a5cbb785bde48522bde7b87c65d3c13>). Gough (2019a), Relative percent cover of plant species for years 2012–2017 in the Arctic Long-Term Ecological Research (ARC-LTER) 1989 moist acidic tundra (MAT89) experimental plots, Toolik Field Station, Alaska. Environmental Data Initiative (<https://doi.10.6073/pasta/f31def760db3f8e6cfee5fee07cc693e>). Gough (2019b), Relative percent cover of plant species for years 2013 2014 2016 2017 in LTER dry heath tundra experimental plots established in 1989, Arctic LTER Toolik, Field Station Alaska. Environmental Data Initiative (<https://doi.10.6073/pasta/25d3f0db55e9df6f99fc3e9596433090>).

ORCID

Austin Roy  <http://orcid.org/0000-0002-2519-6455>
Matthew Suchocki  <http://orcid.org/0000-0002-8321-8640>
Laura Gough  <http://orcid.org/0000-0002-9312-7910>
Jennie R. McLaren  <http://orcid.org/0000-0003-2004-4783>

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