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Limited short-term impact of lemming grazing on vascular plants under experimentally reduced predation in the High Arctic

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Abstract

Population fluctuations of lemmings in the High Arctic appear to be driven by predator–prey interactions. However, lemming grazing can sometimes have a strong impact on the vegetation during population peaks, suggesting a possible role of plant–herbivore interactions. We use a large-scale experiment where predators were excluded to investigate whether predator reduction could have cascading effects on the vegetation through an increase in lemming densities in the Canadian Arctic. Morphological traits and biomass of *Salix arctica* and the biomass of *Poaceae* and *Juncaceae* were sampled inside and outside lemming exclosures. We detected signs of lemming grazing on the number of buds and catkins of *S. arctica* at snowmelt, and stem length, stem growth, and number of leaves during the summer but the impact was relatively small. We did not detect an impact of grazing on plant biomass during the summer. We also found limited evidence that the impact of grazing was higher in the predator exclosure even though lemming density increased up to two-fold. Our results suggest that the short-term impact of lemmings on vascular plants is relatively small and that an experimental increase in lemming density did not have a cascading effect on the plants consumed by these herbivores in the Canadian Arctic.

Key words: small mammals, predation, population dynamics, plant–herbivore interactions, arctic willow, trophic cascade

Résumé

Les fluctuations de population de lemmings dans l'Extrême-Arctique semblent être déterminées par les interactions prédateur-proie. Cependant, le broutement des lemmings peut parfois avoir un fort impact sur la végétation lors des pics de population, suggérant un rôle possible des interactions plantes-herbivores. Nous utilisons une expérience à grande échelle où les prédateurs ont été exclus pour déterminer si la réduction des prédateurs pourrait avoir des effets en cascade sur la végétation par le biais d'une augmentation des densités de lemmings dans l'Arctique canadien. Les traits morphologiques et la biomasse de *Salix arctica* et la biomasse de *Poaceae* et de *Juncaceae* ont été échantillonnés à l'intérieur et à l'extérieur d'exclos à lemmings. Nous avons détecté des signes de broutement par les lemmings sur le nombre de bourgeons et de chatons de *S. arctica* à la fonte des neiges, et sur la longueur de la tige, la croissance de la tige et le nombre de feuilles pendant l'été, mais l'impact était relativement faible. Nous n'avons pas détecté d'impact du broutement sur la biomasse végétale pendant l'été. Nous avons également trouvé peu d'évidence que l'impact du broutement était plus élevé dans l'exclos à prédateurs même si la densité de lemmings a augmenté jusqu'à deux fois. Nos résultats suggèrent que l'impact à court terme des lemmings sur les plantes vasculaires est relativement faible et qu'une augmentation expérimentale de la densité de lemmings n'a pas eu d'effet en cascade sur les plantes consommées par ces herbivores dans l'Arctique canadien. [Ceci est une traduction fournie par l'auteur du résumé en anglais.]

Mots-clés : petits mammifères, prédation, dynamique de population, interactions plante-herbivore, saule Arctique, cascade trophique

Introduction

Biotic interactions play a key role in structuring the tundra food web (Legagneux et al. 2014; Barrio et al. 2016). Plant–herbivore interaction has long been thought to be a dominant interaction of the Arctic tundra on the premise that the primary production is too low to support an herbivore biomass large enough to sustain viable predator populations (Oksanen et al. 1981; Oksanen and Oksanen 2000).

Small mammals, and in particular lemmings, are among the most important herbivores of the tundra and are well known for their periodic population fluctuations of large amplitude (Gilg et al. 2003; Gruyer et al. 2008; Gauthier et al. 2024). Some studies supported the hypothesis that lemming population dynamics is primarily driven by plant–herbivore interactions and that population crashes following a peak are due to an exhaustion of the food supply caused by overgrazing (Turchin et al. 2000; Pitelka and Batzli 2007; Oksanen et al. 2008). In accordance with this idea, several studies documented a negative impact of lemmings on plant communities in Fennoscandia and Alaska, both in the short term (Moen et al. 1993; Olofsson et al. 2012; Villarreal et al. 2012) and the long term (Virtanen et al. 1997; Johnson et al. 2011; Olofsson et al. 2014).

In recent decades, however, an increasing number of studies in the Canadian Arctic and in Greenland have found that lemming populations are primarily limited by predators (Reid et al. 1995; Wilson et al. 1999; Gilg et al. 2003; Fauteux et al. 2016). Multi-site food web modelling further confirmed that predator–prey interactions can be a dominant force in structuring tundra food webs (Krebs et al. 2003; Legagneux et al. 2014). According to Legagneux et al. (2014), small body-size species of the tundra such as rodents tend to be more controlled by predators, whereas large body-size ones such as ungulates tend to be more food-limited. Therefore, unlike the situation of voles in boreal and sub-Arctic regions, where there is an emergent consensus that predators control their population dynamics (Korpimäki and Norrdahl 1998; Klemola et al. 2000; Korpimäki et al. 2004), factors controlling lemming populations remain controversial (Gauthier et al. 2009; Oksanen et al. 2009; Krebs 2011).

Field experiments are a powerful tool to disentangle factors controlling animal populations (Huitu et al. 2003; Krebs 2011). In food webs composed of three levels, the removal of predators could lead to a trophic cascade by allowing herbivores to reach densities high enough to negatively impact the vegetation (Oksanen et al. 1981; Oksanen and Oksanen 2000). Large-scale experiments performed in northern Europe revealed that predator removal can change the phase of vole population cycles (Korpimäki and Norrdahl 1998) and increase their densities high enough to induce negative grazing impacts on vegetation, especially in winter (Klemola et al. 2000; Huitu et al. 2003). Experimental removal of predators in northern Canada increased survival and densities of cyclic lemming populations, and delayed population crashes (Wilson et al. 1999; Fauteux et al. 2016), but the effect of such experiments on vegetation has yet to be examined. In one of the rare studies in the Canadian Arctic, Bilodeau et al. (2014) could not detect any impact of lemming grazing on both vascular plants and mosses during a lemming peak. However, lemming densities during peak years in the High Arctic are inferior than those at low Arctic sites (Ekerholm et al. 2001; Gilg 2002; Pitelka and Batzli 2007; Fauteux et al. 2015) where impacts of lemming grazing have been documented (Moen et al. 1993; Villarreal et al. 2012). It is thus relevant to examine whether experimentally increased lemming densities due to predator removal could lead to a significant impact on the vegetation in the High Arctic.

Lemming activities in winter are concentrated in patches of deep snow characterized by a heterogenous microtopography (i.e., snowbeds; Duchesne et al. 2011; Reid et al. 2012). This, in combination with the absence of plant growth during the long Arctic winter, may make lemmings especially susceptible to food depletion at this time of the year. Several studies have showed that winter grazing by Norwegian lemmings (*Lemmus lemmus*) can have a strong impact on snowbed vegetation and reduces the availability of palatable plant species (Moen et al. 1993; Virtanen et al. 1997, 2002). Snow conditions in the basal layers may also hinder the ability of lemmings to feed on high quality plants in winter, either by reducing their functional habitat or limiting access to food resources (Korslund and Steen 2006; Poirier et al. 2019, 2021).

In this study, we use a large-scale experiment where most lemming predators were excluded and which resulted in a two-fold increase in lemming abundance at peak densities compared to the control (Fauteux et al. 2016). This manipulation allowed us to investigate whether predator reduction could have cascading effects on the vegetation through an increase in lemming densities (Schmitz et al. 2000; Huitu et al. 2003). Our study is the first one in the High Arctic to examine the effect of lemming grazing on the vegetation using a two-factor experimental setup where either predators or herbivores alone or both predators and herbivores are excluded. In this study, we focus on the quantitative impact of lemming grazing by examining plant biomass and abundance or size of specific plant parts. We hypothesized that if predator reduction allows lemmings to reach densities high enough to become food limited, we should detect a grazing impact on their most important food items in winter, such as willows (Soininen et al. 2015), at snowmelt and after the summer regrowth. We thus predicted that the impact of lemming grazing (1) should be higher when predation is reduced because of higher lemming densities and (2) should be proportional to variations in lemming densities through the various phases of their population cycle; additionally, (3) grazing impact should be most intense in snowbeds, a habitat preferred by lemmings in winter and prone to resource overuse. Our results should help determine whether food limitation could be a density-dependent factor capable of stopping lemming population growth during peak years.

Materials and methods

Study area

The study took place on Bylot Island, Nunavut, Canada (73°08′N, 80°00′W) from 2014 to 2016. The ground is generally snow-free from mid-June to beginning of October with a mean temperature of −14.5 °C annually and 6.3 °C during July, and rainfall from June to August averaging 91 mm (Gauthier et al. 2011). The area corresponds to bioclimatic subzone C of Walker et al. (2005). The study site is located in upland areas dominated by mesic tundra, which account for 85% of the landscape of the area (Bilodeau et al. 2014). Mesic tundra is characterized by hummocky terrain on plateaus and gentle slopes and is crossed by numerous small streams draining the surrounding landscape into low-elevation wetlands through gullies. The mesic tundra plant community is dominated by shrubs (mostly *Salix arctica*, but also *Salix herbacea* and *Salix reticulata*, *Dryas integrifolia* and *Cassiope tetragona*), graminoids (*Arctagrostis latifolia*, *Alopecurus alpinus*, *Poa arctica, Luzula confusa*, and *Luzula nivalis*), sedges (*Eriophorum angustifolium, Carex* spp.), and herbs (*Stellaria longipes*, *Oxyria digina*, *Polygonum viviparum*, *Potentilla* spp., *Ranunculus* spp. *Pedicularis* spp., and *Saxifraga* spp.). Field research on Bylot Island was conducted in accordance with permits delivered by Parks Canada for Sirmilik National Park.

The region hosts two species of rodents, the Nearctic brown lemming (*Lemmus trimucronatus*), which shows large amplitude population cycles with a periodicity of 3–4 years, and the Nearctic collared lemming (*Dicrostonyx groenlandicus*), which shows fluctuations of small amplitude (Gruyer et al. 2008). Lemming densities found on Bylot Island are typical of those found at other High Arctic sites (e.g., in Greenland; Gauthier et al. 2024) but are inferior to those found at low Arctic sites in Alaska or Fennoscandia (Ekerholm et al. 2001; Pitelka and Batzli 2007). The other important herbivore, the greater snow goose (*Anser caerulescens atlanticus*), is only present during the summer and primarily feeds in wet habitats. Other herbivores such as rock ptarmigans (*Lagopus mutus*) and Arctic hares (*Lepus arcticus*) are rare in the area and large mammalian herbivores are absent. Predators of lemmings are mainly American ermines (*Mustela richardsonii*), arctic foxes (*Vulpes lagopus*), snowy owls (*Bubo scandiaca*), rough-legged hawks (*Buteo lagopus*), long-tailed jeagers (*Stercorarius longicaudus*), and glaucous gulls (*Larus hyperboreus*) (Legagneux et al. 2012). According to the literature, the diet of brown lemmings is dominated by grasses, sedges, and mosses and the one of collared lemmings by dicotyledons (Batzli and Jung 1980; Batzli and Pitelka 1983; Rodgers and Lewis 1985). However, DNA metabarcoding analyses identified *Salicaceae* as the most consumed vascular plant family by both lemming species on Bylot Island in winter, with a smaller proportion of *Poaceae* and *Juncaceae* (Soininen et al. 2015).

Predator exclosure

At the end of summer 2013, we established a predator exclosure preventing access to all lemming predators except ermines on an 8.6 ha (360 m × 240 m) area of mesic tundra. Arctic foxes were excluded from the area by a 1.4–2 m high fence—a variation caused by terrain unevenness—made of chicken wire (2.5 cm × 2.5 cm mesh size) and maintained by steel T-posts. This mesh size allowed lemmings to move freely through the fence, but potentially also ermines although no physical signs (i.e., feces, carcasses) or visual observations were ever noted inside the fenced area. Avian predators were kept out of the exclosure by a roof of nylon fishing lines crisscrossing each other every 0.5 m over the complete area of the exclosure and supported by steel rods. In winter, the net also acted as a protection against foxes that could have penetrated the fenced area from above due to snow drifts. Additional details and pictures of the predator exclosure can be found in Fauteux et al. (2016).

Lemming densities

We estimated lemming density each summer from 2011 to 2017 by live trapping them in two grids, one inside the predator exclosure (experimental grid) and one in a control site also located in mesic habitat 600 m away. The experimental trapping grid had 96 traps (8 × 12), whereas the control grid had 144 traps (12 × 12; traps spaced every 30 m in both sites). Lemmings were captured for three consecutive days during three periods in mid-June, mid-July, and mid-August. Traps were checked twice daily, and all individuals captured were identified to the species and either marked with a passive integrated transponders or an ear tag with a unique number. These data allowed an estimation of population density using spatially explicit capture–recapture models with the package “secr” integrated in the R software (Efford 2024). More details on field methods and statistical analyses can be found in Fauteux et al. (2015). Capture of animals was approved by ethical committees of Université Laval in accordance to the Canadian Council on Animal Care guidelines.

We estimated the density of lemming winter nests from an exhaustive sampling of the area delimited by the trapping grids in early July, shortly after snowmelt. We systematically walked the grids along parallel lines separated by 10 m and all nests found were counted, identified to the species based on feces color and shape (Duchesne et al. 2011; Soininen et al. 2015) and destroyed to avoid re-sampling the following year. For each trapping grid, the total number of nests of each lemming species was divided by the grid size (nest/ha).

Lemming exclosures

We randomly selected sites located inside the predator exclosure ($n = 16$) and within the limits of the control trapping grid where predators had access ($n = 8$). Each site consisted of a grazing exclusion plot of 70 cm × 70 cm (referred as lemming exclosure) paired with a control plot of similar size exposed to lemmings (referred as grazed plot) located within a 5 m radius. The control plot was located in an area of similar plant composition compared to its paired lemming exclosure to avoid too much spatial heterogeneity (e.g., we avoided pairing a plot with only shrubs with one with only graminoids). We equally split the sites between inside and outside snowbeds, which are highly used by lemmings in winter due to the favourable conditions provided by a thick snow cover (Duchesne et al. 2011; Reid et al. 2012). Permanent lemming exclosures were installed over the grazing exclusion plots at the end of the summer 2013 and were 1 m × 1 m or 2 m × 2 m in size. They were made of galvanized welded wire (1.25 cm × 1.25 cm mesh size) 1 m high and buried at least 10 cm into the soil to prevent lemming intrusions. Exclosures were checked every summer to make sure the frost–defrost action of the soil did not push the fence out of the soil. No sign of lemming presence (e.g., feces, fresh tunnels, or grazing marks) were ever detected inside lemming exclosures. Control plots outside the predator exclosure were further fenced with chicken wire (2.5 cm × 2.5 cm mesh size) to prevent grazing by greater snow geese or other herbivores, which were also excluded by our predator exclosure. However, these exclosures did not prevent grazing by lemmings, which could move through this mesh size.

Table 1. Description of the traits measured on marked individual shoots of *Salix arctica* and of the biomass measured on selected plants in 70 cm × 70 cm plots (dependent variables) and when the sampling was carried out during the season.

Variables	Description	Timing
Salix arctica		
Number of buds	Count of the number of buds before blooming	Snowmelt
Number of catkins	Count of the number of inflorescences (male + female)	Snowmelt and end of summer growth
Number of leaves	Count of the number of green leaves	End of summer growth
Stem diameter	Measurement of the basal stem diameter at moss level (±0.01 mm)	End of summer growth
Stem length	Measurement of maximal stem length from moss level to the tip (±0.01 mm)	End of summer growth
Stem growth	Maximal growth of the stem during the summer measured by the length of the new, light green stem section (±0.01 mm)	End of summer growth
New ramifications	Count of the number of new (light green) ramifications of the stem	End of summer growth
All ramifications	Count of the total number of ramifications of the stem, including new ones	End of summer growth
Vascular plant species		
Biomass	Aboveground biomass (g/m^2) estimated by point intercept sampling for major taxa	End of summer growth

Vegetation sampling

Salicaceae is the most important food item consumed by lemmings at our study site during winter (84% in collared lemmings and 56% in brown lemmings; 76% if we exclude mosses for the latter species; Soininen et al. 2015). Among the three *Salicaceae* species at our study site (see above), *Salix arctica* is by far the most abundant (Duclos 2002; Bilodeau et al. 2014). Cafeteria trial experiments also confirmed that brown lemmings readily eat *S. arctica*, especially buds, catkins, and roots (Fauteux et al. 2017). Therefore, we paid special attention to this important food item.

We examined the impact of lemming grazing on individual shoots of *S. arctica*. In early summer 2014, we randomly selected five individual shoots in every plot and marked them with small metal bands loosely tied at their base. At the end of June 2015 and 2016, shortly after snowmelt, we recorded physical signs of winter grazing by lemmings (clipped stems or buds) and we counted the number of buds and catkins on marked shoots in grazed plots. We also counted fresh lemming feces in grazed plots to confirm lemming activity at these sites. Number of feces piles were counted individually for each species and number of feces in each pile was estimated on a logarithmic scale. At the end of July or early August 2014, near the end of the growing season, we measured the stem diameter, length and growth, and counted the number of leaves, total ramifications, and new ramifications of all marked shoots (see Table 1 for measurement descriptions) in both grazed and ungrazed (i.e., lemming exclosures) plots. The same shoots were repeatedly sampled in 2015 and 2016, unless they were completely grazed by lemmings, in which case they were replaced (3% of the shoots were replaced).

We examined the impact of grazing on the biomass of the most important vascular plants consumed by lemmings in winter, *Salicaceae*, *Juncaceae*, and *Poaceae* (collectively, these three families account for >87% of vascular plants consumed; Soininen et al. 2015). We estimated plant abundance with a non-destructive point intercept sampling method derived from the ITEX protocol (Henry and Molau 1997) in all lemming exclosures and plots exposed to grazing at the end of July or early August in 2014 and 2015. The sampling was performed with a 100 points square grid (70 cm × 70 cm) composed of two superposed and parallel layers of string spaced every 7 cm. The frame supporting the grid was horizontally leveled before each sampling and settled every year in the same position in the center of the plots. Plant hits were identified at the species level according to the top-bottom method sampling where only the first and last species touched by the needle was noted for a total of 200 records per frame (May and Hollister 2012). We also determined whether the plant parts were alive or dead, and for woody plants whether the plant parts were woody (lignified) or non-woody (leaves, buds, and flowers). Total aboveground biomass of each taxon was then estimated from pointing data using formulas validated and calibrated in the field in summer 2015 (see Supplementary methods and Table S1 for details). Biomass was estimated at the species level (except for *Poaceae*), and for *Salicaeae*, we divided biomass into non-woody and woody parts. *Juncaceae* was the sum of *L. confusa* and *L. nivalis*, *Poaceae* included several species but mostly *Arctagrostis latifolia*, *Alopecurus alpinus*, and *Poa arctica*, and *Salicaceae* was the sum of *S. arctica* and *S. herbacea*. For *Poaceae* and *Juncaceae*, we used total biomass (combination of live and dead vegetation). However, analyses based on only live biomass yielded the same results (results not shown).

Statistical analyses

We used χ^2 tests to compare the proportion of marked *S. arctica* shoots in plots exposed to lemmings showing signs of grazing at snowmelt between inside/outside the predator exclosure, inside/outside snowbeds and years (2015 vs. 2016). We used linear mixed effects (LME) models to examine the influence of predation (inside vs. outside the predator exclosure), habitat (inside vs. outside snowbeds), and year (2015 vs. 2016) on the number of buds and catkins at snowmelt in plots exposed to lemming grazing. All analyses were conducted at the plot level and thus measurements from the five individual shoots within the same plot were averaged and expressed as means per plot to avoid pseudoreplication (Hurlbert 1984). Another advantage of using the mean value per plot was that the distribution of count data was rather continuous. We used the sampling site (i.e., a pair of lemming exclosure and control plot) as the random effect variable because the same sites were sampled annually (Pinheiro and Bates 2000). Year was used as a fixed effect to account for the different phases of the lemming cycle. We applied a logarithm transformation to dependent variables to improve normality and the residual distribution. Normality was respected based on the Shapiro–Wilk test. We used a simple linear regression to examine the relationship between the mean number of buds and catkins (combined) per plot and the log number of lemming feces at each plot.

We examined the effect of lemming grazing on *S. arctica* morphological traits and vascular plant biomass at the end of the growing season by comparing grazed vs. ungrazed plots with LME models using again the site as a random effect. Linear models were used in biomass analyses for *S. arctica* wood and *S. herbacea* because too few plots with these plant items were sampled in both years. Variables that did not respect normality of the residuals were log- (number of leaves, stem diameter, stem growth, and biomass of *S. herbacea*, *Poaceae*, and *Juncaceae*) or square root-transformed (all and new ramifications and non-woody biomass of *S. arctica*) to improve normality. Normality was respected based on the Shapiro–Wilk test except in one case (number of catkins, $p < 0.01$) where we used a Wilcoxon rank sum test.

To provide a more direct assessment of the treatment effects (predation, habitat, and year) on the impact of lemming grazing on *S. arctica* morphological traits and plant biomass at the end of the growing season, we calculated the difference (D) between paired lemming exclosures (ungrazed, U) and control plots (grazed, G) for each variable i ($D_i = U_i - G_i$). A positive D_i value would indicate a reduction of this trait in grazed plots due to lemmings and we will refer to this variable as lemming grazing impact below. We used LME models to examine the influence of predation (inside vs. outside the predator exclosure), habitat (inside vs. outside snowbeds), and year (2014, 2015, and 2016 for morphological traits; 2014 and 2015 for biomass) on D_i with site as a random effect. We applied a logarithm transformation to the stem diameter to improve normality and the residual distribution. Normality was respected based on the Shapiro–Wilk test. Because *S. arctica* wood and *S. herbacea* were absent from several sampling sites, these sites were excluded from the biomass analysis for these variables as they contributed no information. This reduced the number of sites sampled repeatedly, which is why site was not used as a random factor for these two variables. Finally, because *S. herbacea* was almost exclusively found in snowbeds, the factor habitat was excluded from the analysis for this species.

We created a set of candidate models including various combinations of our three main factors and of two-way interactions that we applied to all dependent variables analysed (Table S2). We selected the best model using the Akaike information criterion corrected for small sample sizes (AIC$_c$). When no single model in the candidate set had a clear support (AIC$_c$ weights < 0.90), we performed model-averaging on estimates and their confidence intervals using models with ΔAIC$_c$ < 4. All analyses were performed using R statistical software version 4.4.0 (R Core Team 2024). LME's parameters were estimated with the "nlme" package (Pinheiro and Bates 2024) and the "AICcmodavg" package was used for model selection and multimodel inference (Mazerolle 2023).

Results

Lemming population dynamics

Summer densities of brown lemmings were high in 2011 but subsequently crashed and were very low in 2012 and 2013 (Fig. 1). Brown lemmings peaked again in 2014, stayed relatively high in 2015 and 2016, and finally crashed in 2017. From 2014 to 2016, brown lemming densities were much higher in the predator exclosure than in the control site at most trapping sessions (Fig. 1). The same was true for winter nest densities except during winter 2013–2014 when they were high both inside and outside the predator exclosure. Summer densities of collared lemmings were low in all years in the predator exclosure and were higher in the control grid than the predator exclosure from 2014 to 2016 (Fig. 1). Brown lemming densities were always several times higher than those of collared lemmings except in crash years when both species were virtually absent.

Grazing impact on *Salix arctica* at snow melt

We frequently detected signs of lemming grazing at snowmelt on marked *S. arctica* shoots (clipped stems and buds) in the control plots but never in lemming exclosures. The proportion of shoots showing signs of grazing ($n = 203$) did not differ between the predator exclosure and the control site (0.23 vs. 0.24, $\chi^2_{(1)} = 0.04$, $p = 0.84$), but was significantly higher inside than outside snowbeds (0.30 vs. 0.17, $\chi^2_{(1)} = 4.82$, $p = 0.03$) and in 2015 than in 2016 (0.47 vs. 0.08, $\chi^2_{(1)} = 41.6$, $p < 0.001$). A total of seven shoots (5.8% of all marked shoots) were found completely clipped at moss level after snowmelt. The seven shoots were all in snowbeds and three of them inside the predator exclosure.

The number of *S. arctica* buds at snow melt in grazed plots varied according to predation and habitat, and habitat and year in interaction (Tables 2 and S3). The number of buds was lower in presence of predation than in absence inside snowbeds, whereas the reverse was true outside snowbeds. The number of buds was also lower in 2015 than in 2016 inside snowbeds but not outside (Fig. 2). The number of *S. arctica* catkins in grazed plots was negatively influenced by predation only (Tables 2 and S3) as it was lower in presence than in absence of predation (Fig. 2). The combined number of *S. arctica* buds and catkins at snowmelt was negatively related to the number of lemming feces measured in grazed plots ($\beta = -0.80$, 95% CI $= -0.03, -1.56$; Fig. 3).

Grazing impact on *Salix arctica* traits at the end of the summer

Stem length, number of leaves, and stem growth of *S. arctica* were all significantly higher in plots protected from

Fig. 1. Summer density (±SE) and winter nest density of brown and collared lemmings in presence (control site) and absence (predator exclosure) of predation on Bylot Island, Nunavut, from 2011 to 2017. Gray areas indicate winters. The vertical dashed line is when the predator exclosure was set up. Note the scale difference on the *Y* axis between the two graphs. Jn = June; Jl = July; Au = August; W = Winter.

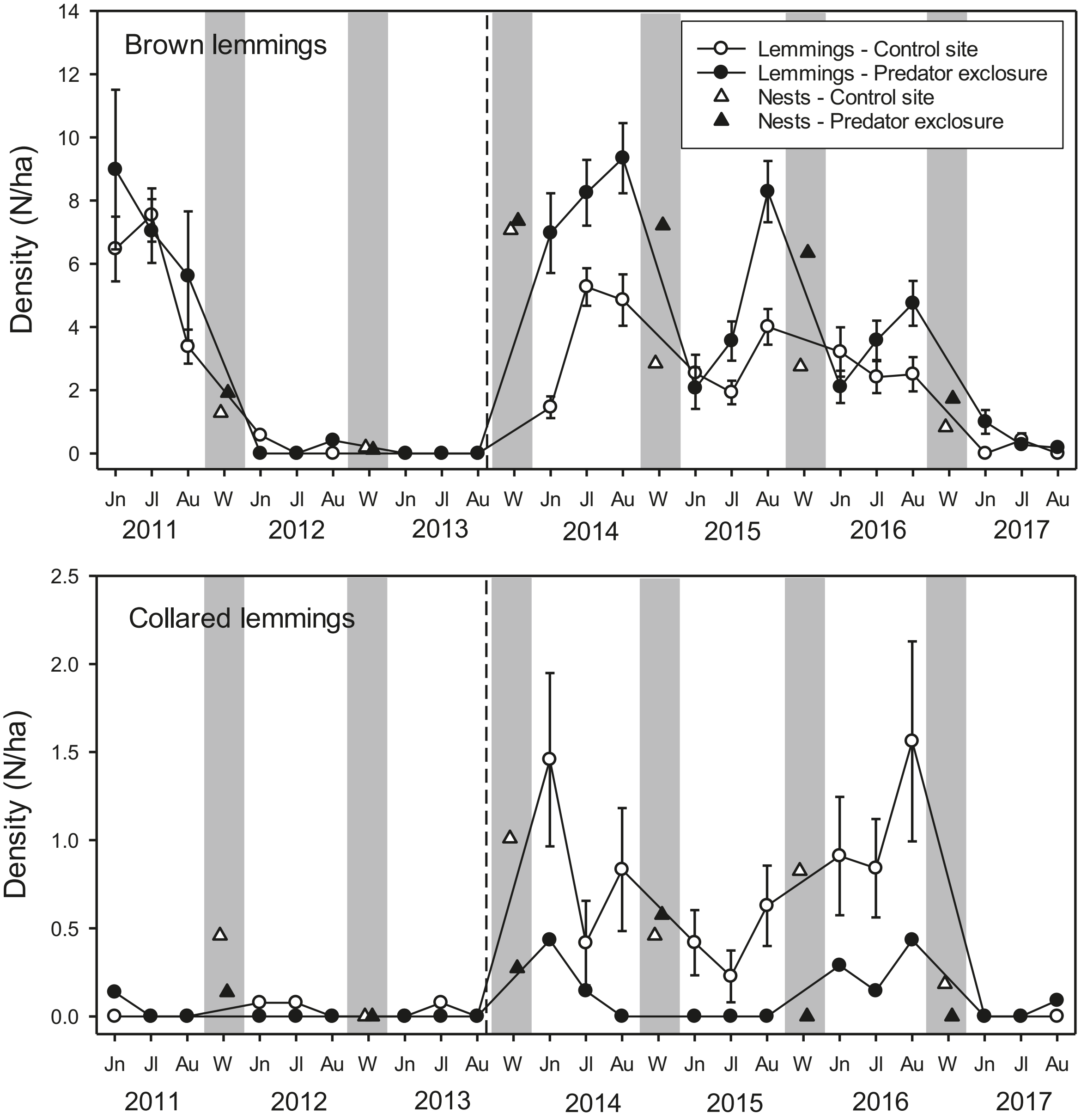


Table 2. Parameter estimates with 95% confidence intervals of the influence of predation, habitat, and year on the number of buds and catkins of *Salix arctica* at snow melt in plots exposed to lemming grazing on Bylot Island, Nunavut, 2015–2016 ($n = 40$), based on model-averaging (models with $\Delta AIC_c < 4$, Table S3).

Variable	Predation[a]	Habitat[b]	Year[c]	Predation × habitat	Predation × year	Habitat × year
Buds	−0.11 (−0.53, 0.31)	**−0.54 (−1.00, −0.08)**	0.08 (−0.26, 0.41)	**−1.13 (−1.85, −0.40)**	−0.07 (−0.42, 0.28)	**0.49 (0.14, 0.84)**
Catkins	**−0.28 (−0.53, −0.02)**	−0.08 (−0.33, 0.15)	0.09 (−0.13, 0.31)	NA	NA	NA

Note: Values in bold are significant (confidence interval excludes zero). NA = not retained in the most parsimonious models.

[a] Predator exclosure (predation absent) is the level of reference.

[b] Outside snowbed is the habitat of reference.

[c] Year 2015 is the year of reference.

lemmings than in those exposed to them at the end of summer growth (Fig. 4; Table S4). However, stem diameter and number of ramifications did not differ between ungrazed and grazed plots. These results indicate that our sampling design was sufficient to detect an impact of lemming grazing on some *S. arctica* traits.

Fig. 2. Mean number (±SE) of buds or catkins of *Salix arctica* at snowmelt in absence (predator exclosure) or presence (control site) of predation, inside or outside snowbeds, and in 2015 and 2016 in plots exposed to lemming grazing on Bylot Island, Nunavut ($n = 40$).

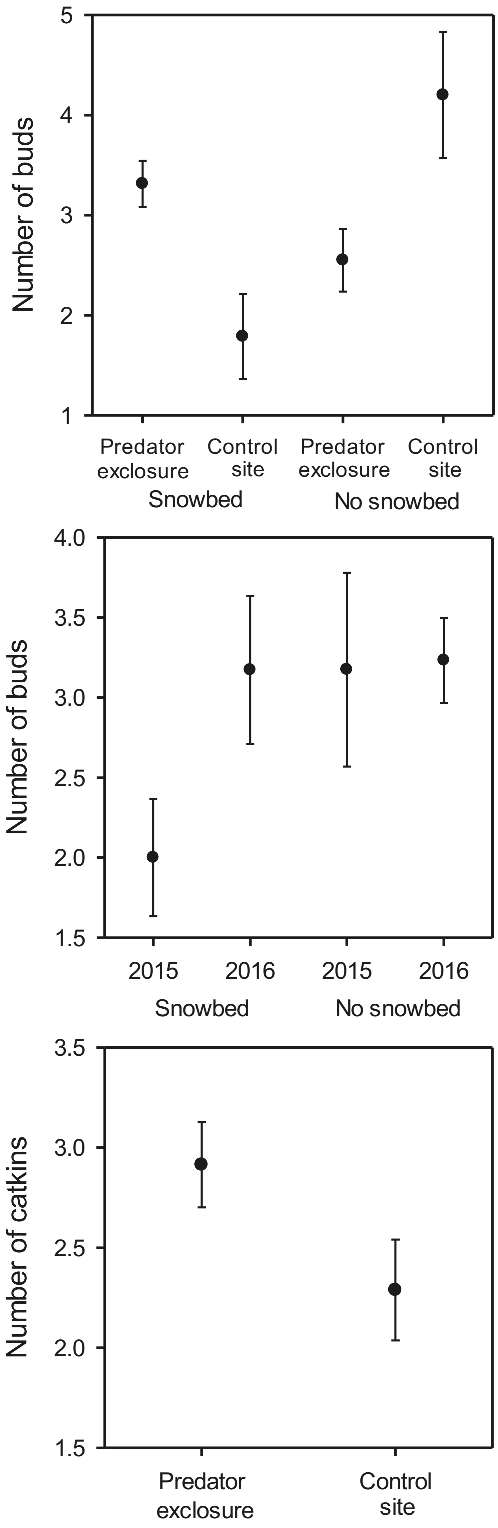
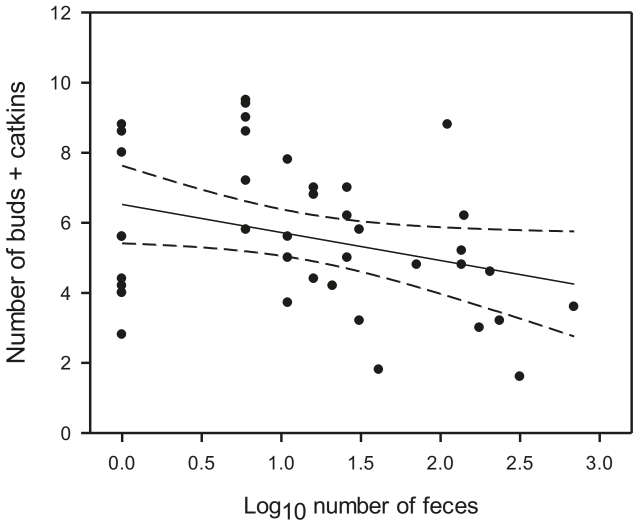


Fig. 3. Mean number of *Salix arctica* buds and catkins (combined) per plot in relation to the number of lemming feces in plots exposed to grazing at snowmelt in 2015 and 2016 on Bylot Island, Nunavut. The dotted lines represent the 95% confidence interval.



Overall, none of the treatments (i.e., predation, habitat, or year) had a consistent influence on the grazing impact of lemmings on various morphological traits of *S. arctica* (Table S5). Predator exclusion affected grazing impact on catkins and all ramifications. In presence of predation, grazing impact on catkins was reduced but the grazing impact on the number of ramifications was higher in presence than in absence of predation (Table 3; Fig. 5). Grazing impact was higher on stem diameter in 2016 than in 2014, higher on stem length in 2015 and 2016 than in 2014, and higher on stem growth in 2015 than in 2014 (Table 3; Fig. 5). Finally, there was no difference in lemming grazing impact between inside and outside snowbeds for any *S. arctica* morphological traits (Table 3).

Grazing impact on plant biomass at the end of the summer

No difference in aboveground biomass was found at the end of summer growth between plots ungrazed (i.e., inside lemming exclosures) and grazed by lemmings for all taxa analyzed (*Salicaceae*, *Poaceae*, and *Juncaceae*; Table S6). On average, the percentage difference in biomass between ungrazed and grazed plots ranged from +0.1 to −10.3% except for *S. herbacea* (+22.7%; Table S7). These results suggest that lemming grazing was globally quite small and not high enough to allow our sampling design to detect its impact on plant biomass.

Predation (presence vs. absence of predators), habitat (inside vs. outside snowbeds), and year had little influence on the difference in aboveground biomass between ungrazed and grazed plots for all taxa (Tables 4 and S8). Difference in *S. herbacea* biomass between ungrazed and grazed plots tended to be greater in absence of predation than in presence and difference in *Juncaceae* biomass between ungrazed and grazed plots was greater in 2014 than in 2015 (Table 4; Fig. 6).

Discussion

Our experimental design allowed us to detect an impact of lemming grazing on some *S. arctica* morphological traits,

Fig. 4. Comparison of number of leaves, stem length, and stem growth of *Sakix arctica* at the end of the summer between plots ungrazed (lemming exclosures) and grazed by lemmings from 2014 to 2016 on Bylot Island, Nunavut. Values are the mean (±SE), $n = 64$ in each treatment.

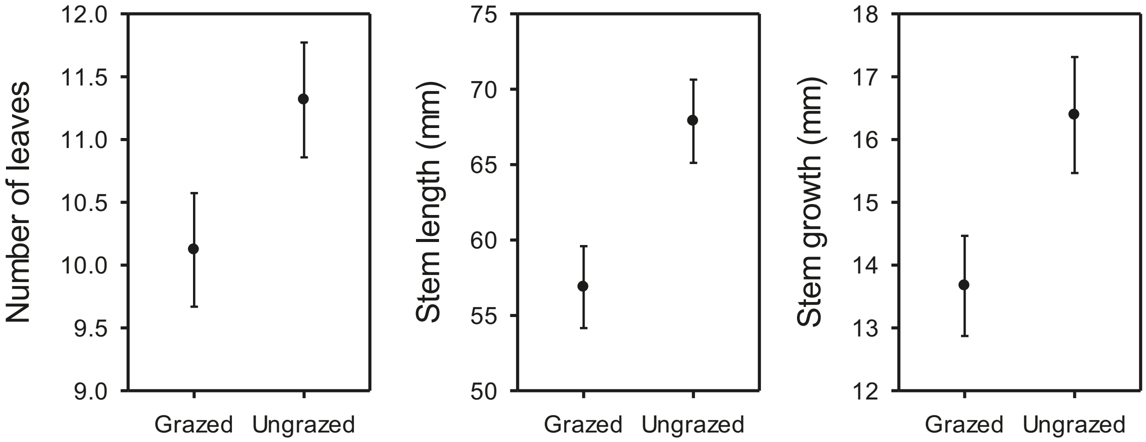


Table 3. Parameter estimates with 95% confidence intervals of the influence of predation, habitat, and year on the difference in various *Salix arctica* morphological traits at the end of the summer between plots ungrazed (lemming exclosures) and grazed by lemmings on Bylot Island, Nunavut, 2014–2016 ($n = 64$ except new ramifications, $n = 48$) from model-averaging (models with $\Delta\text{AIC}_c < 4$, Table S5).

Morphological trait	Predation[a]	Habitat[b]	Year 2015[c]	Year 2016[c]
Number of catkins	**−0.14 (−0.27, −0.01)**	0.04 (−0.08, 0.17)	NA	NA
Number of leaves	2.15 (−1,17, 5.46)	1.37 (−1.82, 4.56)	NA	NA
Stem diameter	0.02 (−0.15, 0.19)	−0.10 (−0.26, 0.05)	0.03 (−0.07, 0.12)	**0.14 (0.03, 0.23)**
Stem length	0.16 (−18.63, 18.96)	3.51 (−14.17, 21.20)	**8.89 (2.68, 13.09)**	**11.88 (5.67, 18.08)**
Stem growth	−0.02 (−4.41, 4,36)	1.74 (−2.34, 5.86)	**4.88 (1.74, 8.04)**	2.83 (−0.32, 5.98)
All ramifications	**0.73 (0.01, 1.46)**	0.16 (−0.56, 0.87)	NA	NA
New ramifications	0.219 (−0.14, 0.58)	−0.07 (−0.41, 0.28)	–	0.07 (−0.20, 0.33)

Note: Values in bold are significant (confidence interval excludes zero). NA = not retained in the most parsimonious models and – = not included in the set of candidate models.

[a] Predator exclosure (predation absent) is the level of reference.

[b] Outside snowbed is the habitat of reference.

[c] Year 2014 is the year of reference except for new ramifications for which 2015 is the year of reference.

such as on the number of buds and catkins at snowmelt or stem length, stem growth, and number of leaves during the summer regrowth. However, we could not detect any impact of lemming grazing on the biomass of their main food plants (*Salicaceae*, *Poaceae*, and *Juncaceae*) at the end of the growing season. Our predator exclosure was successful in increasing brown lemming density up to two-fold compared to the control sites (see also Fauteux et al. 2016). However, we found limited evidence that the impact of lemming grazing on *S. arctica* morphological traits or plant biomass was higher in the predator exclosure compared to the control site during the first 3 years of the experiment, contrary to our initial prediction. Therefore, our results suggest that the short-term impact of lemming grazing on their preferred winter food plants is relatively small compared to other Arctic sites (Thompson 1955; Moen et al. 1993; Virtanen et al. 2002; Villarreal et al. 2012) and this impact was not significantly enhanced by an experimental increase in lemming density.

During the increase phase, Arctic lemmings often reach high densities in late winter under the snow due to intense winter reproduction (Henttonen and Kaikusalo 1993; Gilg 2002; Fauteux et al. 2015). Because of the absence of plant growth in winter, the impact of grazing should be highest at that time of the year (Soininen and Neby 2024). This can explain why the number of willow buds and catkins, the plant parts preferred by brown lemmings (Fauteux et al. 2017), were reduced at snow melt in individual plots where lemming activity was highest. In contrast, at a larger spatial scale, increased lemming density in the predator exclosure did not reduce the number of catkins at snowmelt, which was in fact higher in absence than in presence of predators. Although the number of buds was lower in the predator exclosure than the control site outside snowbeds, the trend was reversed in snowbeds, the preferred winter habitat of lemmings (Duchesne et al. 2011; Reid et al. 2012). Therefore, artificially increasing lemming density had no consistent effect on *S. arctica* buds at snowmelt.

Fig. 5. Difference between plots ungrazed (lemming exclosures) and grazed by lemmings in the number of (A) catkins and (B) all ramifications of *Salix arctica* in absence (predator exclosure, $n = 40$) or presence (control) of predation ($n = 24$), and in (C) stem diameter, (D) stem length, and (E) stem growth (all in mm) of *S. arctica* at the end of the summer according to the sampling year (2014: $n = 16$, 2015 and 2016: $n = 24$ each) on Bylot Island, Nunavut. Values are the mean difference (±95% confidence intervals). A positive difference indicates a reduced value in grazed plots.

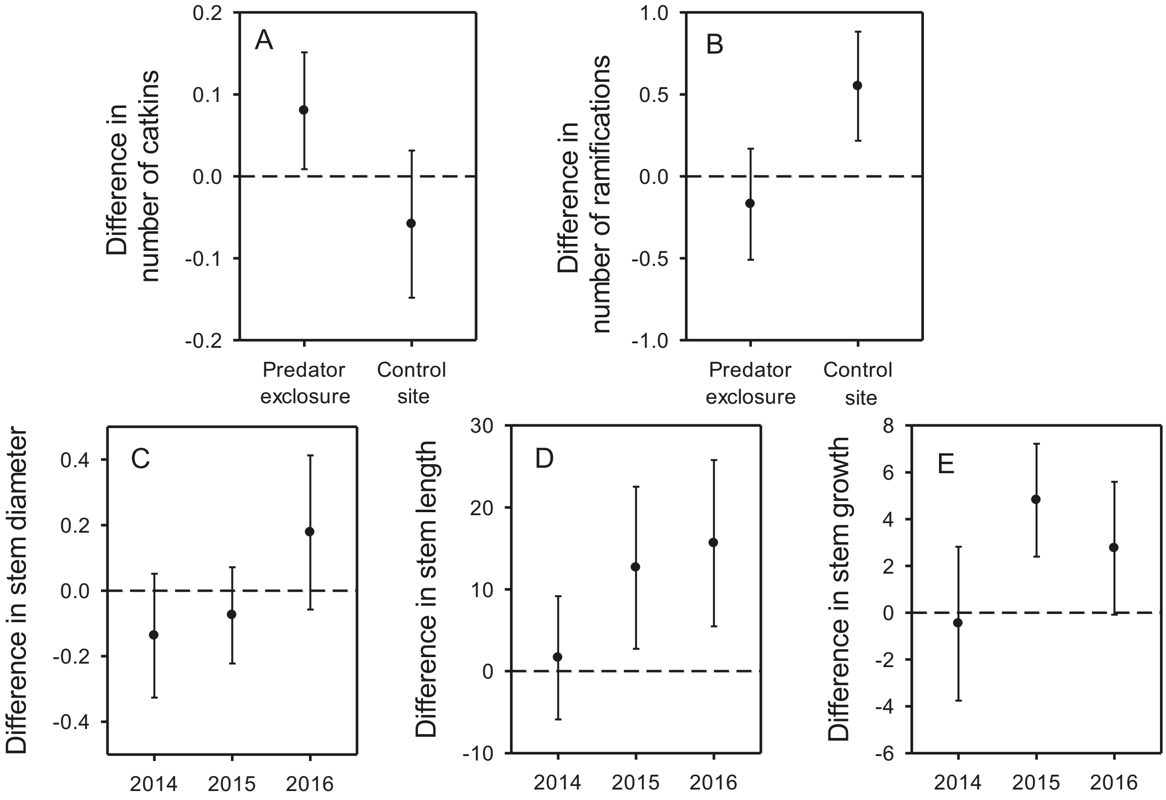


Table 4. Parameter estimates with 95% confidence intervals of the influence of predation, habitat, and year on the difference in total aboveground biomass of different taxa at the end of the summer between plots ungrazed (lemming exclosures) and grazed by lemmings on Bylot Island, Nunavut, 2014–2015 ($n = 40$ except *Salix arctica* wood, $n = 34$ and *Salix herbacea*, $n = 27$) from model-averaging (models with $\Delta AIC_c < 4$, Table S8).

Plant taxa	Predation[a]	Habitat[b]	Year 2015[c]
S. arctica wood	2.91 (−1.45, 7.27)	2.70 (−1.53, 6.93)	−1.08 (−5.71, 3.55)
S. arctica non wood	1.54 (−1.87, 4.95)	1.63 (−1.70, 4.96)	−0.50 (−3.51, 2.51)
S. arctica total	5.09 (−1.74, 11.92)	3.07 (−3.66, 9.80)	−0.26 (−5.67, 5.16)
S. herbacea non wood	−2.40 (−5.01, 0.22)	–	1.06 (−1.69, 3.80)
Salicaeae non wood	−0.35 (−3.99, 3.29)	−0.76 (−4.28, 2.77)	0.25 (−2.93, 3.43)
Poaceae	−1.26 (−4.41, 1.88)	−1.72 (−4.67, 1.24)	1.18 (−0.42, 2.78)
Juncaceae	0.33 (−0.49, 1.14)	−0.02 (−0.81, 0.77)	**−0.99 (−1.67, −0.30)**

Note: Values in bold are significant (confidence interval excludes zero). – = not included in the set of candidate models.

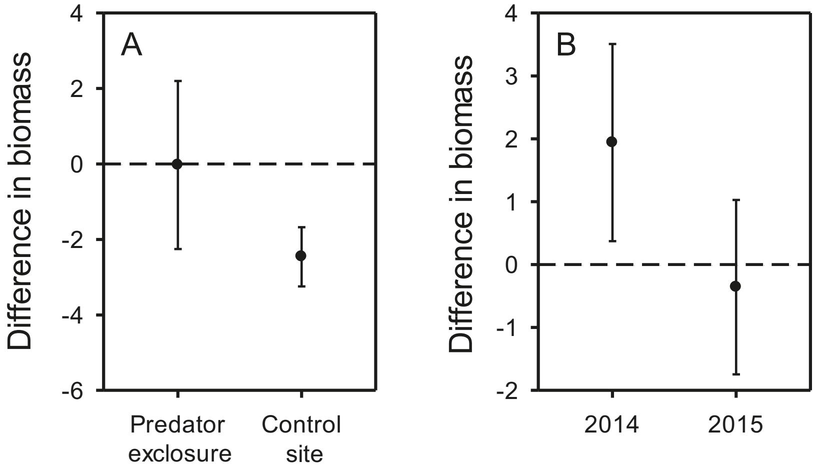
[a] Predator exclosure (predation absent) is the level of reference.

[b] Outside snowbed is the habitat of reference

[c] Year 2014 is the year of reference.

We found an impact of lemming grazing on some *S. arctica* morphological traits at the end of the summer as the number of leaves, stem length, and stem growth were reduced outside areas protected from lemming grazing. This suggests that plant recovery after winter grazing was affected. However, the grazing impact on these traits was not higher in the predator exclosure, where lemming density was twice higher than in presence of predators. The grazing impact on catkins at the end of the summer was higher in the predator exclosure than the control site, but the converse was true for new ramifications. Contrary to our initial prediction, the grazing impact on *S. arctica* morphological traits was not greatest in the year of highest lemming abundance (2014). However, it is interesting that grazing impact on some traits (stem

Fig. 6. Difference between plots ungrazed (lemming exclosures) and grazed by lemmings in total aboveground biomass (g/m^2) of (A) *Salix herbacea* in absence (predator exclosure, n = 15) and presence (control site) of predation (n = 12) and (B) *Juncaceae* in 2014 (n = 16) and 2015 (n = 24) at the end of the summer on Bylot Island, Nunavut. Values are the mean difference (±95% confidence intervals). A positive difference indicates a reduced value in grazed plots.



diameter, length, and growth) gradually increased from 2014 to 2016. This indicates a possible cumulative impact of grazing on plant recovery during the summer as lemming density was still relatively high in 2015 and moderate in 2016. However, some studies suggested that *S. arctica* could withstand well-sustained grazing (Boulanger-Lapointe et al. 2016)

Despite the impact of lemming grazing on some *S. arctica* morphological traits, we could not detect any impact on both woody and non-woody biomass of this species at the end of the growing season, and we found no difference between the predator exclosure and the control site. The same applies to other important food plants of lemmings in winter, *Poaceae* and *Juncaeae*, although in the latter case a reduction in biomass in grazed plots was detected in the year of highest lemming abundance (2014). This suggests that regrowth of these species is not affected by lemming grazing with the possible exception of *Juncaceae*, a result similar to the one of Bilodeau et al. (2014). *Salix herbacea* is the only species that showed a tendency for an effect of the predator exclosure on the difference in biomass between grazed and ungrazed site. This species is generally found in snowbeds (Beerling 1998; Aiken et al. 2007; this study) and is thus potentially exposed to high lemming densities. However, the exact contribution of this species to the lemming diet compared to the more abundant *S. arctica* is unknown because diet analysis based on DNA metabarcoding could not distinguish *Salix* species (Soininen et al. 2015). Some studies suggest that *S. herbacea* is regularly grazed by both mammals and insects (Wijk 1986; Beerling 1998), possibly because the species is less woody than other *Salix*, which could increase its palatability.

Although brown lemmings were much more abundant in the predator exclosure than the control site, we note that the pattern was reversed for the less abundant collared lemming (Fig. 1). The reason for that is not entirely clear although interspecific competition with the more abundant brown lemming, which is the dominant species (Morris et al. 2000), may have depressed collared lemming populations in the predator exclosure. Because *Salicaceae* makes up a greater proportion of the winter diet of the collared lemming compared to the brown (Soininen et al. 2015), the relatively high density of collared lemmings in the control site may have weakened the differences in grazing impact on *S. arctica* between the predator exclosure and the control site. It is unlikely that other herbivores affected our results because control plots located outside the predator exclosure were protected from grazing by other vertebrate herbivores, such as geese, ptarmigans, or hares, by chicken wire, which allowed lemming grazing. Finally, insect herbivory appears insignificant at the site (Rheubottom et al. 2019).

Highly significant grazing impact of lemmings on tundra vegetation during years of peak abundance has been reported at other Arctic sites. This includes brown lemmings in Alaska, where close to 100% of graminoids can be clipped during winter (Thompson 1955; Pitelka and Batzli 2007; Villarreal et al. 2012) and Norwegian lemmings, which can graze up to 50% of the vegetation in snowbeds of Fennoscandia during winters of peak abundance (Moen et al. 1993; Virtanen et al. 2002). Lemming grazing has also been shown to reduce the number of *Salix* recruits in Norway (Ravolainen et al. 2014). These results contrast with the situation on Bylot Island where the largest effect was found on stem length and growth of *S. arctica* at the end of the summer, which were reduced by only 16% on average by lemming grazing (see also Bilodeau et al. (2014) for similar results). A possible explanation is that lemmings never reach densities high enough in the High Arctic to have a strong impact on the vegetation, which is reinforced by our manipulation that doubled the lemming population without much consequence on plants. At our study site, lemming densities reached a maximum of ~10 lemmings/ha over seven peaks, which is typical in the High Arctic (Gauthier et al. 2024) compared to >100 lemmings/ha in Alaska (Pitelka and Batzli 2007). Direct comparison with Fennoscandia is more difficult because absolute densities are not reported in most studies, only abundance indices, However, peak densities of Norwegian lemmings are likely much higher than those of High Arctic lemmings (Ekerholm et al. 2001; L. Oksanen, pers. comm.).

Severe damage to the vegetation during years of peak abundance has been invoked as the primary mechanism driving population crashes of lemmings in Alaska (Pitelka and Batzli 2007) and Fennoscandia (Turchin et al. 2000), although Soininen and Neby (2024) argued that critical evidence to support this hypothesis is lacking. Plant recovery following heavy grazing needs to be sufficiently slow to generate population cycles in small mammals through a delayed density-dependent effect (Turchin and Batzli 2001). Considering the relatively small impact of lemmings on vegetation documented in this study and by Bilodeau et al. (2014), and the good summer regrowth of plants during the peak abundance phase, plant–herbivore interaction is unlikely to drive the population dynamics of lemmings at our study site. These results are consistent with other studies showing that predators are likely to drive the population dynamics of lemmings in the High Arctic (Gilg et al. 2003; Fauteux et al. 2016; Bergeron et al. 2025; Bolduc et al. 2025). Limitation by predation can explain why lemmings never reach densities high enough to significantly deplete their food supply on Bylot Island. Even though lemming density doubled in the predator exclosure, dispersal outside the exclosure or possible invasion of the exclosure by ermines may have prevented populations from reaching levels high enough to severely impact the vegetation (Fauteux et al. 2016). However, we cannot exclude that in some years, local depletion of some plant parts (e.g., *S. arctica* buds or catkins) due to winter grazing may be an additional density-dependent factor reducing the growth potential of lemming populations.

Even though plant–herbivore interactions may not drive lemming population dynamics in our system, grazing still has the potential to affect vegetation in the long term. Exclusion of lemmings for ≥10 years has shown that their periodic outbreaks can change vegetation composition in Alaska and Fennoscandia even at moderate population peaks (Virtanen et al. 1997; Virtanen 2000; Johnson et al. 2011; Olofsson et al. 2014). The trend that we detected of an increased impact on some *S. arctica* morphological traits (stem diameter, length, and growth) after 2 years of high lemming density may also point in that direction. Long-lasting effects may occur if lemmings selectively graze some plant species, thereby favouring the growth of other species or functional groups (Virtanen 2000; Olofsson et al. 2014). However, it is also possible that grazing stimulates plant growth by speeding up nutrient cycling through the release of urine and feces in the nutrient-poor tundra (Gough et al. 2012; Tuomi et al. 2019; Roy et al. 2022). Clearly, long-term effects of lemming grazing on the vegetation deserve more study.

In conclusion, although our predator removal experiment was successful in increasing the abundance of lemmings, we found little evidence that this had a cascading effect on the main food plants consumed by these herbivores in the short term (<3 years), in contrast to the results of a similar experiment in subarctic voles (Huitu et al. 2003). However, it will be interesting to see if a trophic cascade could emerge if predator exclusion is maintained in the long term (10+ years). A diverse guild of predator species, each with complementary adaptations, is needed to stop lemming population growth through top-down processes and to generate cycles (Gilg et al. 2003; Bergeron et al. 2025). Changes to the predator community brought by climate change thus have the potential to destabilize the system and initiate a trophic cascade if lemmings escape predator control, which could have a lasting effect on Arctic plant communities.

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Data availability

Lemming data are available on NordicanaD (https://nordicana.cen.ulaval.ca/dpage.aspx?doi=45400AW-9891BD76704C4CE2). Plant data are provided as supplementary material to the paper.

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Competing interests

The authors declare there are no competing interests.

Supplementary material

Supplementary data are available with the article at https://doi.org/10.1139/as-2024-0076.

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