

## RESEARCH ARTICLE

Functional Ecology



# Long-term heavy reindeer grazing promotes plant phosphorus limitation in arctic tundra

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## Abstract

1. The potential of large mammalian herbivores to shift plant communities between nitrogen (N) and phosphorus (P) limitation has received little attention so far. However, herbivores can influence the cycling of these growth-limiting nutrients, and thereby affect plant nutrient limitation and productivity. Tundra ecosystems are nutrient-poor and commonly grazed by large herbivores like reindeer and may thus be responsive to such changes.
2. Here, we examined the effect of long-term light and heavy reindeer grazing on nutrient limitation of plant growth in a Scandinavian arctic tundra. We are the first to conduct a factorial N and P fertilization experiment across the two grazing regimes in two functionally contrasting vegetation types: heath and meadow.
3. Annual primary productivity (APP) showed contrasting responses to our fertilization treatments under light and heavy grazing. Under light grazing, APP increased in response to N + P additions in both the heath and meadow. Under heavy grazing, APP increased in response to N in the heath, with an additional positive effect of N + P combined, while APP increased in response to P and N + P additions in the meadow.
4. These results clearly show that an increase in the grazing intensity of reindeer facilitated a shift towards more P-limited conditions in Scandinavian arctic tundra, by increasing N cycling without having a corresponding positive effect on P cycling. In the N-poor heath, reindeer increased soil N availability at least partly due to a shift towards more N-rich graminoids, while in the meadow, reindeer decreased soil P availability. The mechanisms behind this decrease remain unclear, but reindeer may simply export more P from the system than N due to their large P demand for the production of their antlers.
5. *Synthesis.* We conclude that heavy and long-term reindeer grazing promoted a more P-limited tundra, thus experimentally confirming the potential of large mammalian herbivores to influence nutrient limitation of plant growth.

## KEYWORDS

fertilization experiment, herbivory, nitrogen, nutrient limitation, plant-herbivore interactions, primary productivity, stoichiometry

## 1 | INTRODUCTION

Large mammalian herbivores are key drivers of plant communities and ecosystem functioning in many terrestrial ecosystems (Estes et al., 2011; Wise & Abrahamson, 2005). It is well known that herbivores influence nutrient cycling and availability in soils through several pathways, such as returning nutrients in the form of dung and urine, altering plant community composition and litter quality, and/or influencing physical properties, such as soil porosity (Bardgett & Wardle, 2003; Schrama et al., 2013; Sitters & Olde Venterink, 2015). Herbivores thus have the potential to change the availability of plant nutrients, such as nitrogen (N) and phosphorus (P) (Sitters et al., 2017). Since N and/or P commonly limit plant growth (Aerts & Chapin, 2000; Elser et al., 2007), herbivore-induced changes in soil N:P stoichiometry are likely to affect plant nutrient limitation and productivity (Sitters et al., 2017). So far, however, studies on the effects of herbivores on nutrient availability in terrestrial ecosystems have been carried out predominantly on N (e.g., Frank & Evans, 1997; Olofsson, Kitt, Rautiainen, Stark, & Oksanen, 2001; Pastor, Cohen, & Hobbs, 2006; Singer & Schoenecker, 2003). The few studies that have focused on both N and P have found that mammalian herbivores can promote P limitation of the vegetation (Bai et al., 2012; Frank, 2008), but that the effect depends on environmental conditions (Bai et al., 2012). The opposite has, however, also been found; the exclusion of red deer browsing in a birch forest resulted in a decrease in foliage N:P ratios, suggesting that the browsed areas were less P-limited (Carline, Jones, & Bardgett, 2005). Additionally, these studies predicted nutrient limitation based on foliar N:P ratios. Even though this is an established method (Güsewell, 2004; Koerselman & Meuleman, 1996; Olde Venterink, Wassen, Verkroost, & de Ruiter, 2003), care needs to be taken as “critical N:P ratios,” below which plant growth is limited by N and above which plant growth is limited by P, vary among plant species and ecosystems (Güsewell, 2004). Especially, it has not been studied if critical N:P ratios remain constant across herbivore grazing treatments. Thus, nutrient addition experiments that alleviate N and/or P limitation are needed to robustly assess nutrient limitation to plant growth (Harpole et al., 2011).

Reindeer (*Rangifer tarandus*) are an important herbivore in tundra ecosystems and are known to affect nutrient availability (Olofsson et al., 2001; Olofsson, Stark, & Oksanen, 2004; Sitters, te Beest, Cherif, Giesler, & Olofsson, 2017; Stark, Mannisto, & Smolander, 2010; Stark, Strommer, & Tuomi, 2002; Van der Wal & Brooker, 2004) and potentially plant nutrient limitation. Numerous fertilization experiments in tundra ecosystems have shown strong effects of fertilization on plant biomass, productivity and community composition. These experiments suggest that tundras are limited by N or sometimes co-limited by N and P (Gough, Osenberg, Gross, & Collins, 2000; Shaver & Chapin, 1980; Sundqvist, Liu, Giesler, & Wardle, 2014), while recent studies indicate that meadow tundra might be more constrained by P (Giesler, Esberg,

Lagerstrom, & Graae, 2012; Sundqvist, Wardle, Vincent, & Giesler, 2014).

In an earlier paper, we showed that long-term heavy reindeer grazing in a Scandinavian arctic tundra increased extractable N:P ratios in the soil, suggesting that reindeer could promote a shift towards P limitation of plant growth (Sitters et al., 2017). Here, we examined the effect of long-term light and heavy reindeer grazing on nutrient limitation of plant growth in the same tundra. We conducted a factorial N and P fertilization experiment across the two grazing regimes in two functionally contrasting vegetation types: heath and meadow. We hypothesize that under light grazing plant communities in the heath will be more responsive to N addition, while P fertilization will have a stronger effect on plant communities in the meadow. Under heavy grazing, we hypothesize that both vegetation types will become more responsive to P addition, as soil extractable N:P is increased and hence P-limited conditions for plant growth (Sitters et al., 2017).

## 2 | MATERIALS AND METHODS

### 2.1 | Study area

The study was performed on treeless tundra in Reisadalen, Troms Fylke, northern Norway (69°30'N, 27°30'E), situated between 500 and 700 m a.s.l., about 100 m above the local timberline. The area experiences a suboceanic climate with an annual precipitation of 935 mm and an annual mean temperature of −0.6°C (gridded data, 2006–2015, Norwegian Water Resources and Energy Directorate, [www.senorge.no](http://www.senorge.no)). The mean annual precipitation and temperature in 2013 and 2014 (the years in which this study was performed) were fairly normal for the last decade, but since mean annual temperatures have increased over the last 50 years at a rate of almost 1° per decade, these years were warmer than the long-term averages (Ylänne, Olofsson, Oksanen, & Stark, 2018). The study site is divided by a reindeer fence, established in the 1960s to help keep the reindeer within their legal summer ranges. The fence is built of wire attached to 1–1.5 m wooden poles and runs for 18 km across the tundra. The fence divides the area into a very lightly grazed migration pasture during spring and autumn and a heavily grazed summer pasture (Olofsson et al., 2001; te Beest, Sitters, Menard, & Olofsson, 2016). In our selected study sites, reindeer on the heavily grazed side of the fence were primarily present in the beginning and end of summer, indicating that there is no significant temporal difference in reindeer presence between the lightly and heavily grazed sites. Reindeer density in the heavily grazed summer pasture was 10.1 reindeer/km<sup>2</sup> (2010–2014; Parsons, 2016), which is among the highest reindeer densities found in Scandinavia (Bråthen et al., 2007). Since the lightly grazed sites are in a migration area, similar density calculations are not meaningful, but measurements on dung deposition suggest very low reindeer densities; average of 1 g dung/m<sup>2</sup> on the lightly grazed side of the fence compared to 17 g dung/m<sup>2</sup> on the heavily grazed side of the fence (te Beest et al., 2016).

## 2.2 | Experimental set-up

In June 2013, we selected two functionally contrasting vegetation types for this study: heath vegetation dominated by slow-growing deciduous and evergreen dwarf shrubs, such as *Betula nana*, *Empetrum hermaphroditum* and *Vaccinium vitis-idaea*, and meadow vegetation dominated by the graminoids *Carex bigelowii*, *Agrostis mertensii* and *Deschampsia flexuosa* and the forb *Bistorta vivipara*. The vegetation types were identified by the vegetation on the lightly grazed side of the reindeer fence. The plant community composition has changed substantially on the heavily grazed side, and especially graminoids (e.g., *Festuca ovina*, *Poa alpina* and several *Carex* species) and forbs (e.g., *B. vivipara* and *Viola biflora*) are more abundant (Olofsson et al., 2001; Sitters et al., 2017; te Beest et al., 2016). Soil N availability is high in the meadow vegetation and low in the heath vegetation, but in the latter only under light grazing, as heavy grazing increases soil N to levels found in the meadow vegetation (Sitters et al., 2017). Both soil moisture and temperature are higher in the meadow vegetation compared to the heath vegetation and higher on the heavily grazed side of the fence (te Beest et al., 2016).

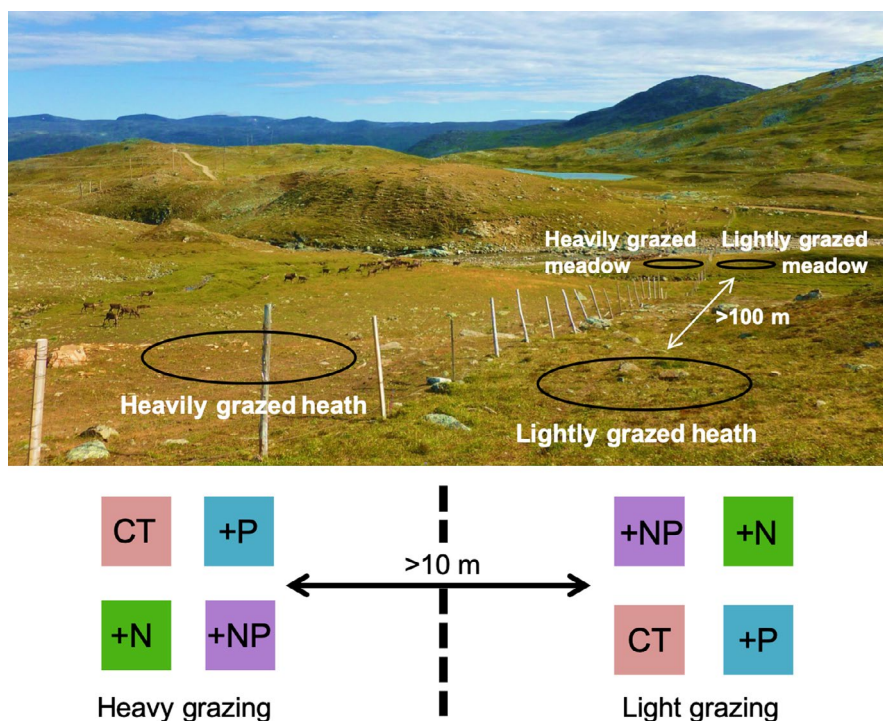
We selected eight sites per vegetation type, four on each side of the fence. For each vegetation type, sites were selected as pairs across the fence line to be as topographically and edaphically uniform as possible. The distance between paired sites was about 10 m, while the distance between one pair of sites and the next was about 100 m (Figure 1). Within each site, we established four plots of 1 × 1 m with the outer 10 cm as a buffer. The distance between these plots was 2 m, which was similar to distances used in other fertilization experiments in arctic tundra (Gough, Moore, Shaver, Simpson, & Johnson, 2012; Shaver et al., 1998). In total, we had 64 plots across the two grazing regimes and vegetation types (Figure 1).

In each vegetation type, the four plots on either side of the fence were randomly assigned to one of four fertilization treatments: (a) no fertilization (control), (b) N addition, (c) P addition or (d) N and P addition. In 2013 and 2014, we added 10 g N/m<sup>2</sup> as ammonium nitrate (NH<sub>4</sub>NO<sub>3</sub>) and 5 g P/m<sup>2</sup> as monosodium phosphate dihydrate (NaH<sub>2</sub>PO<sub>4</sub>(H<sub>2</sub>O)<sub>2</sub>). These fertilization rates are similar to other studies focusing on plant nutrient limitation in arctic tundra (e.g., Jonasson, 1992; Mack, Schuur, Bret-Harte, Shaver, & Chapin, 2004; Sundqvist et al., 2014). In 2013, half of the annual amount was added on June 15 and the other half on July 27. In 2014, the full annual amount was added between June 23 and July 8 depending on snow-melt conditions, which differed between plots. After fertilization in 2014, plots on the heavily grazed side of the fence were protected from grazing by temporary exclosures until vegetation sampling (ca. 1.5 month). On the lightly grazed side, no reindeer were present in 2014 before vegetation sampling.

## 2.3 | Vegetation sampling

To assess the effect of the fertilization treatments on tundra vegetation, we clipped all above-ground biomass in a square of 25 × 25 cm in each plot in August 2014 (between 10 and 15 August 2014; 1 year and 2 months after our first fertilization treatment). The clipped biomass was sorted to the level of plant functional type (i.e., deciduous shrub, evergreen shrub, forb and graminoid). For the shrub species, we separated the present year's growth (new leaves and stems) from all previous years' growth using the bud scars on the stems. For forbs, all above-ground biomass was classified as present year's growth, while for graminoids, new leaves were separated from old dead leaves. The present year's growth was used to estimate annual primary productivity (APP) of each plant functional

**FIGURE 1** A photograph of the arctic tundra in Reisadalen (Norway) showing the long-term reindeer fence and the set-up of the fertilization experiment. Four replicate sites of two functionally contrasting vegetation types, heath and meadow, were selected on either side of the fence; one replicate site per type is shown as a circle. In each site, we established four plots of 1 × 1 m as is shown below the photograph. The dashed line represents the fence separating the lightly grazed from the heavily grazed side. The four plots on either side of the fence were randomly assigned to a fertilization treatment: no fertilization (CT), N addition (+N), P addition (+P), or N and P addition (+NP)



type. All biomass was thereafter dried (60°C, 48 hr) and weighed. We focus on APP instead of total standing biomass as this is a better measure for the plant response to fertilization, especially since there is considerable variation in plant growth forms (i.e., shrubs vs. graminoids) between the vegetation types and grazing regimes (but for results on total biomass see Figure S1 in Appendix; Shaver & Chapin, 1991).

## 2.4 | Statistical analyses

We analysed the effects of vegetation type, grazing regime and fertilization treatment on total APP using a linear-mixed effects model that allowed for random effects of sites to vary between grazing regimes and vegetation types. We used this random structure because we expected (from Sitters et al., 2017) that meadow vegetation would show more uniform total APP and that heavy grazing would decrease spatial variability in total APP; indeed, total APP was much less variable between heavily grazed meadow sites than between other sites (Figure S2). Our spatial variance-covariance structure in random effects allows for these different site variances in different vegetation type  $\times$  grazing regime combinations. We used Tukey's HSD tests for post hoc comparisons between different grazing regimes and fertilization treatments.

To take a closer look at the fertilization responses of each plant functional type (i.e., deciduous shrubs, evergreen shrubs, forbs and graminoids), we used a compound Poisson linear-mixed model with a spatial variance-covariance structure. The compound Poisson model is particularly adapted for plant biomass data including zeros (i.e., the absence of a plant). We used the same random structure as for total APP taking different variances for different vegetation type  $\times$  grazing regime combinations into account (Figure S3). In our model, we included vegetation type, grazing regime, plant functional type and fertilization treatment, and all their interactions, as fixed factors. We then performed a model selection procedure that tested all combinations of these fixed factors and scored models based on Akaike's information criterion (AIC). The three best models (with lowest AIC scores) contained the interaction between vegetation type  $\times$  grazing regime  $\times$  plant functional type (Table S1), and therefore, we looked more specifically into the effects of fertilization treatment for each plant functional type separately, within each vegetation type  $\times$  grazing regime combination. Unfortunately, it is not yet possible to do post hoc pairwise comparisons on compound Poisson models fitted with the "cpglmm" function from the "cplm" package in R (version 3.4.3; R Core Team, 2017). Thus, these comparisons were done qualitatively by plotting the mean values and their 95% Wald confidence intervals (CI) for each fertilization treatment. When lower 95% CI values for fertilized treatments (+N, +P, +NP) were located above the upper value for the control treatment (CT), there were potentially significant differences between these treatments and their control. All data were log-transformed to meet assumptions of normality and homogeneity of variance. A link to the R scripts used can be found under "Data accessibility."

## 3 | RESULTS

Total APP showed contrasting responses to our fertilization treatments under light and heavy reindeer grazing (Table 1). Under light grazing, total APP increased in response to N and N + P additions in comparison with the control (i.e., single N limitation; Figure 2a). Under heavy grazing, APP increased in response to N and P added alone, but increased synergistically to their combined addition (i.e., independent co-limitation of N and P; Figure 2b). Independent co-limitation means that the vegetation responded to the single addition of N and P, but synergistically to both nutrients when added together (see Harpole et al., 2011 for definitions), indicating that P became more limiting under heavy grazing. Per vegetation type, we observed an increase in APP in both the lightly grazed heath and meadow following N + P additions, and a slight (but not significant) increase when adding N alone (i.e., simultaneous co-limitation of N and P; Figure 3). In the heavily grazed heath, APP did increase following N addition alone, but increased more with the combined N + P addition (i.e., serial N limitation; Figure 3a). Serial limitation means that the vegetation only responded to the addition of P after our fertilization treatment alleviated limitation by the primary nutrient N, indicating that under heavy grazing P was less available than under light. Annual primary productivity in the heavily grazed meadow increased in response to P and N + P additions with no response to adding N alone (i.e., single P limitation; Figure 3b).

The lightly grazed heath vegetation was strongly dominated by deciduous and evergreen dwarf shrubs, while forbs and graminoids were rare. The lightly grazed meadow, on the other hand, was dominated by graminoids and forbs, while deciduous and evergreen dwarf shrubs were rare. After decades of heavy grazing, both vegetation types were strongly dominated by graminoids (Figure 3). The response of graminoids to the different fertilization treatments under light and heavy reindeer grazing followed the same pattern as total APP (Figure 4). Annual primary productivity

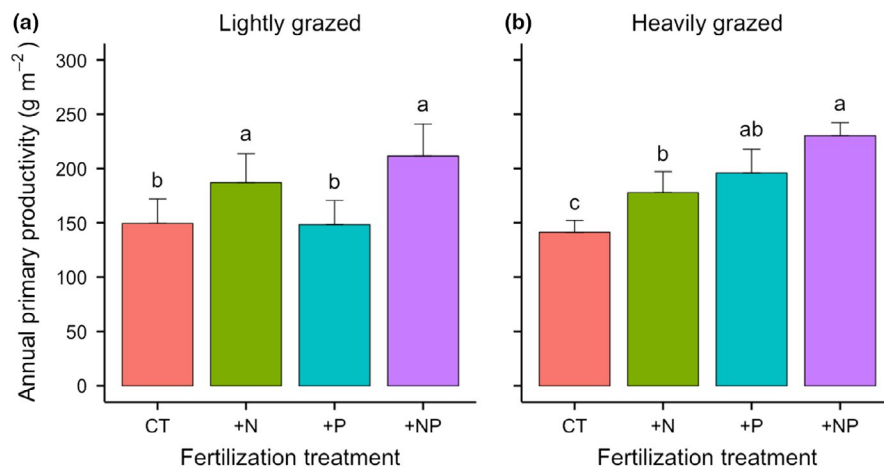
**TABLE 1** ANOVA results for the effects of vegetation type, grazing regime and fertilization treatment on annual primary productivity (APP) ( $n = 4$ )

	df	F-value	P-value
Vegetation type	1,45	4.70	0.036
Grazing regime	1,45	0.01	0.937
Fertilization treatment	3,45	23.60	<0.001
Vegetation type $\times$ grazing regime	1,45	4.28	0.044
Vegetation type $\times$ fertilization treatment	3,45	1.68	0.186
Grazing regime $\times$ fertilization treatment	3,45	4.16	0.011
Vegetation type $\times$ grazing regime $\times$ fertilization treatment	3,45	2.12	0.112

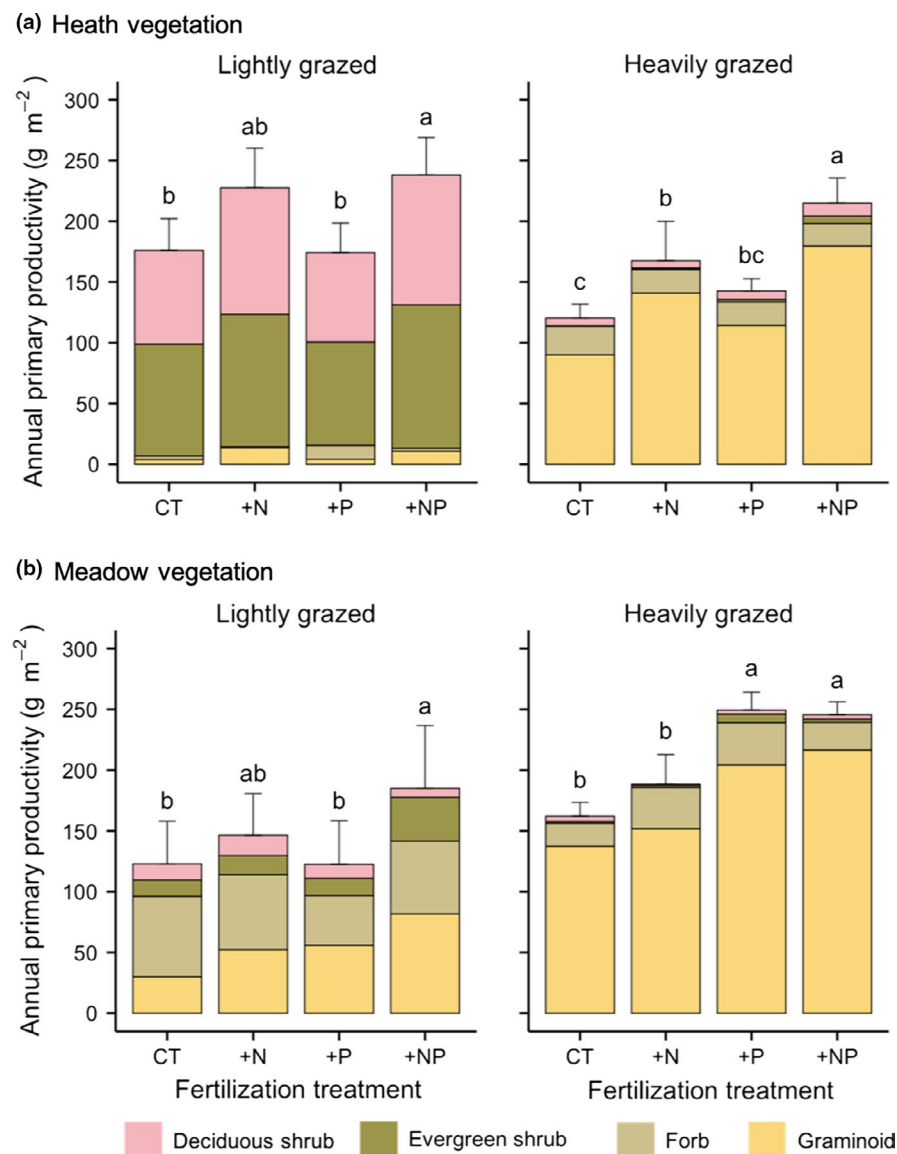
Note: Significant effects are printed in bold.



**FIGURE 2** The effects of fertilization treatment on annual primary productivity ( $\text{g}/\text{m}^2$ ; mean  $\pm$  SE;  $n = 4$ ) in (a) lightly and (b) heavily grazed plots (including both heath and meadow vegetation). Plots were either not fertilized (CT) or fertilized with N (+N), P (+P), or N and P (+NP). Bars not connected by the same letter indicate significant differences between fertilization treatments

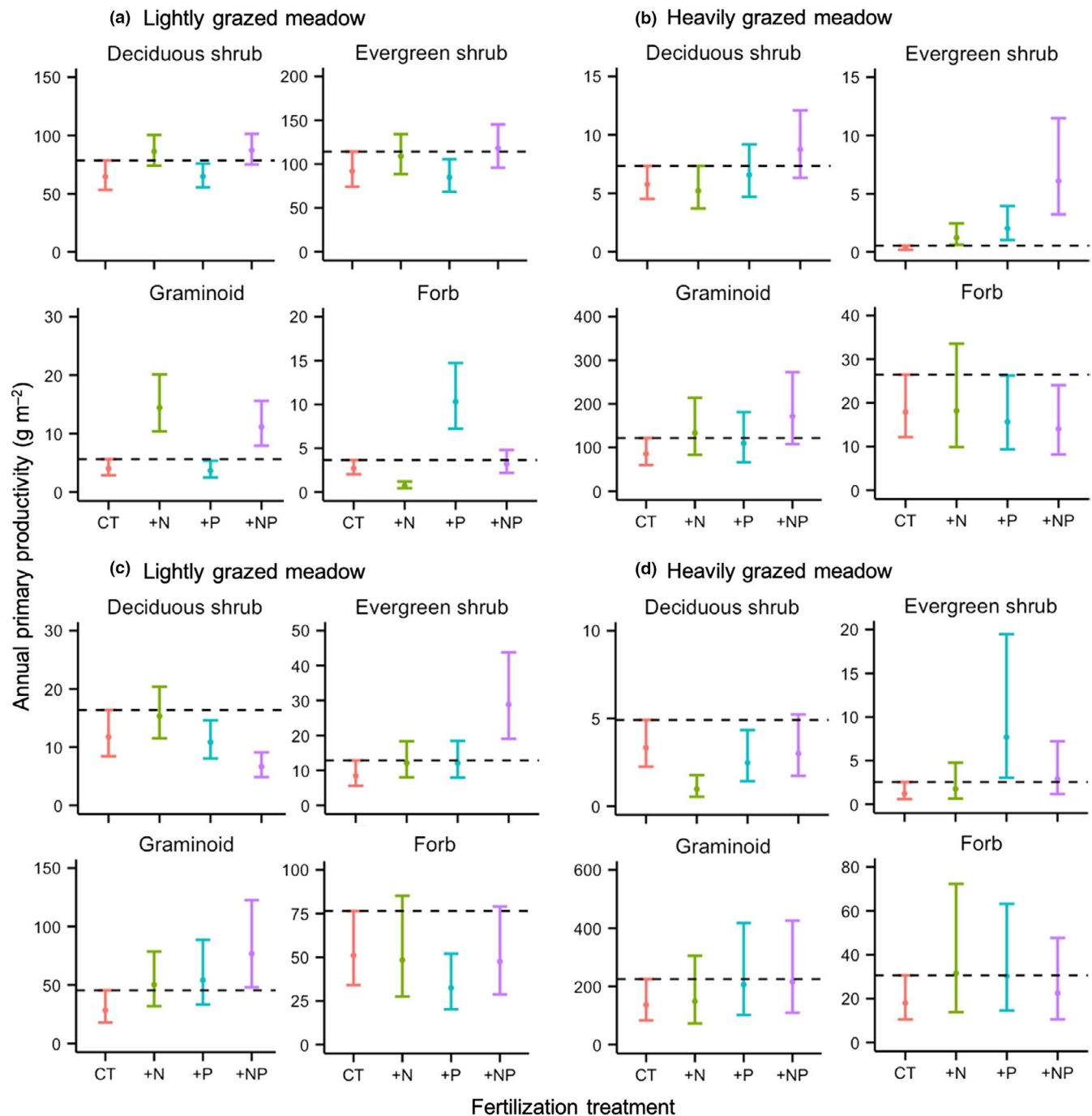


**FIGURE 3** The effects of fertilization treatment on annual primary productivity ( $\text{g}/\text{m}^2$ ; mean  $\pm$  SE;  $n = 4$ ) separated by plant functional type in lightly and heavily grazed heath (a) and meadow plots (b). Plots were either not fertilized (CT) or fertilized with N (+N), P (+P), or N and P (+NP). Bars within a vegetation type and grazing regime not connected by the same letter indicate significant differences between fertilization treatments



of graminoids increased in the lightly grazed heath following N and N + P additions (Figure 4a), while under heavy grazing, only N + P additions tended to increase APP (Figure 4b). In the meadow

vegetation, graminoids responded most strongly to N + P additions under light grazing (Figure 4a), while under heavy grazing, they responded to both P and N + P additions (Figure 4b). The



**FIGURE 4** Annual primary productivity ( $\text{g/m}^2$ ) per plant functional type in lightly and heavily grazed heath (a, b) and meadow vegetation (c, d) under different fertilization treatments ( $n = 4$ ). Plots were either not fertilized (CT) or fertilized with N (+N), P (+P), or N and P (+NP). Error bars represent the 95% Wald confidence interval for each fertilization treatment, and the dotted line is located at the upper value for the control treatment (CT)

same pattern was found for deciduous and evergreen shrubs in the heath vegetation; under heavy grazing, the strongest increase of APP was observed when adding N + P, while under light grazing, the addition of N alone was also important (Figure 4). In the meadow vegetation, evergreen shrubs responded more strongly to P addition under heavy grazing compared to light grazing (Figure 4c,d). Lastly, we observed a strong response in forb APP under P addition in the lightly grazed heath (Figure 4a).

## 4 | DISCUSSION

In accordance with our hypotheses, heavy and long-term grazing by reindeer promoted P limitation of above-ground primary production (Figures 2 and 3). Only a few studies have addressed the effects of herbivores on nutrient limitation of vegetation in terrestrial ecosystems (Sitters et al., 2017). Corresponding to our results, two previous studies also revealed that long-term, heavy grazing by large

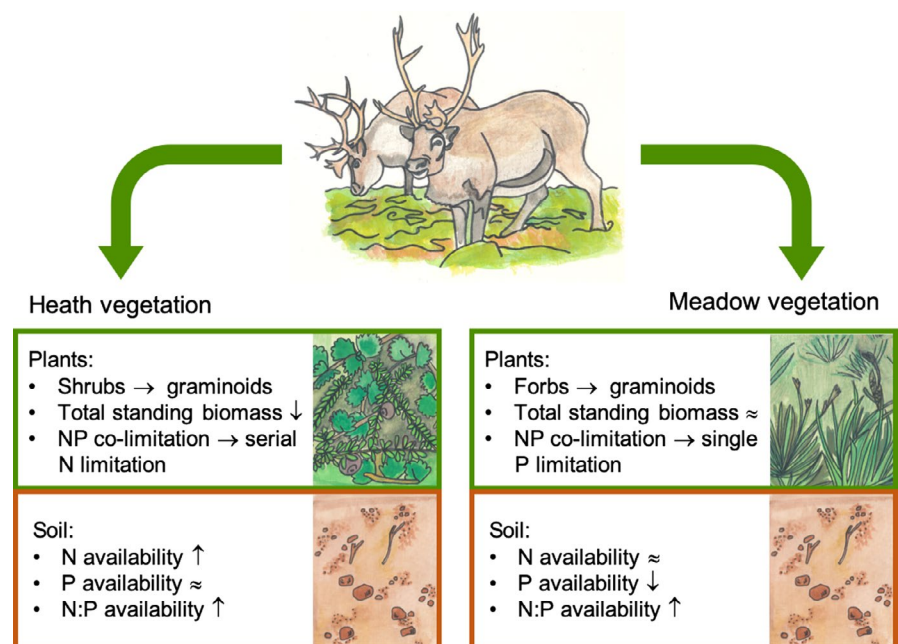
herbivores has the potential to promote P limitation using data on plant N:P ratios. Elk and bison promoted P limitation of plants in a temperate grassland (Frank, 2008), and domestic grazers promoted P limitation of plants in a meadow steppe (Bai et al., 2012). Whether or not the effect of herbivores on N:P stoichiometry is realized depends on environmental conditions, as in Bai et al. (2012) herbivores only seemed to increase N:P ratios at higher precipitation, which were the habitats where herbivores strongly reduced plant biomass. The opposite pattern was, however, also recorded since red deer were found to promote N limitation of birch trees (*Betula pubescens*) in a regenerating woodland (Carline et al., 2005). It is not clear whether this result is in contrast with the other studies mentioned above, since the impact of grazing versus browsing herbivores on nutrient cycling might differ (Pastor et al., 2006). Additionally, the N:P ratios of single plants can respond differently than the N:P ratio of the whole community to herbivory (Bai et al., 2012), and only a few plant functional types responded in accordance with total APP in this study as well.

The promotion of P limitation of plants by long-term heavy reindeer grazing was expected based on several earlier findings in our arctic tundra. Firstly, we observed an increase in extractable soil N:P with heavy grazing in both the heath and meadow vegetation (Sitters et al., 2017), indicating that there was relatively more N than P available for plants when reindeer were present in high densities. Secondly, phosphatase activity in heath soil was higher under heavy grazing (Stark & Vaisanen, 2014). This extracellular enzyme is involved in the breakdown of organic P (Duff, Sarath, & Plaxton, 1994) to enhance local P supplies for plants. Finally, there was an increase in the colonization of arbuscular mycorrhizal fungi (AMF) in heavily grazed heath sites (Barthelemy, Stark, Kytöviita, & Olofsson, 2017). These AMF, with their known propensity for P acquisition, may be indicative of a decreased P availability. Hence, under heavy reindeer grazing, plants (and/or microbes) are allocating more resources to

organic P acquisition (Richardson, George, Hens, & Simpson, 2005; Turner, 2008), strategies that suggest limitation of plant available P.

Although heavy reindeer grazing promoted plant P-limited conditions in our system in general, the mechanisms behind the shift towards these conditions were likely different for the heath and meadow vegetation (Figure 5). A positive effect of herbivores on N availability, without a correspondingly positive effect on P availability, seems to be a major driver for the promotion of P limitation of plants in several ecosystems (Bai et al., 2012; Frank, 2008). In our system, this mechanism probably plays a driving role in the heath, as high reindeer densities increased mineral N availability in the soil (Egelkraut et al., 2018; Sitters et al., 2017; Stark & Vaisanen, 2014), likely due to a shift towards more N-rich graminoids that produce more easily decomposing litter (Olofsson & Oksanen, 2002). The shift towards more P-limited conditions in the meadow is, contrastingly, related to reduced P availability in the soil (Egelkraut et al., 2018; Sitters et al., 2017). The mechanisms behind this reduction are not known, but large ungulates have a high relative P demand due to their fairly robust skeleton, and the annual production and shedding of their antlers (Moen, Pastor, & Cohen, 1999; Sterner & Elser, 2002). This should be especially true for reindeer, since both sexes have antlers, and the antlers are large compared to their body weight (Moen et al., 1999). Reindeer do not shed their antlers in summer grazing ranges, as the one that we have studied, but rather in autumn/winter in other places along their migration routes. Heavy grazing by reindeer might thus export large amounts of P from our study system. If the effect of reindeer on plant N:P stoichiometry is the opposite in areas where they shed their antlers remains to be studied. Conceptual models focusing on the impact of large ungulates on plant nutrient limitation also predict that because of their high bone mass and P demand they should recycle more N than P and consequently facilitate P-limited conditions (Sterner & Elser, 2002). Furthermore, changes in soil chemical properties

**FIGURE 5** Illustration of changes in the plant and soil compartments as a consequence of heavy and long-term reindeer grazing for heath and meadow vegetation. The plant compartments show changes in dominant plant functional type and nutrient limitation from lightly to (→) heavily grazed sites. Total plant biomass decreases (↓) or remains the same (≈) due to heavy grazing in heath and meadow vegetation, respectively. The soil compartments show increases (↑), decreases (↓) or no changes (≈) in nutrient availability due to heavy grazing. The plant compartment is based on data from this study, and the soil compartment is based on data from Sitters et al. (2017)



due to trampling-induced soil compaction might also be important (Schrama et al., 2013; Sitters et al., 2017), and in order to unravel the mechanisms behind the impact of herbivores on P cycling, we strongly urge future studies to take this element into account.

At the functional group level, responses of the dominant plant functional types (graminoids under heavy grazing in both vegetation types and shrubs in the lightly grazed heath; Figure 4) likely drove the changes in total APP in our sites. This is in accordance with the mass ratio hypothesis and highlights the importance of dominant species for ecosystem functioning as well as ecosystem responses to perturbations (Grime, 1998). That graminoids would respond to our fertilization treatments was expected, since they have been found to be the plant functional type which increases the most following fertilization (Dormann & Woodin, 2002). The responses of deciduous and evergreen shrubs to fertilization were also expected, although deciduous shrubs have often been recorded to respond more positive to fertilization than evergreen (Dormann & Woodin, 2002; Gough et al., 2012; Grellmann, 2002). We also observed fertilization responses from subdominant plant functional types. For example, forbs increased with P addition in the lightly grazed heath, which was also observed for non-mycorrhizal and  $N_2$ -fixing forbs in an alpine tundra, and was related to their higher P requirements (Theodose & Bowman, 1997). We also observed an increase in evergreen shrubs in the lightly grazed meadow and heavily grazed heath following addition of both N and P, and even a reduction in deciduous shrubs after N addition in the heavily grazed meadow (Figure 4). These responses also contributed to the patterns observed at the total APP level and might not only be related to the nutrient that limited growth but also to competitive interactions among plants, which strongly regulate the response of subdominant plants or functional types to fertilization (Bret-Harte et al., 2004).

In conclusion, we show that heavy and long-term reindeer grazing not only alters soil nutrient availabilities (Sitters et al., 2017) but also facilitates shifts in nutrient limitation of arctic plant communities. High reindeer density promoted a more P-limited tundra, which large ungulates seem to do, at least in all studies we are aware of that have taken a whole ecosystem approach (Bai et al., 2012; Frank, 2008). These studies have in common that they are long-term studies in heavily grazed areas, seemingly indicating that heavy grazing for a long time is necessary for these stoichiometrical effects to be apparent. Shifts in N:P stoichiometry can have significant ecological impacts, ranging from changes in plant species composition and success of alien plant species (Sardans, Rivas-Ubach, & Penuelas, 2012a), to a decreased response of the ecosystem to N deposition and increased N run-off into surface waters (Britton & Fisher, 2007).

Reindeer densities in the heavily grazed sites are among the highest found in Scandinavia (Bråthen et al., 2007), and probably high compared to densities in the rest of the arctic tundra. However, it is presently not known how the impact of reindeer or other large herbivores on vegetation and soils varies across the Arctic, as densities of reindeer/caribou are not easy to compare, since data are provided in different formats and at different spatial scales. The effects presented here could thus potentially be

greater than in the rest of the Arctic, but this is simply not known. Understanding the importance of reindeer-induced changes in plant nutrient limitation across the whole range of reindeer densities found in the arctic tundra is therefore an important challenge in the future. The manifestations of shifts in nutrient limitation are likely to vary across environmental gradients because the nature of nutrient limitation is expected to shift with changes in climate and soil bedrock (Sardans, Rivas-Ubach, & Penuelas, 2012b). Since the effect of herbivores on N and P availability can vary depending on the type of herbivore considered, soil characteristics, environmental conditions and grazing regime, all these factors have to be considered before our results can be generalized across more ecosystem types where ungulates form a significant part of the grazing community.

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## AUTHOR'S CONTRIBUTIONS

J.S., J.O., M.C. and R.G. conceived the ideas and designed the study. J.S., D.E. and M.C. performed the experiment and collected the data. J.S. and M.C. analysed the data. J.S. led the writing of the manuscript. All authors contributed critically to the draft and gave final approval for publication.

## DATA ACCESSIBILITY

Data and R scripts deposited in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.jp55n53> (Sitters, Cherif, Egelkraut, Giesler, & Olofsson, 2019).

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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