

Mammalian herbivory exacerbates plant community responses to long-term increased soil nutrients in two Alaskan tundra plant communities

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Abstract: The interaction between bottom-up and top-down forces in regulating plant communities is a long-standing topic of interest in ecology. Factorial field experiments examining these factors have been relatively few, but recent meta-analyses provide predictions that can be tested in a range of ecosystems. We tested the prediction that added nutrients would reduce species richness and evenness, while herbivore activity would offset those changes in two tundra plant communities after 11 years. In moist acidic tundra (MAT), herbivores reduced richness more in fertilized plots when mammals were present compared with fertilized plots without herbivores. In dry heath (DH), evenness was significantly reduced in fertilized plots only when herbivores were present, also providing evidence that herbivores enhanced community changes caused by greater nutrient availability. The difference in response between MAT and the meta-analysis predictions appears to be driven by *Betula nana*, the species that dramatically increased with added nutrients in MAT. Unlike in similar studies and in DH, *B. nana* is not as palatable as most of the species in the community and is generally avoided by herbivores. These results highlight how the effects of herbivory and nutrients differ across communities and can be affected by the traits of the species present.

Key words: herbivory, nutrients, tundra, species richness, species evenness.

Résumé : L'interaction entre les forces ascendantes (ressources) et descendantes (prédateurs) dans la régulation de communautés végétales est depuis longtemps un sujet d'intérêt en écologie. Les expériences factorielles sur le terrain examinant ces facteurs ont été relativement peu nombreuses, mais les méta-analyses récentes fournissent des prédictions qui peuvent être vérifiées au niveau de divers écosystèmes. Nous avons vérifié la prédiction selon laquelle des substances nutritives ajoutées réduiraient la richesse et la régularité des espèces tandis que les activités des herbivores pallieraient ces changements chez deux communautés végétales de toundra après onze ans. Dans la toundra acide humide (TAH), les herbivores ont davantage réduit la richesse dans les parcelles fertilisées lorsque les mammifères étaient présents en comparaison des parcelles fertilisées sans herbivores. Dans les landes sèches (LS), la régularité a été significativement réduite au niveau des parcelles fertilisées seulement lorsque les herbivores étaient présents, fournissant aussi la preuve que les herbivores ont amélioré les changements des communautés végétales en raison de plus grande disponibilité nutritive. La différence de la réponse entre la TAH et les prédictions des méta-analyses semble être déterminée par *Betula nana*, l'espèce qui a dramatiquement augmenté avec l'ajout de substances nutritives dans la TAH.

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Contrairement aux études semblables et dans les LS, un facteur était que *B. nana* n'est pas aussi agréable au goût que la plupart des espèces de la communauté végétale et est généralement évité par les herbivores. Ces résultats mettent en évidence la façon dont les effets de l'herbivorie (« herbivory ») et des substances nutritives diffèrent à travers les communautés végétales et peuvent être affectés par les caractéristiques des espèces présentes. [Traduit par la Rédaction]

Mots-clés : herbivorie (« herbivory »), substances nutritives, toundra, richesse spécifique, régularité des espèces.

Introduction

For several decades, ecologists have attempted to determine how bottom-up resource limitation of plant communities interacts with top-down limitation via herbivory (Turkington 2009). Meta-analyses of empirical manipulations of nutrient availability and herbivore pressure have focused on responses of community productivity and biomass (Gruner et al. 2008) and species diversity (Gough et al. 2000; Hillebrand et al. 2007). Results suggest that the direction and magnitude of change can be influenced by productivity of the ecosystem, type of herbivore, evenness of the plant community, and ecosystem type (i.e., terrestrial or aquatic) (e.g., Wardle et al. 2004; Stark et al. 2015).

Most field studies conducted to examine nutrient limitation do not simultaneously limit herbivore access to these plant communities (e.g., data included in Hillebrand et al. 2007), so interactions cannot be assessed. Given the current increase in nutrient loading across the globe (Rockström et al. 2009), predictions of ecosystem changes may be misleading because herbivore activity under different nutrient regimes is not well understood. Herbivores may respond to greater nutrients by increasing their rate of plant biomass removal (e.g., Borer et al. 2014b). They may also change their herbivory patterns and may target particular species, altering species composition and potentially removing plant species with important ecosystem functions (Huntly 1991; Schmitz 2008).

Understanding how community composition is regulated by nutrient limitation and herbivore pressure is essential for determining how the ecosystem responds to changes in these factors particularly in light of climate change. Hillebrand et al. (2007) approached this important question by analyzing species composition data from multiple experiments manipulating these variables singly and in combination. Predictions derived from that study for terrestrial ecosystems suggest that both richness and evenness should increase slightly in the presence of herbivores and significantly decrease when nutrients are added. In addition, their results suggest that herbivores should offset the declines in richness with fertilization (also see Borer et al. 2014a). However, as mentioned above, their data set included many studies that were single-factor manipulations, and thus conclusions regarding the interaction between nutrients and herbivory were limited. For example, only one factorial manipulation from a high-latitude ecosystem met the criteria for inclusion (Grellmann 2002).

Our goal was to determine if an unusually long-term (11 year) factorial nutrient addition and mammalian herbivory (hereafter herbivory) study in arctic Alaska met the predictions described above from Hillebrand et al. (2007). Although their conceptual model assumed that low productivity was associated with aquatic ecosystems, our study sites are on the very low end of the terrestrial (and wetland) productivity gradient (45–150 g m⁻² year⁻¹; Shaver et al. 2014). We report results from two arctic tundra plant communities, moist acidic tussock (MAT) tundra and dry heath (DH), that differ in productivity, biomass, and response to these manipulations (Chapin and Shaver 1996; Gough et al. 2007, 2012b). The DH community is comprised of dwarf evergreen shrubs and lichens under ambient nutrients but becomes dominated by *Hierochloe alpina*, a tussock-forming grass (hereafter *Hierochloe*),

when fertilized (Gough et al. 2002, 2012b). In contrast, the MAT community supports relatively equal abundance of tussock-forming sedges, dwarf deciduous and evergreen shrubs, and *Sphagnum* mosses. When fertilized, this community becomes dominated by *Betula nana*, a dwarf deciduous shrub (hereafter *Betula*), and *Rubus chamaemorus*, a perennial forb (Shaver et al. 2001; Gough et al. 2012b). Previously, we reported effects of these manipulations on individual plant growth of several common species (Gough et al. 2007) as well as productivity and biomass (Gough et al. 2012b). Here we test the following specific predictions for community structure based on Hillebrand et al.'s (2007) meta-analysis findings for terrestrial ecosystems.

1. Alleviating nutrient limitation decreases species richness and evenness; thus, we predicted both would be lower in fertilized plots relative to control plots.
2. The activities of herbivores slightly increase species richness and evenness relative to areas without herbivores, such that plots with herbivores present should have higher values than those inside exclosures.
3. Herbivores offset the negative effects of added nutrients on species richness and evenness. Specifically, we predicted that fertilized plots with herbivores should have higher richness and evenness values than fertilized plots without herbivores.

Materials and methods

Study sites

This research was conducted at the Arctic Long Term Ecological Research (LTER) site at Toolik Lake, Alaska (68.2°N, 149.6°W; 760 m asl). In 1996, a factorial design was implemented in both MAT and DH to determine how the presence or absence of mammals affected plant and soil responses to added nutrients (10 g m⁻² year⁻¹ as NH₄NO₃ and 5 g m⁻² year⁻¹ as P₂O₅ applied annually in granular form in early June following snowmelt). Earlier fertilization studies have demonstrated that these communities are colimited by N and P (Chapin et al. 1995; Gough et al. 2002). The plots themselves are part of a larger experimental setup established in 1989. At that time, separate blocks (rows) of 5 m × 20 m plots separated by 2 m walkways were established in homogeneous vegetation at both sites: four blocks in MAT and three blocks in DH. The plots studied here were maintained with no manipulation until 1996. At that time, within each block, one plot was randomly assigned N and P addition (+NP) and the other had no added nutrients (CT). Only three blocks from MAT were included in this analysis (LTER Blocks 2–4).

In 1996, half of each 5 m × 20 m plot (one CT and one +NP) in each block was left unfenced allowing mammals access to the vegetation, while the remaining 5 m × 10 m area was enclosed in a large-mesh fence excluding only caribou (15.2 cm × 15.2 cm openings, approximately 1.2 m in height; also see Gough et al. 2008). Within this larger caribou enclosure, a 5 m × 5 m area consisting of a smaller-mesh fence (1.3 cm × 1.3 cm openings, approximately 0.8 m in height) was built to exclude all mammals. This smaller-mesh fence was buried in the soil to at least 10 cm at construction to prevent small mammals from burrowing into the plots. For this study, we did not consider the effects of small and large mammals separately; all data for areas lacking herbivores (–H) were collected from areas with both small and large mammal exclusion. Each block therefore contained all four treatment combinations of herbivore exclusion and fertilization: CT, +NP, –H, and –H + NP. While there are herbivorous insects in these communities, their effect on leaf biomass appeared to be minimal (personal observation). Additionally, these plots may retain snow on the immediate northern edge of fences for 2–3 days longer in the season relative to unfenced areas (personal observation). To avoid confounding effects of this snow accumulation, all sampled plants were at least 0.5 m from the edge of the fence.

Mammalian herbivores

Several microtine rodent species are common in communities near the Arctic LTER (Batzli and Lesieutre 1995). In MAT, tundra voles (*Microtus oeconomus*) are commonly seen along with evidence of their presence (burrows in *Eriophorum* tussocks, hay piles, trails, and fecal deposits; Johnson 2008) and undergo periodic population outbreak years (Batzli and Lesieutre 1995). Singing voles (*Microtus miurus*) and collared lemmings (*Dicrostonyx rubricatus*) have been recorded in rocky areas very near DH (Batzli and Henttonen 1990; Johnson 2008). Batzli and Henttonen (1990) suggested that rodent densities near the LTER are generally limited by food availability, particularly during outbreak years; however, they may also be limited top-down by predators similar to lemmings in coastal tundra (e.g., Batzli et al. 1980; Berg et al. 2008).

While transient, caribou (*Rangifer tarandus*) are commonly sighted near the Arctic LTER and traverse the area across both communities studied here (personal observation). Although the LTER lies within the range of the Central Arctic Herd (Lenhart 2002), the herd's primary calving grounds are far to the north. Thus, caribou are not considered common foragers of plants in MAT. However, in DH, caribou feces can be seen following snowmelt, and DH may be an occasionally important winter grazing area for caribou because snow cover is often less there than in surrounding areas.

Data collection

Plant relative abundance

To estimate relative abundance, we conducted nondestructive sampling of the vegetation in all treatment combinations and replicates at both MAT and DH during peak plant growth in late July 1998, 2004, 2005, and 2006. In 1998, to establish an approximate baseline of pretreatment plant community structure, we established permanent randomly located sampling points in each 5 m × 10 m plot (5 m × 5 m inside the exclosures). At each point, eight adjacent 1 m × 1 m quadrats with 20 cm × 20 cm subquadrats marked to aid estimations were censused for relative cover of each vascular plant species as well as mosses, lichens, and other ground cover (e.g., bare ground). Vascular plant species were identified according to Hultén (1968). We regularly standardized cover value estimates among observers to minimize bias. Cover was then summed for each quadrat, and cover estimates for each species or ground cover measure were divided by this sum and multiplied by 100 to generate relative abundance for each species in each individual sample quadrat. Quadrats were nested in block ($n = 3$) for statistical analyses (see below).

Species richness and evenness

We used the relative abundance data collected in the four years described above to calculate measures of plot-level diversity. Species richness (S) was determined by counting the number of vascular plant species recorded in each 1 m² quadrat. Evenness (E) was calculated based on Simpson's dominance index (D) following Mulder et al. (2004):

$$E = D/S = \left(\frac{1}{\sum_{i=1}^S p_i^2} \right)$$

where p_i is the proportion of vascular plant cover comprised by species i .

Dominance–diversity curves

Relative cover data from 2006 were also used to construct dominance–diversity curves to qualitatively examine resulting community change after 11 years of experimental manipulation. Relative cover of each species within each 1 m² quadrat was summed across all replicate quadrats across blocks within each treatment (total area: 24 m²). Species were then

ranked in order from most abundant to least abundant based on their relative cover in each treatment.

Data analysis

Generally, we considered the 1998 data to approximate baseline. Statistical analysis for data collected over the four years reported here was conducted with year both to assess the change from baseline and to determine if the treatment responses differed across year. Relative cover of *Betula*, species richness, and evenness were analyzed using nested repeated-measures ANOVAs with block, community (DH or MAT), fertilization, and herbivore exclusion as main effects, quadrats nested within block, and all possible interactions among main effects. Relative cover of *Eriophorum* and *Hierochloe* was analyzed without the main effect of community, since these species only occurred in one site. Relative cover was arcsine square root transformed prior to analysis. Normality and homogeneity of variance were confirmed for all ANOVAs, and Wilks' Lambda was used to test within-subject effects in the repeated-measures analyses. SAS version 9.2 for Windows (SAS Institute, Cary, NC) was used for all analyses. Data used in these analyses are archived at <http://arc-iter.ecosystems.mbl.edu/terrestrial-data>.

Using species richness and evenness results for 2006 only, we calculated the log ratio effect sizes according to Hillebrand et al. (2007) for each community for comparison with their meta-analysis results. The quadrats within each block were averaged prior to calculating the effect size for each block.

Results

Dominance–diversity and relative abundance

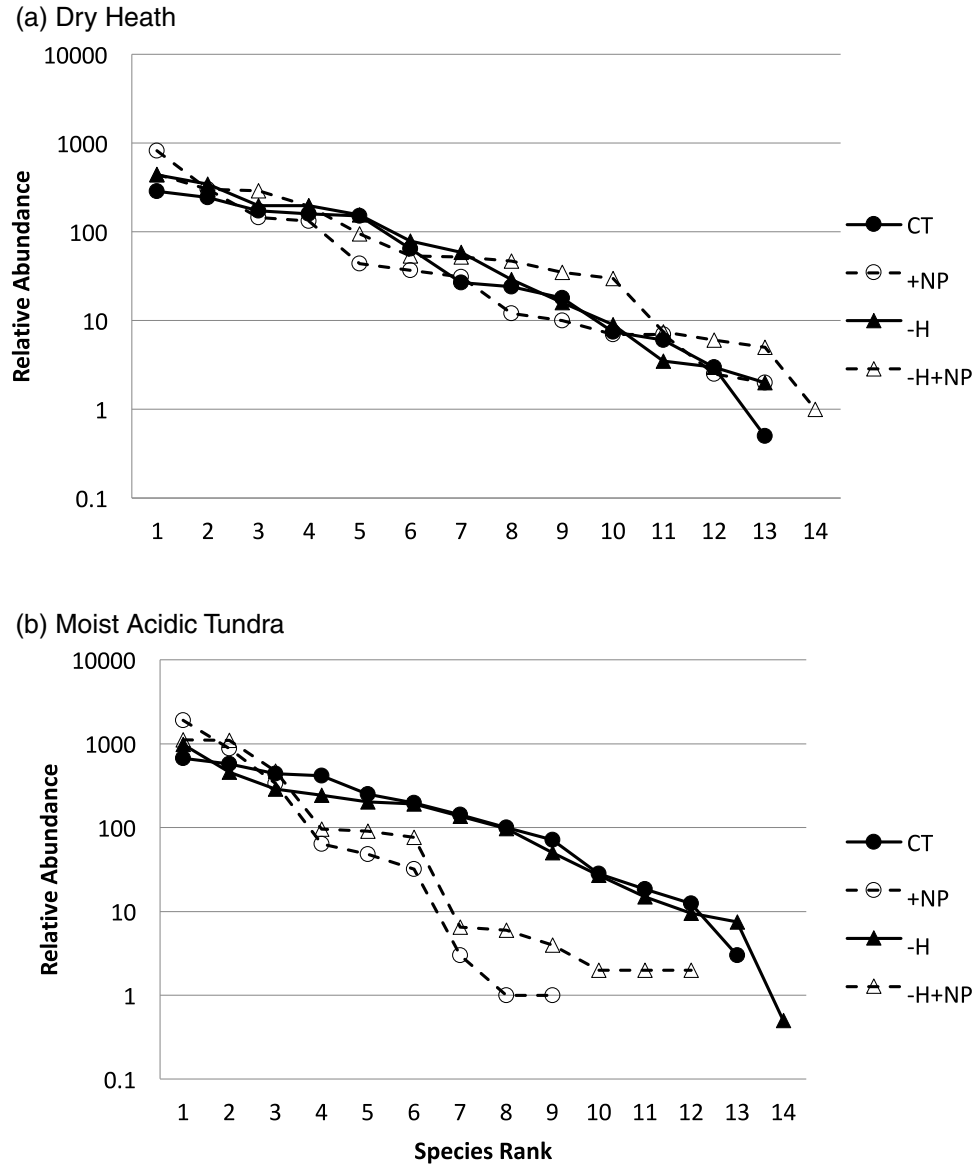
Dry heath

The community changes in fertilized DH plots were the result of an increase in abundance of a tussock-forming grass, a smaller increase in a dwarf deciduous shrub, and a decrease in evergreen shrubs and lichens (see Gough et al. 2012b for biomass responses by growth form). Dominance–diversity curves based on proportional abundance of each vascular species recorded in 2006 were used to qualitatively examine patterns of dominance at a larger spatial scale to compare with the quadrat-level quantitative analyses described below. In DH, all four treatments were somewhat similar (Fig. 1a). The greater dominance of the most abundant species in fertilized plots with herbivores present (*Hierochloe*) along with somewhat reduced evenness is evident, while there is a suggestion of greater evenness in the –H + NP treatment relative to the others.

Under ambient environmental conditions (CT), the tussock-forming grass *Hierochloe* is relatively rare in DH, the eighth most abundant species out of 13, with low relative cover. This species became the most abundant species when fertilized, increasing from 10% in 1998 (the third year of the experiment) to ~32% cover in +NP and ~20% in –H + NP in 2006 (significant year \times fertilization \times herbivory: $F_{3,67} = 4.75$, $p = 0.005$; fertilization \times herbivory: $F_{1,69} = 5.02$, $p = 0.03$; fertilization: $F_{1,69} = 351.76$, $p < 0.0001$; herbivory: $F_{1,69} = 11.91$, $p = 0.001$) (Fig. 2a). When herbivores were excluded, *Hierochloe* abundance was similar unless soil nutrients were also increased.

Dwarf birch also positively responded to added nutrients by 2004 (Fig. 2b) in DH. Analyzed across both communities simultaneously, the significant increase in abundance (changing in rank from seventh in CT to second most abundant species in +NP in DH) differed in magnitude between communities but was significant as a main effect (fertilization: $F_{1,153} = 117.70$, $p < 0.0001$; community \times fertilization: $F_{1,153} = 5.74$, $p = 0.02$) (Fig. 3b). Protection from herbivores did not affect *Betula* relative cover in DH (Fig. 2b);

Fig. 1. Dominance–diversity curves for (a) dry heath and (b) moist acidic tundra based on relative abundance of vascular plant species in 24 m² areas where mammalian herbivory and soil nutrients were manipulated for 11 years. CT, control; +NP, annually added N and P; –H, mammalian herbivores excluded.

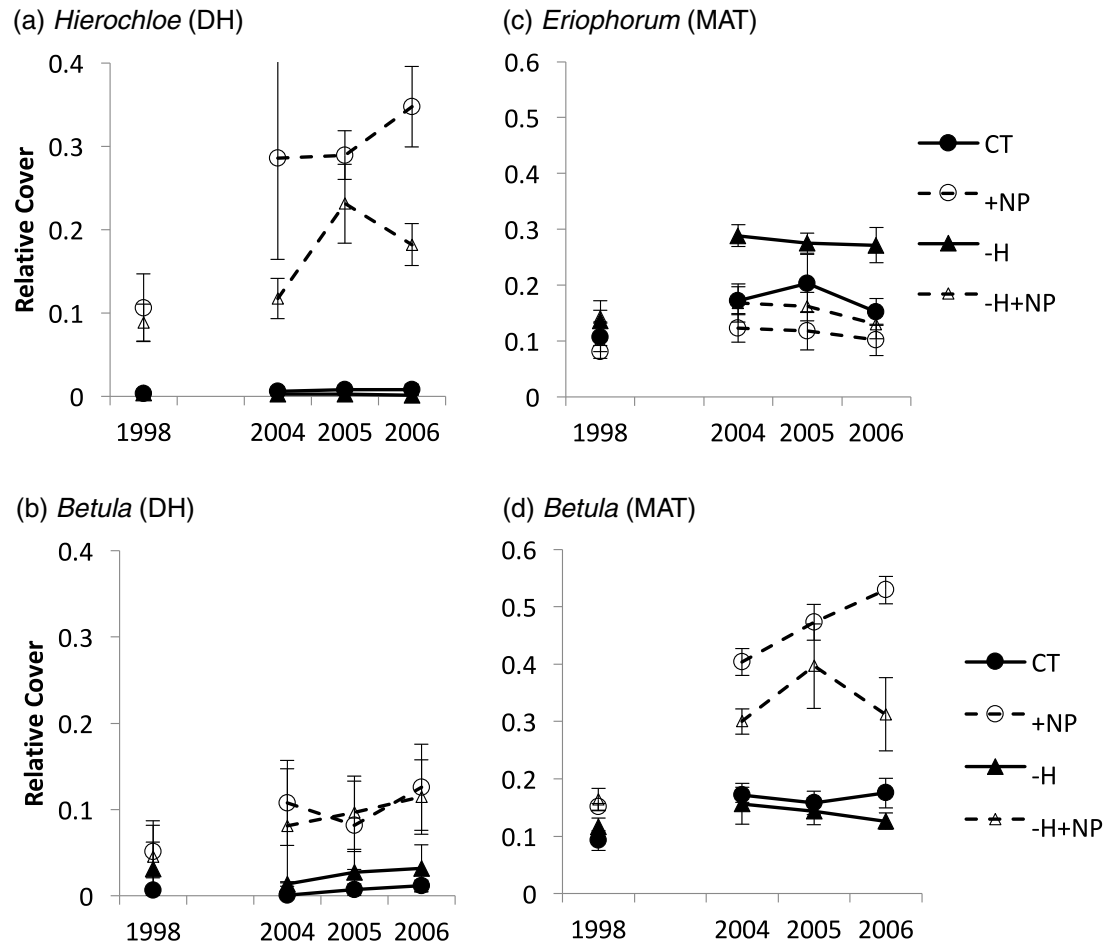


therefore, the different response of *Hierochloe* between +NP and –H + NP appeared to drive the different community-level responses to those treatments.

Moist acidic tundra

In contrast with DH, the dominance–diversity curves for the MAT treatments showed dramatic responses to the addition of nutrients, with both +NP and –H + NP having fewer species at this scale and reduced evenness. In particular, at this 24 m² scale, three fewer species were recorded in +NP compared with –H + NP (Fig. 1b), suggesting that the same species were locally extirpated from +NP plots, while in the –H + NP plots, a few species

Fig. 2. Mean (± 1 SE) relative cover for (a) *Hierochloe alpina* and (b) *Betula nana* in dry heath (DH) and (c) *Eriophorum vaginatum* and (d) *B. nana* in moist acidic tundra (MAT). Treatments began in 1996. For treatment abbreviations, see Fig. 1.



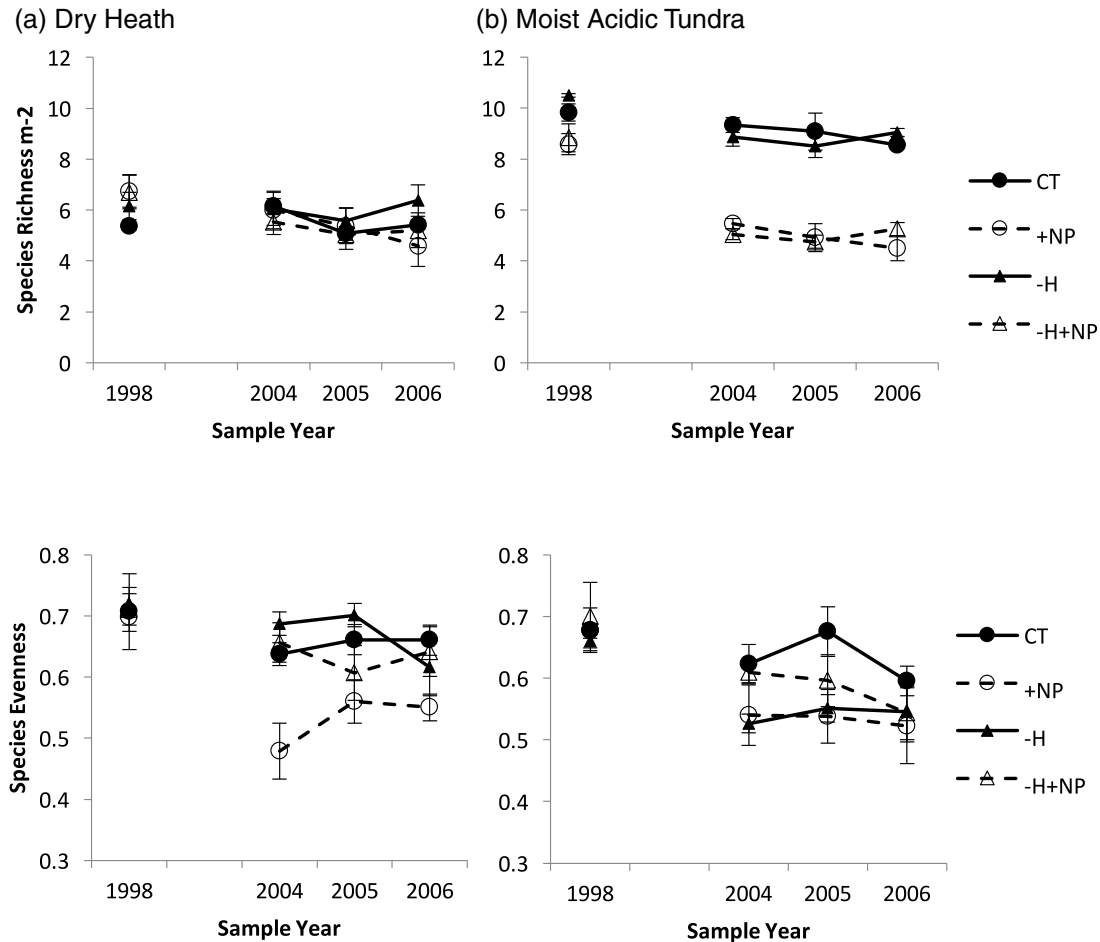
persisted infrequently. Evenness at this scale also appeared similar in these two treatments, as at the plot scale described in the next section.

These dramatic changes in fertilized MAT plots were driven by a fivefold increase in *Betula* in +NP plots and greater cover in -H + NP compared with CT in 2006 (Fig. 2d) (see statistical results above). Protection from herbivores did not significantly affect *Betula* relative cover under ambient nutrients, although there was a suggestion in 2006 that cover when exposed to herbivores was greater, just as in fertilized plots. In contrast, the abundant tussock-forming graminoid *Eriophorum* did not respond positively to added nutrients and achieved greatest cover at ambient soil nutrient levels when herbivores were excluded (herbivory \times fertilization: $F_{1,69} = 5.16$, $p = 0.03$) (Fig. 2c). The species that were locally extirpated from fertilized plots were often evergreen shrubs and forbs, although one forb, *R. chamaemorus*, responded positively (see Gough et al. 2012b).

Plot-level species richness and evenness

Treatments did not affect species richness and evenness consistently across both communities. By 2004, species richness was dramatically lower in fertilized plots in MAT but

Fig. 3. Mean (± 1 SE) species richness (top panels) and species evenness (bottom panels) in 1 m² plots over time in (a) dry heath and (b) moist acidic tussock tundra undergoing chronic herbivore exclusion and nutrient addition since 1996. For treatment abbreviations, see Fig. 1.



was not significantly affected in DH, driving a significant year \times community \times fertilization interaction that also resulted in significant community \times fertilization, year \times community, and year \times fertilization interactions and significant overall effects of fertilization and year (Table 1; Fig. 3). In 2006, the 11th year of treatment, fertilized plots in both communities had significantly fewer species ($p < 0.05$ for both) than ambient nutrient plots, although the magnitude of reduction was greater in MAT (approximately five species lost compared with approximately one lost in DH; Fig. 3). Herbivory significantly decreased species richness in both 1998 and 2006 ($p < 0.05$ in both years, significant year \times herbivory; Table 1), when plots exposed to herbivores had fewer species than plots from which herbivores were excluded (Fig. 1). Significantly more species in control and exclosure plots in MAT compared with fertilized MAT plots and all DH treatments drove a significant main effect of community (Fig. 3). The log response ratios calculated for species richness based on the 2006 data overlapped with zero in DH but were significantly negative for the main effects of herbivory and fertilization in MAT (Table 2).

Table 1. Source table for repeated-measures analysis of species richness and Simpson's evenness calculated at the 1 m² scale.

Source	df	Richness		Evenness	
		F	p	F	p
Year	3, 151	73.53	<0.0001		<0.0001
Year × block	9, 368				
Year × quadrat (Quad) (block)	84, 453				
Year × community (Comm)	3, 151	12.19	<0.0001		
Year × herbivory (H)	3, 151	9.88	<0.0001		
Year × fertilization (F)	3, 151	27.29	<0.0001	2.95	0.03
Year × Comm × H	3, 151				
Year × Comm × F	3, 151	3.39	0.02		
Year × H × F	3, 151				
Year × H × F × Comm	3, 151				
Block	3, 153	10.82	<0.0001		
Quad (block)	28, 153				
Community	1, 153	196.13	<0.0001	5.15	0.02
Herbivory	1, 153				
Comm × H	1, 153			9.52	0.002
Fertilization	1, 153	189.32	<0.0001	14.12	0.0002
Comm × F	1, 153	162.67	<0.0001	4.81	0.03
H × F	1, 153			19.80	<0.0001
Comm × H × F	1, 153				

Note: Only effects significant at $p < 0.05$ are included in the table.

Table 2. Mean ($n = 3$ blocks) effect size (log response ratio with 95% confidence interval) (calculated following Hillebrand et al. 2007).

Main effect	Dry heath		Moist acidic tundra	
	Richness	Evenness	Richness	Evenness
Herbivory	−0.15 (0.18)*	−0.04 (0.05)	−0.09 (0.08)	0.03 (0.02)*
Fertilization	−0.19 (0.35)	−0.07 (0.15)	−0.59 (0.14)*	−0.07 (0.10)
Interaction	0.03 (0.22)*	−0.11 (0.05)	−0.02 (0.07)*	−0.07 (0.28)*

Note: Confidence intervals for values in bold do not include zero. Asterisks indicate that effect is the same sign (or not different from zero) as results of the meta-analysis presented in Hillebrand et al. (2007).

Patterns resulting from manipulations were more complicated for species evenness than for species richness. Species evenness decreased with added nutrients in DH whereas MAT showed little response (significant community × fertilization interaction; Table 1), the opposite pattern as seen for species richness (Fig. 3). This decrease in evenness in DH caused by fertilization was significant by 2004 and helped drive a significant main effect of fertilization (significant year × fertilization, fertilization; Table 1). The two communities also differed in response to herbivory: excluding herbivores resulted in greater species evenness in DH, while in MAT, the absence of herbivores did not affect evenness (significant community × herbivory). In general, species evenness was greater in DH compared with MAT (significant effect of community; Table 1; Fig. 3).

An intriguing interaction effect on species evenness was found between herbivory and fertilization (Table 1) across all years and both communities. In plots with no added nutrients, exposure to herbivores promoted greater evenness. This relationship switched in fertilized plots, where herbivores instead *reduced* evenness. This pattern suggests that herbivore activity in combination with greater nutrients facilitated dominance of particular species, which in turn reduced evenness (Fig. 3).

The log response ratios for species evenness (from 2006) highlighted some of the community differences described above. In DH, the interaction term between fertilization and herbivory was negative, while it was not different from zero in MAT (Table 2). Herbivory had a positive effect on evenness in MAT but not in DH.

Discussion

Dramatic community-level responses to added soil nutrients

Across both communities studied here, added soil nutrients caused strong vegetation compositional responses. However, alleviating nutrient limitation significantly decreased species richness in MAT but not in DH and did not consistently alter species evenness in either community, contrary to our first prediction derived from Hillebrand et al. (2007) that both variables would decline. In general, adding nutrients tends to increase community biomass with a concomitant decrease in species richness (e.g., Gough et al. 2000). Here, MAT followed this pattern (also see Gough et al. 2012b for biomass results). In fact, species were lost at the scale of 1 m² and the entire plot, resulting in a significantly negative response ratio for species richness, while evenness was less affected. In contrast, live biomass actually declined with fertilization in DH because the increase in grass abundance did not offset the loss of wood biomass as ericaceous shrubs died (Gough et al. 2012b), and this community shift did not result in local species losses. Species evenness was reduced with nutrient addition, suggesting that *Hierochloe* was changing the pattern of dominance, but the response ratio did not differ from zero (Table 2). Although we do not report light data here, these findings are similar to those by Borer et al. (2014a) in which communities that experienced light limitation following nutrient addition showed greater reductions in species richness. At MAT, *Betula* is capable of growing up and out, intensifying light competition with added nutrients (Bret-Harte et al. 2001; Gough et al. 2012a), whereas *Heirochloe* is more limited in its morphology and restricted to a tussock growth form. The differences in the growth forms of these particular species that increased in abundance affected the difference in the response of community structure between DH and MAT presumably via different competitive effects on coexisting species.

Subtle mammalian herbivore effects on community structure

In general, the exclusion of herbivores had less of an effect on plant community structure than adding nutrients, in line with our second prediction from Hillebrand et al. (2007). In these low-productivity tundra systems, community-level responses to herbivore exclusion continue to develop over long time scales (Turkington et al. 2002; Johnson et al. 2011; Olofsson et al. 2014). Our response ratio for species richness was not different from zero in DH, as in the meta-analysis, and had a slight negative trend in MAT (Fig. 3). Evenness response ratio was also not different from zero in DH, but slightly positive in MAT, at a lower magnitude than in the meta-analysis (Table 2).

These communities may experience different degrees of herbivore pressure because of the location and plant species available: in some years, tundra vole abundance is higher in MAT than in DH, but caribou frequent DH more often than MAT (Johnson 2008). Evidence suggests that the effects of these herbivores may be relatively slight when averaged across years, although further study is needed to better document their impacts on the plant communities and to tease out differences in herbivore pressure by the different mammals (Olofsson et al. 2013). For example, the only individual plant species focused on here that responded positively to herbivore exclusion at ambient soil nutrients was *Eriophorum* in MAT; as discussed earlier, this species is targeted by small mammals, although it can regrow following tiller removal (e.g., Chapin 1980) and thus can withstand some herbivory each year yet persist (Johnson and Gough 2013).

Presence of mammals exacerbates community response to nutrients

Our third prediction that herbivores would offset the negative community responses to added nutrients was not supported in MAT: there was no significant interaction between herbivory and fertilization for species richness at the 1 m² scale, and the log response ratio for the interaction term was not significantly different from zero (for species richness or evenness). The dominance–diversity curves suggest that the presence of herbivores in MAT instead exacerbated community response at the plot scale by reducing evenness, promoting *Betula* dominance while negatively affecting *Eriophorum* (Gough et al. 2007), and reducing species richness even more than occurred with nutrient addition in the absence of mammals. This subspecies of *Betula* contains a variety of secondary compounds that make it generally unpalatable to herbivores (Graglia et al. 2001; Christie et al. 2015); thus, although the community was more productive, it was dominated by a plant species avoided by herbivores. In addition, although *Eriophorum* is known to tolerate repeated biomass clippings (Chapin 1980; Archer and Tieszen 1983), tundra voles in MAT may graze *Eriophorum* below the meristem as they use the tussocks for shelter and perhaps through repeated grazing also negatively affect particular individuals. The fact that *Eriophorum* did not increase in relative cover under increased nutrients and herbivore exclosure, conditions that promoted the greatest growth of individual tillers (Gough et al. 2007), may be the result of competition from *Betula* (Bret-Harte et al. 2001). This interaction between herbivore pressure and plant competition has been shown to be important in other tundra communities (e.g., Olofsson et al. 2002).

In DH, in contrast, the log response ratio for the interaction term for species evenness was significantly negative (Table 2). When herbivores were excluded, species evenness was the same in ambient and enriched nutrient plots (Fig. 1a), suggesting that the addition of nutrients did not affect the relative apportionment of cover among species in the absence of herbivores. However, when mammals were present, the addition of soil nutrients significantly decreased evenness. *Hierochloa* was able to expand into the available open space when fertilized by producing tussocks from scattered small individuals, and its dominance was further stimulated by the presence of herbivores (Johnson 2008), perhaps because of fecal deposition or because trampling disrupts intrat tussock and intraspecific competition (van der Wal 2006; Gough et al. 2012b). However, as mentioned earlier for fertilization, this change was not large enough to cause a decrease in species richness.

Conclusions

In contrast with conclusions from other arctic studies (Eskelinen et al. 2012; Kaarlejärvi et al. 2013), we found that mammal activity exacerbated the community shifts caused by increased soil nutrient availability in two tundra plant communities instead of negating these changes. In DH where bare space is more readily available, the community transitioned from one dominated by evergreen shrubs and lichens to a grassland when fertilized, and these changes were exacerbated by the presence of mammalian herbivores, mainly through the stimulation of growth of a grazing-tolerant tussock-forming grass (Johnson and Gough 2013). In the more closed-canopy MAT community, the tussock-forming sedge was negatively affected by nutrient addition and the presence of herbivores because an unpalatable dwarf deciduous shrub was able to take advantage of the nutrients and mammalian activity and grow taller and larger, overtopping the tussocks (Gough et al. 2012b).

The responses to treatments in these two tundra plant communities also contradict predictions derived from a broad meta-analysis (Hillebrand et al. 2007). The reasons for this likely differ between the two communities. In DH, significant changes to richness were not observed even after 11 years, suggesting that competitive exclusion has not yet occurred, perhaps because of the limits imposed by abiotic conditions in this

low-productivity community. In contrast, plant traits at MAT likely prevented herbivory from counteracting the decline in richness that occurred with fertilization; the dominant *Betula* is not palatable and herbivores in northern Alaska will not consume it if given a choice. Herbivory affecting plant communities in habitats that differ in fertility in distinct ways has been documented in other tundra systems (e.g., Stark et al. 2015) and has implications for how herbivores may or may not offset increased shrub abundance associated with climate warming and greater soil nutrient availability (Pajunen et al. 2012; Zamin and Grogan 2013; Christie et al. 2015; Vowles et al. 2017). These results when compared with Hillebrand et al. (2007) also suggest that specific plant traits may result in unexpected responses to increased nutrients and herbivory.

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