Caribou exclusion during a population low increases deciduous and evergreen shrub species biomass and nitrogen pools in low Arctic tundra

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Summary

1. Increased shrub growth has been observed across the Arctic with recent climate warming trends, whilst many populations of caribou and reindeer (*Rangifer*) have been in decline. Paradoxically, our current understanding of the impacts of caribou and reindeer in altering trajectories of Arctic vegetation change is almost entirely dependent on studies with relatively high density semi-domesticated herds in Fennoscandia. With many wild herd populations across the Arctic presently at much lower densities, it is important to understand the impact of low intensity browsing on shrub biomass and the soil nutrient pools that fuel it.

2. We used exclosures that have been in place for 5 years in mesic birch hummock tundra in the central Canadian low Arctic to investigate the impact of caribou exclusion on tundra shrub biomass, tissue chemistry and plant and soil nitrogen (N) pools. Over the study period, the migratory tundra caribou herd in the region declined from 25% to 7% of its previous population maximum.

3. Caribou exclusion significantly enhanced the above-ground biomass components of one deciduous shrub (*Betula glandulosa*) and two evergreen shrubs (*Vaccinium vitis-idaea* and *Rhododendron subarcticum*). In particular, exclusion doubled *B. glandulosa* leaf biomass and increased *V. vitis-idaea* old leaf biomass 1.7 times, with the strongest effects in evergreens present in tissues > 1 year old, indicating a legacy of browsing from the earlier years of the experiment when the caribou population was higher. Meanwhile, *Vaccinium uliginosum* biomass and overall vascular plant diversity tended to decline with exclusion. Caribou exclusion increased *B. glandulosa* leaf N pools by 0.15 g N m^{-2} (equivalent to 12% of the total vascular plant community annual N requirement for apical growth). Altogether exclusion did not alter total above-ground N pools, but rather led to a redistribution of shoot biomass and N, enhancing spatial variability in a key growth-limiting resource for tundra plants.

4. *Synthesis*. Excluding caribou during a population low resulted in ecologically significant changes in the distribution of plant above-ground biomass and nitrogen, further increasing the dominance of the three most abundant shrubs. These findings demonstrate that, despite uncertainty in herd recovery, *Rangifer* browsing impacts to both deciduous and evergreen shrub species should be considered for more robust projections of Arctic vegetation change.

Key-words: arctic tundra, caribou, determinants of plant community diversity and structure, herbivory, nitrogen pool, phenolics, productivity, reindeer, shrub expansion

Introduction

Arctic shrub growth has been increasing over the past 50 years whilst mean annual temperatures in the region have also been rising (Goetz *et al.* 2005; Tape, Sturm & Racine 2006; Forbes, Fauria & Zetterberg 2009; Jia, Epstein & Walker 2009; Elmendorf *et al.* 2012; Epstein *et al.* 2012), but many populations of caribou and reindeer (*Rangifer tarandus* L.) have been in decline (Vors & Boyce 2009). The potential role of herbivory in these past shrub dynamics and in future trajectories is only beginning to be recognized (Post &

Pedersen 2008; Olofsson *et al.* 2009; Yu *et al.* 2011). Whilst substantial impacts of caribou and reindeer browsing on shrub biomass and productivity over multiple decades have been well documented (Manseau, Huot & Crete 1996; Väre, Ohtonen & Mikkola 1996; Olofsson *et al.* 2001; Olofsson 2006; Kitti, Forbes & Oksanen 2009), many herd numbers are presently much lower than they have been in recent decades. Whether caribou and reindeer at low population densities are a significant control on tundra productivity and shrub expansion is unknown, yet highly relevant to projections of future Arctic vegetation change.

Robust projections of Arctic shrub expansion require understanding of the effects of herbivores not only on shrub

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biomass, but on plant and soil nutrient pools. Arctic shrub growth is most strongly limited by soil nutrient availability (Chapin *et al.* 1995; Jonasson *et al.* 1999; Shaver & Jonasson 1999; Bret-Harte *et al.* 2001; Bret-Harte, Shaver & Chapin 2002; van Wijk *et al.* 2004; Zamin & Grogan 2012), which itself may be influenced by herbivores (Hobbie 1992; Hobbs 1996; Bardgett, Wardle & Yeates 1998). Complex feedbacks characterize the relationships between herbivores, vegetation community composition and nutrient availability, in which herbivores impact soil fertility, and yet, soil fertility determines the direction and magnitude of these impacts (McNaughton 1979; Cargill & Jefferies 1984; Pastor *et al.* 1993; Olofsson *et al.* 2001; Pastor, Cohen & Hobbs 2006). Furthermore, climate warming is projected to increase soil fertility in the Arctic through enhanced microbial decomposition of organic matter (Nadelhoffer *et al.* 1991; Chapin *et al.* 1995). There is then a strong potential for the 'top-down' process of herbivory to interact with the 'bottom-up' process of increased nutrient availability and either exacerbate or mediate these changes in soil fertility and correspondingly vegetation.

Caribou and reindeer (herein referred to as *Rangifer* for clarity) browsing may be expected to strongly impact upon deciduous shrubs, as these are preferred summer forage, generally comprising 35–50% of diets (Boertje 1984; Crête, Huot & Gauthier 1990). In particular, *Betula glandulosa* is heavily selected by caribou in eastern Canada (Bergerud 1972; Crête, Huot & Gauthier 1990; Manseau, Huot & Crete 1996), whilst *Salix spp.* are strongly selected by caribou in Alaska (White & Trudell 1980; Boertje 1984), and species of both genera are considered preferred reindeer forage in Fennoscandia (Mårell, Ball & Hofgaard 2002). Evergreen shrubs have lower digestibility (White & Trudell 1980; Johnstone, Russell & Griffith 2002) and are a marginal part of summer diets (Bergerud 1972; Boertje 1984; Crête, Huot & Gauthier 1990), but may be used heavily in the spring, autumn and winter during the absence of deciduous leaves (Bergerud 1972; Boertje 1984). Nonetheless, selection for preferred forage species may be particularly strong when herbivore populations are low, as these species then experience the highest level of tissue removal per plant (Augustine & McNaughton 1998).

Past research on *Rangifer* browsing impacts on Arctic tundra has been dominated by studies on semi-domesticated herds in Fennoscandia, with comparatively little research on the impacts of wild herds in western and eastern North America (see citations in following sentences). Exclosure studies in northern Norway, Sweden and Finland ranging from 1 to 50 years of treatment indicate that caribou browsing can substantially decrease shrub biomass, particularly in *Salix* species (Väre, Ohtonen & Mikkola 1996; Grellmann 2002; den Herder, Virtanen & Roininen 2004, 2008; Pajunen, Virtanen & Roininen 2008; Kitti, Forbes & Oksanen 2009), and can either increase or decrease soil nutrient availability (Väre, Ohtonen & Mikkola 1996; Stark & Grellmann 2002; Stark *et al.* 2003; Olofsson, Moen & Ostlund 2010; Stark, Mannisto & Smolander 2010) with impacts varying between sites and ecosystems. In the North American Arctic, although there have been observational studies (Klein 1987; Henry &

Gunn 1991; Manseau, Huot & Crete 1996; Post & Klein 1996; Crête & Doucet 1998), the only published caribou exclosure study is at Toolik Lake, Alaska, where 10 years of exclosure treatment caused no impact on live vegetation, 17 years of exclusion led to an increase in total live biomass and lichen biomass, and impacts to the soils were not measured (Gough *et al.* 2008).

Current understanding of *Rangifer* browsing impacts on plant community composition and soil nutrient pools are then highly geographically biased, with the Fennoscandian sites generally having lower fertility than North American low Arctic mesic tundra sites (Giblin *et al.* 1991; Chapin *et al.* 1995; Grellmann 2002; Olofsson, Stark & Oksanen 2004b; Olofsson *et al.* 2004a; Chu & Grogan 2010; Vankoughnett 2010), generally higher summer herbivore densities (Wegener & Odasz-Albrigtsen 1998; Adamczewski *et al.* 2009; Kitti, Forbes & Oksanen 2009), and browsing by semi-domesticated *Rangifer* whose impacts on ecosystems varying in time and space between that of wild and domesticated animals (Suominen & Olofsson 2000). With an estimated 1.8 million semi-domesticated reindeer in Fennoscandia and Russia and 4.4 million wild caribou and reindeer throughout Russia and North America (Russell & Ulvevadet 2004), it is clear that our comparatively good understanding of the impacts of semi-domesticated *Rangifer* on plant communities and ecosystem processes may not apply to the majority of animals across their circumarctic range.

Populations of wild *Rangifer* are known to fluctuate over multidecadal time scales (Gunn 2003; Payette *et al.* 2004; Zalatan, Gunn & Henry 2006), and yet, widespread declines over the past several decades have left many populations at low numbers during a time when the intensity and scale of industrial development, human presence and climatic changes in their range are unprecedented (Vors & Boyce 2009; Festa-Bianchet *et al.* 2011). Herd recovery will be highly dependent on management actions (Vors & Boyce 2009; Festa-Bianchet *et al.* 2011). As caribou impacts on the landscape can vary substantially with browsing intensity (Olofsson *et al.* 2001, 2004a; Olofsson, Stark & Oksanen 2004b; Cooper 2006; Hansen *et al.* 2007), it is important to understand the role of these comparatively small populations on ecosystem processes. The question is then: 'Could wild caribou at present low densities influence shrub expansion either directly via selective browsing or indirectly through their effects on soil nutrient availability?'

Most past research has examined effects at the species or functional group level, which limits interpretation of the mechanisms and potential extrapolation to system-wide nutrient cycling feedbacks. Here, we investigate the impact of caribou exclusion on tundra vegetation community composition at high-resolution (age- and tissue-specific levels for vascular plants and species level for lichens), plant tissue chemistry and plant and soil nutrient pools in the central Canadian low Arctic using exclosures that have been in place for 5 years. During this time, the caribou herd in the region was in continual decline, with the population at the start of the study at 25% of its previously recorded maximum and by the end of

the study period at 7% of its previous maximum and its lowest size on record (Adamczewski *et al.* 2009). We tested the following hypotheses:

1. Exclusion of caribou during a population low increases *B. glandulosa* leaf and stem biomass and total lichen biomass, but does not affect the other common deciduous and evergreens shrub species (*Vaccinium uliginosum*, *Vaccinium vitis-idaea* and *Rhododendron subarcticum*), such that total deciduous shrub biomass and total above-ground vegetation biomass increase modestly with exclusion but species diversity is unchanged.

2. Excluding caribou increases the tissue nitrogen concentration and decreases phenolic concentrations in *B. glandulosa* but does not alter tissue chemistry in the other shrub species.

3. Through the above effects on biomass and nitrogen concentrations, caribou exclusion increases *B. glandulosa* nitrogen pools and the potential for litter nitrogen return to the soil, and consequently increases total above-ground vegetation nitrogen pools.

Materials and methods

SITE DESCRIPTION

This study was conducted in the central Canadian low Arctic near the Tundra Ecosystem Research Station at Daring Lake, Northwest Territories (64° 52′ N, 111° 33′ W). Temperatures range from an annual minimum of -39 ± 0.7 °C in January to a maximum of 20 ± 0.4 °C in July, and mean annual rainfall is about 142 ± 14 mm (Bob Reid, Indian and Northern Affairs Canada, unpublished data 1996–2009). This research was conducted in mesic birch hummock tundra, part of the erect dwarf shrub tundra category of Arctic vegetation types (CAVM 2003), where the maximum shrub height was around 30 cm. The vegetation is dominated by evergreen shrubs and lichens, each of which constitutes around 35% of the vegetation community (data from this study). The most abundant evergreens include Labrador tea (*R. subarcticum* (Harmaja) [formerly *Ledum decumbens* (Ait.)]]) and mountain cranberry (*V. vitis-idaea* L.), and the lichen community is dominated by *Cladina* and *Cetraria* species. The deciduous shrubs dwarf birch (*B. glandulosa* Michx.) and bog blueberry (*V. uliginosum* L.) comprise around 11% of the vegetation biomass and graminoids, such as *Eriophorum vaginatum* L., *Carex bigelowii* Torr. ex Schwein. and *Carex rotundata* Wahlenb. account for < 1% of the community. Lastly, a variety of mosses comprise about 17% of vegetation biomass. *Salix spp.* are extremely rare at this site and were not present in any of the plots.

Daring Lake Research Station lies in the centre of the Bathurst caribou (*Rangifer tarandus groenlandicus*) herd's summer range. The Bathurst herd population has declined linearly from its peak in 1986 at $472\,000 \pm 72\,900$ to $31\,900 \pm 10\,900$ individuals in 2009 (Adamczewski *et al.* 2009). Nonetheless, over our study period from 2004 to 2009, small groups of caribou were regularly observed passing through the site, with at least one animal observed in the research valley daily throughout August 2009 when the data for this study were collected.

Experimental caribou exclosure plots were constructed in the mesic birch hummock tundra in August 2004. Ten large patches of representative and fairly homogenous vegetation of similar gentle slope and aspect that were each around 100–200 m apart were identified and assigned alternately to exclosure treatment or control ($n = 5$; see Fig. S1 in Supporting Information for map). Large exclosures of metal range fencing (19.8 m × 19.8 m × 1.2 m height) were constructed (aperture 15 × 20 cm) to exclude caribou but readily permit entry of other herbivores (e.g. hares, lemmings). As the range fencing has large aperture, snow does not preferentially accumulate along the fences. Lastly, the site is at the south-western limit of muskox distributions (Fourier & Gunn 1998), and muskox are rarely seen at the site (Steve Matthews, Government of the Northwest Territories, *personal communication*).

VEGETATION SAMPLING AND ANALYSIS

Vegetation composition was assessed using the point intercept method (Jonasson 1988; Bean & Henry 2003), with a randomly selected 1.0 m^2 area measured within each plot between August 4 and 12, 2009. Treatments were measured in a random order. The 1.0 m^2 plots were unmarked initially and then marked with thin bamboo stakes that were not visibly obvious for a maximum of 11 days. A small (40 × 40 cm) harvest of all biomass above-ground (i.e. down to the transition of the green-brown moss layer) was taken from within each point-framed area on August 13 or 15, 2009 to calibrate the species-level point framing hits data to biomass. 'Above-ground' biomass for vascular shoots was delineated by the transition of green to brown in the moss layer, by structural changes in the shoot, or by the presence of fine roots, whichever indicators were available. The harvested shoot biomass was separated into species and then into new vs. old growth using current year's bud scars on the stems. New growth was then separated into leaves and stem. Therefore, new growth included all apical tissue that had grown within the current growing season, but did not include secondary stem growth. Old growth was also separated into leaves (evergreens only) and stems and included all past years' live tissues.

To calibrate the point framing hits data to biomass, we used a power model as it yielded higher explained variance for our data than a linear model (Jonasson 1988). The power model corresponded to a linear model after natural logarithmic transformation of both variables (Jonasson 1988; see Table S1 in Supporting Information for equations). Separate calibrations were run for leaf and stem tissue in the shrub species. All linear regression parameters are listed in Table S1. After having extrapolated the total leaf and total stem biomass for a given species to the 1.0 m^2 scale, we used the treatment:average ratio of its new leaves:old leaves and new stem:old stem in the 0.16 m^2 harvest to calculate the amount of new leaves, old leaves (evergreens only), new stem and old stem at the 1.0 m^2 scale.

Chemical analyses were performed on the age- and tissue-type-differentiated samples, for example, new leaves separately from old leaves and new stem separately from old stems, with the exception of graminoids, mosses and lichen which were analysed at the functional group level. Sorted samples were oven dried at 40 °C and then ground to a 0.5 mm particle size (IKA MF 10 Microfine grinder, Staufen, Germany) and analysed for total C and N on a LECO CNS (St. Joseph, MI, USA) and for total phenolics using the Folin–Ciocalteu assay (Folin & Ciocalteu 1927; Bärlocher & Graça 2005) and a spectrophotometer (SpectraMax Plus[384], Molecular Devices, Sunnyvale, CA, USA). Nitrogen pool sizes were calculated by multiplying the biomass of a given tissue by its N concentration. Nitrogen concentration data for new stems of both *Vaccinium* species and for *Rubus chamamemorus* in the exclosures are not reported due to insufficient sample available for analysis. Therefore, new stem N pools for both *Vaccinium* species were omitted from the analysis, and N pools for *Rubus* used the N concentration from the control plots alone.

SOIL SAMPLING AND ANALYSES

One organic soil core (5×5 cm $\times$ 10 cm depth) was taken from each plot on August 12, 2010. If the organic layer was shallower than 10 cm, underlying mineral soil was discarded. Soils were kept in coolers and/or a cold room (4 °C) for 6 days before processing. All above-ground plant material and lichens were cut-off, the soil core was weighed for bulk density determination, and then all roots > 2 mm were removed. The soil was then homogenized by hand and subsampled for soil solution extraction and soil moisture determination. Extractions were conducted by adding 50 mL of 0.5 M K_2SO_4 to 10 g of fresh soil, shaking the samples for 1 h at low speed on a mechanical shaker, letting the samples sit for 30 mins and then filtering through glass fibre filters (Fisher G4; 1.2 µm pore space) using a vacuum. NH_{4+} -N and NO_{3-} -N in the extracts were determined colourimetrically using automated flow analysis (Bran-Leubbe Autoanalyser III, Norderstadt, Germany) and the indophenol and sulphanilamide methods (Mulvaney 1996). Dissolved total carbon (DOC) and dissolved total nitrogen (DTN) in the extracts were determined by oxidative combustion and infrared (Nelson & Sommers 1996) or chemiluminescence analysis, respectively (TOC-TN autoanalyser, Shimadzu, Kyoto, Japan). Dissolved organic nitrogen (DON) was calculated as the difference between DTN and NH_{4+} -N, as NO_{3-} -N amounts were below detection. The final C and N concentrations in the extracts were corrected for the dilution associated with initial soil moisture in each individual sample and were calculated to areal pool sizes (g m^{-2}) using the bulk density and organic layer depth of each sample. An additional subsample of soil was also oven dried, ground (Retsch PM 200 Planetary Ball Mill, Haan, Germany) and analysed for total C and total N on a LECO CNS.

STATISTICAL ANALYSES

We tested for effects of caribou exclusion on the most common deciduous (*B. glandulosa* and *V. uliginosum*) and evergreen (*V. vitis-idaea* and *R. subarcticum*) shrub species, since these were present in at least four of the five replicate plots. We conducted species-specific multivariate analyses of variance (MANOVA) in which new leaves, old leaves (evergreens only), new stem and old stem were all considered response variables (3–4 tissue types). The MANOVAs allowed us to test for exclusion effects across multiple tissues of a given species within one analysis and did not require the tissues (response variables) to be independent of each other.

We ran separate MANOVAs for each species' biomass, N pools, N concentrations and phenolic concentrations. We also conducted MANOVAs on aggregated total leaf and total stem biomass (two tissue types) and a *t*-test on total biomass (one tissue type) for each species, as the latter is the most commonly reported level of tissue resolution in *Rangifer* herbivory studies (Henry & Gunn 1991; Manseau, Huot & Crete 1996; Grellmann 2002; Olofsson, Moen & Oksanen 2002; Olofsson, Stark & Oksanen 2004b; Olofsson *et al.* 2004a, 2009; Olofsson 2006; Hansen *et al.* 2007; Pajunen, Virtanen & Roininen 2008; Kitti, Forbes & Oksanen 2009). Lastly, we used *t*-tests to investigate exclusion treatment effects on total deciduous leaf biomass, total evergreen leaf biomass and total shrub leaf biomass.

Effects of caribou exclusion on plant functional groups (i.e. deciduous shrubs, evergreen shrubs, graminoids, forbs, mosses and lichens) were tested using two separate MANOVAs on biomass and on N pools. We tested for overall exclusion treatment effects across all groups, as well as effects on each functional group. We did not investigate the tissue chemical variables (N concentration and total phenolics concentration) at the functional group level, since these data were in

concentrations and would have to be calculated out as weighted averages in each functional group, which may have masked any real effects. We tested for exclosure impacts on species diversity by running a MANOVA on the Shannon–Wiener index values for vascular plants and for lichens as response variables. Shannon–Wiener indices were calculated for vascular plant diversity (10 species) and lichen diversity (23 species) using the point framing data from each plots. The effects of caribou exclusion on soil nutrient pools (NH_4-N, DON, DOC) and soil physical properties (bulk density and soil moisture) were assessed in two separate MANOVAs.

We used a principal components analysis (PCA) to investigate the impact of caribou exclusion on community composition and the abundances of each species. The ordination was conducted on the point framing data, with all lichens and almost all vascular plants delineated to the species level, and graminoids, mosses and fungi (fruiting bodies) at the functional group level. The control and exclosure plot points, derived from the species abundance data for each plot, were included in the figure to enable interpretation of any exclosure effect.

Prior to statistical analysis, proportion data were arcsine-square-root-transformed, and all other data were transformed if necessary to achieve normality. In the case of the forb biomass and N pools, transformation to a normal distribution could not be achieved, and so, the data were converted to ranks and analysis performed on the rank data (Akritas 1990). Homogeneity of variances was confirmed before running the MANOVAs. All statistical analyses were performed with R (R Core Team 2012), and ordinations were performed in Canoco 4.5 (Ter Braak & Šmilauer 2002). All significant results are reported in the text.

Results

ABOVE-GROUND BIOMASS AND PRODUCTIVITY

Caribou exclusion for 5 years increased shrub above-ground biomass components in *B. glandulosa*, *V. vitis-idaea* and *R. subarcticum* ($F_{3,6} = 6.1$, $P = 0.030$; $F_{4,5} = 16.1$, $P = 0.005$; and $F_{4,5} = 281.6$, $P < 0.001$, respectively; Fig. 1 and Table S2). Detection of caribou exclusion effects was strongest with analysis using the highest level of tissue resolution (i.e. leaves, new stems, old stems for deciduous species; and new leaves, old leaves, new stems, old stems for evergreen species as separate response variables within the overall MANOVA model for each species; see Table S2).

The exclosure treatment most affected leaf biomass in these three shrub species (Fig. 1). For example, *B. glandulosa* leaf biomass tended to be 2.0 times larger with exclusion ($F_{1,8} = 4.0$, $P = 0.081$), *V. vitis-idaea* old leaves tended to increase 1.7 times ($F_{1,8} = 3.5$ $P = 0.098$), and *R. subarcticum* old leaf biomass increased 1.2 times with caribou exclusion ($F_{1,8} = 6.2$, $P = 0.038$). By contrast, *V. uliginosum* leaves were unaffected, and the overall model for this species indicated that the exclosure treatment reduced biomass ($F_{3,6} = 86.0$, $P < 0.001$), especially for new stems ($F_{1,8} = 5.4$, $P = 0.049$). Analysis of *B. glandulosa* total leaf and total stem data (e.g. aggregation of new and old stem tissues) still yielded a trend for increased biomass in the exclosures ($F_{2,7} = 3.8$, $P = 0.076$; see Table S2), but total *B. glandulosa* biomass was unaffected by the exclosure treatment (see Table S2).
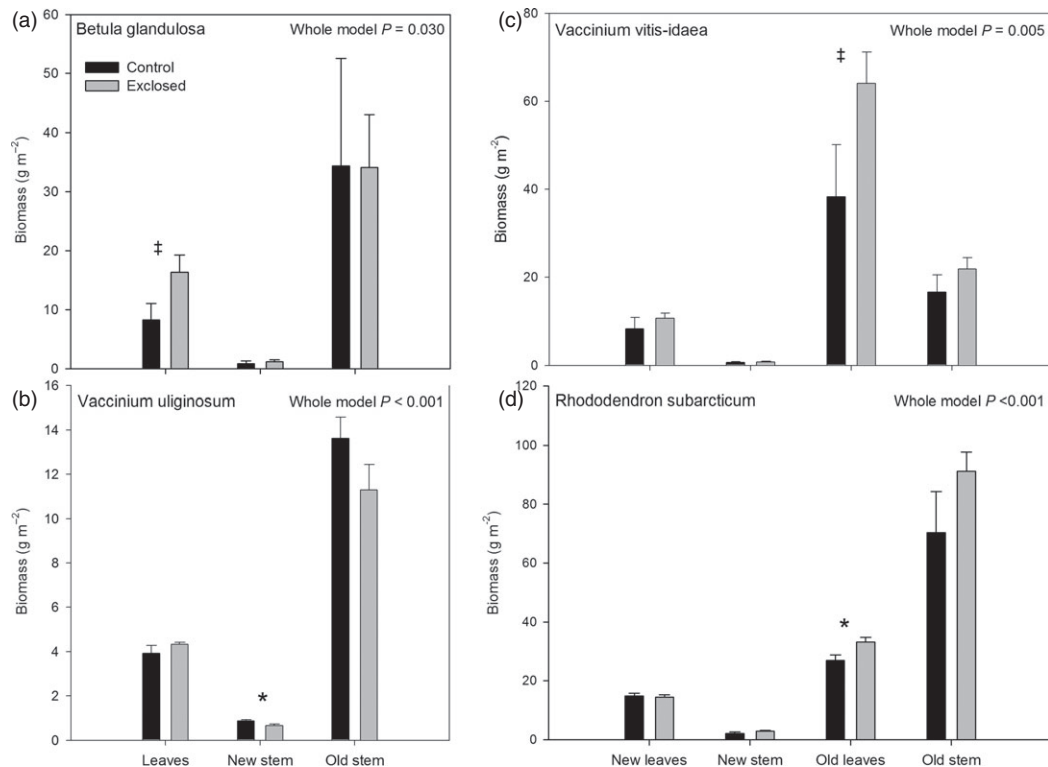
Fig. 1. Above-ground biomass components of the four major shrub species in control and caribou-excluded plots that were established 5 years earlier in mesic birch hummock tundra in the central Canadian low Arctic (n = 5; bars = standard errors). MANOVA whole model effects listed in top right corner, with individual tissue effects: *P < 0.05, ‡P < 0.10.

Caribou exclusion tended to increase total shrub leaf biomass by 43 g m^{-2} or 42% (t = 2.0, P = 0.086), of which 11 g m^{-2} is senesced annually (*V. vitis-idaea* leaf longevity 5 years at this site; *R. subarcticum* leaf longevity 3 years at this site, data this study). At the functional group level, caribou exclusion tended to increase deciduous shrub leaf biomass (t = 2.2, P = 0.061), but did not significantly affect evergreen shrub leaf biomass (t = 1.8, P = 0.123). Nonetheless, exclusion did not affect the total biomass of any functional group or total above-ground vegetation biomass (Fig. S2).

SPECIES DIVERSITY AND COMMUNITY COMPOSITION

Caribou exclusion tended to decrease vascular plant diversity in the exclosure plots ($F_{1,8}$ = 3.5, P = 0.099; Fig. 2), but did not alter lichen diversity. The combined relative abundance of the evergreen shrubs *Andromeda polifolia*, *Empetrum nigrum* and *Loiseleuria procumbens* decreased over 20-fold with the exclusion of caribou, from 9% in the control plots to 0.4% in the exclosed plots, coincident with an increase in the relative abundances of *B. glandulosa*, *R. subarcticum* and *V. vitis-idaea*, which altogether comprised 74% of the browsed community but 87% of the exclosed community.

In the PCA, 50.3% of the variance in the data was explained by axis one, which generally correlated with caribou exclusion (Fig. 3). In addition to the vascular plant associations listed above, this analysis suggested that *Arctostaphylos alpina* was positively associated with the exclosure treatment and that *Rubus chamaemorus* and graminoids were unaffected by exclusion. Lichen species that were positively associated with the exclosure treatment included *Cetraria cucullata*, *C. laevigata*, *C. islandica*, *C. nivalis*, *Cladina mitis*, *Cladina stellaris*, *Cladonia gracilis* and *Cladonia borealis*. Most of the non-*Cetraria* or *Cladonia*/*Cladina* lichens were either unaffected or negatively associated with caribou exclusion. Lastly, PCA axis 2 explained 22.8% of the variance and corresponded best to the moss abundance in each plot.

PLANT TISSUE CHEMISTRY

Five years of caribou exclusion did not alter leaf and stem tissue N concentrations or total phenolic concentrations in *B. glandulosa, V. vitis-idaea* or *R. subarcticum* (Table S3). For *V. uliginosum*, caribou exclusion raised N concentration by 8% in the old stems ($F_{1,3}$ = 13.4; P = 0.035) and tended increase phenolics concentration in new and old stems ($F_{1,3}$ = 6.3; P = 0.088 and $F_{1,3}$ = 8.2, P = 0.065, respectively). Both N and phenolics concentrations were highest in leaves, moderate in new stems and lowest in old stems of each shrub species (see Table S4). In general, shrub leaf phenolic concentrations were highest in the two *Vaccinium* species, moderate in *B. glandulosa* and lowest in *R. subarcticum*, while the shoot phenolic concentrations in the graminoids, mosses and lichens were much lower than that of the shrub species (Table S4).
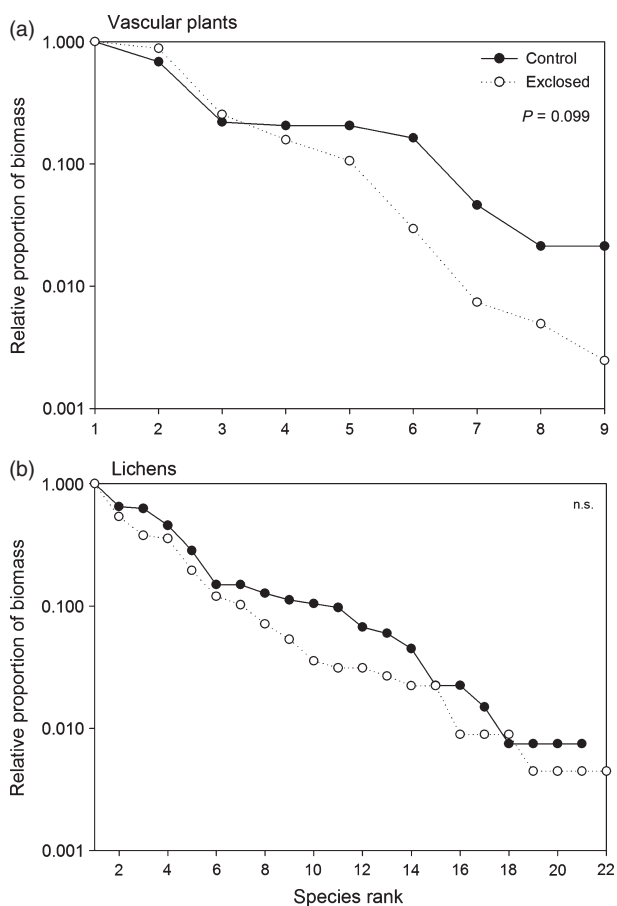
Fig. 2. Species rank abundance curves for vascular plants (a) and lichens (b), in control and caribou-excluded plots. Data are means derived from point framing hits per plot (*n* = 5).

PLANT AND SOIL NUTRIENT POOLS

In accordance with the biomass and N concentration data, the exclosure treatment increased N pools overall in *B. glandulosa*, *V. vitis-idaea* and *R. subarcticum* ($F_{3,6}$ = 8.9, *P* = 0.013; $F_{3,6}$ = 30.9, *P* < 0.001; and $F_{4,5}$ = 10.9, *P* = 0.011, respectively; Fig. 4 and Table S3), whilst *V. uliginosum* N pools were unaffected by the exclosure treatment (Fig. 4). In particular, *B. glandulosa* leaf N pools tended to be 2.0 times larger in the exclosures ($F_{1,8}$ = 3.7, *P* = 0.090), increasing deciduous shrub leaf N pools by 72% or 0.15 g N m^{-2} (*t* = 2.0, *P* = 0.079). Exclusion did not alter evergreen shrub leaf N pools (*t* = 1.3, *P* = 0.256). Whilst total shrub leaf N pools were around 0.40 g N m^{-2} (34%) higher in the exclosures, this effect was not significant (*t* = 1.7, *P* = 0.144). The exclosure treatment did not significantly affect the total N pools of any functional group or total above-ground N pools (Fig. 5). Lastly, mid-August measures of soil nutrient pools, soil bulk density and soil moisture were unaffected by 5 years of caribou exclusion (see Table S5).

Discussion

The substantial increases in *B. glandulosa*, *V. vitis-idaea* and *R. subarcticum* leaf biomass in our 5-year-old exclosures

relative to control plots clearly demonstrate that, even during a severe population low for this herd, browsing pressure on these three species is strong enough to restrict their growth. Nonetheless, excluding caribou through this population low did not alter total community biomass or N pools, as the increases in the above three species were met by decreases in other species, including *V. uliginosum*. These four species are abundant in the 'erect shrub tundra' vegetation class that comprises 26% of the vegetated Arctic (CAVM 2003). Therefore, the implications of *Rangifer* impacts to these species are important to Arctic vegetation change projections, as both deciduous and evergreen shrub growth has been increasing in Arctic tundra over the past 30 years (Elmendorf *et al.* 2012), with strongest increases in plant biomass in the low Arctic (Epstein *et al.* 2012).

It is important to acknowledge that what is being measured inside the exclosures is not an ideal unbrowsed state but rather an uncontrolled recovery phase (Bergström & Edenius 2003), and therefore, short-term browsing impacts are a function of both browsing intensity on the grazed control plots and the rate of recovery in the exclosed plots, although the latter may be the comparatively slower process (Olofsson 2006). Whilst we observed the strongest effects on *B. glandulosa* as originally hypothesized, the effects on the other three shrub species were unexpected and contradicted some of our original hypotheses. To explain them, we propose four possible mechanisms that are discussed below in terms of both browsing in control plots and recovery in the exclosures. These mechanisms include consideration of direct consumption, browsing legacy on individual plants, altered soil fertility and trampling as explanatory components.

BIRCH SHRUB GROWTH INCREASES IN EXCLOSURES

The increase in *B. glandulosa* leaf biomass with caribou exclusion is expected and supports Hypothesis 1. Whilst deciduous shrubs are known to be preferred summer forage (Bergerud 1972; Boertje 1984), previous exclosure studies have found strong browsing effects on *Salix spp.* within 4–5 years (Grellmann 2002; den Herder, Virtanen & Roininen 2008; Kitti, Forbes & Oksanen 2009), but not on *Betula spp.* over these short time scales (Grellmann 2002; Olofsson, Stark & Oksanen 2004b; Olofsson *et al.* 2004a). Nonetheless, substantial reduction in the biomass of *Betula nana* in Fennoscandia and *B. glandulosa* in eastern Canada with long-term *Rangifer* browsing is well known (Manseau, Huot & Crête 1996; Crête & Doucet 1998; Olofsson *et al.* 2001; Olofsson 2006).

For direct consumption to decrease the biomass of deciduous *B. glandulosa*, the leaves must have been consumed sometime between their emergence in mid-June and their measurement in early-mid-August. Dramatic within-season browsing impacts by reindeer have been previously documented on preferred vascular plant species in riparian tundra and a coastal deciduous forest (Bråthen & Oksanen 2001; Ravolainen *et al.* 2011), but have not been reported for mesic or dry tundra sites in the same season (den Herder,
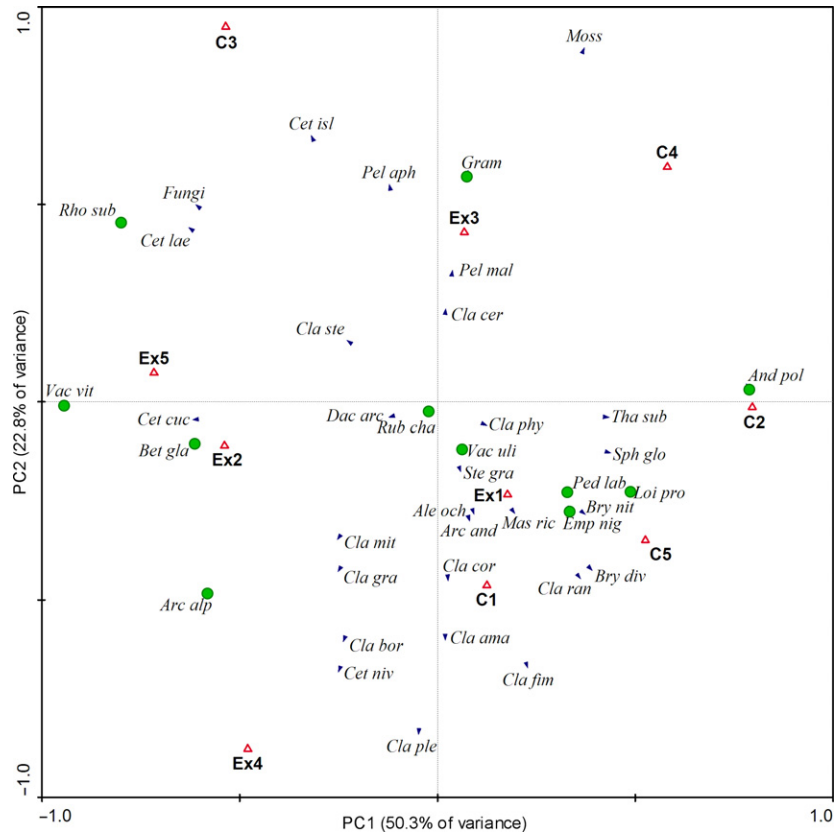
Fig. 3. Principal components analysis (PCA) on all species-level hits. Vascular plant species are delineated with green circles; lichens, fungi (fruiting body) and moss are marked with slanted blue triangles, and plots are indicated with open red triangles. Plot abbreviations include the following: C, control, Ex, exclosed, 1–5, plot replicate number. Species abbreviations include the following: Ale och, *Alectoris ochroleuca*; And pol, *Andromeda polifolia*; Arc alp, *Arctostaphylos alpina*; Arc and, *Arctocetraria andrejevii*; Bet gla, *Betula glandulosa*; Bry div, *Bryocaulon divergens*; Bry nit, *Bryoria nitidula*; Cet cuc, *Cetraria cucullata*; Cet isl, *Cetraria islandica*; Cet lae, *Cetraria laevigata*; Cet niv, *Cetraria nivalis*; Cla ama, *Cladonia amaurocraea*; Cla bor, *Cladonia borealis*; Cla cer, *Cladonia cervicornis*; Cla cor, *Cladonia cornuta*; Cla fim, *Cladonia fimbriata*; Cla gra, *Cladonia gracilis*; Cla mit, *Cladina mitis*; Cla phy, *Cladonia phyllophora*; Cla ple, *Cladonia pleurota*; Cla ran, *Cladina rangiferina*; Cla ste, *Cladina stellaris*; Dac arc, *Dactylina arctica*; Emp nig, *Empetrum nigrum*; Gram, graminoids; Loi pro, *Loiseleuria procumbens*; Mas ric, *Masonhalea richardsonni*; Ped lab, *Pedicularis labradorica*; Pel aph, *Peltigera aphthosa*; Pel mal, *Peltigera malacea*; Rho sub, *Rhododendron subarcticum;* Rub cha, *Rubus chamaemorus*; Sph glo, *Sphaerophorus globosus*; Ste gra, *Stereocaulon grande*; Tha sub, *Thamnolia subuliformis*; Vac uli, *Vaccinium uliginosum*; Vac vit, *Vaccinium vitis-idaea*.

Virtanen & Roininen 2004) or one year later (Grellmann 2002; Olofsson, Stark & Oksanen 2004b; Olofsson *et al.* 2004a). As *Salix spp.* are rare at this site (T. Zamin, *personal observation*), it is possible that browsing pressure on *B. glandulosa* is increased accordingly. Nonetheless, whilst personal observations confirm that several caribou passed through our research valley each day during 2009, the year of data collection when the population was at its lowest size, the likelihood that caribou ate in several of our five 1-m² plots seems low. Therefore, we suspect that in addition to some direct browsing, several of the other mechanisms may also have contributed to the exclosure treatment effects on *B. glandulosa*.

A legacy effect of previous year's browsing may have contributed to the comparatively lower leaf biomass in *B. glandulosa* in the control plots. Following alleviation from high browsing pressure, *B. glandulosa* leaf and stem biomass have been reportedly still low 1–4 years later (Henry & Gunn 1991; Crête & Doucet 1998), whilst in simulated browsing experiments, 100% and 50% defoliation of *Betula pubescens* and *B. glandulosa* led to a substantial reduction in new growth in the following 1–2 years (Hjálten, Danell & Ericson 1993; Manseau 1996). With natural defoliation rates < 6% (Crête & Doucet 1998), it is possible that whilst the loss of leaves affects the plant C budget (Holland, Cheng & Crossley 1996), the cumulative impacts may be slow and subtle and therefore not detected in this 5-year study. Nonetheless, we would expect any effect to be present in the newly grown tissues and not only did *B. glandulosa* leaf biomass double in the exclosures, but new stem biomass also increased by 30%. Whilst the effect on new stems was not statistically significant, this increase may indicate that the cumulative effect of browsing, or lack thereof, may translate to changes in stem biomass over time. Old stems comprise most of the species' above-ground biomass and were entirely unresponsive to the treatment, yet this is likely due to the short duration of the study. Meanwhile, as *B. glandulosa* is the dominant deciduous shrub at this site, this lack of total
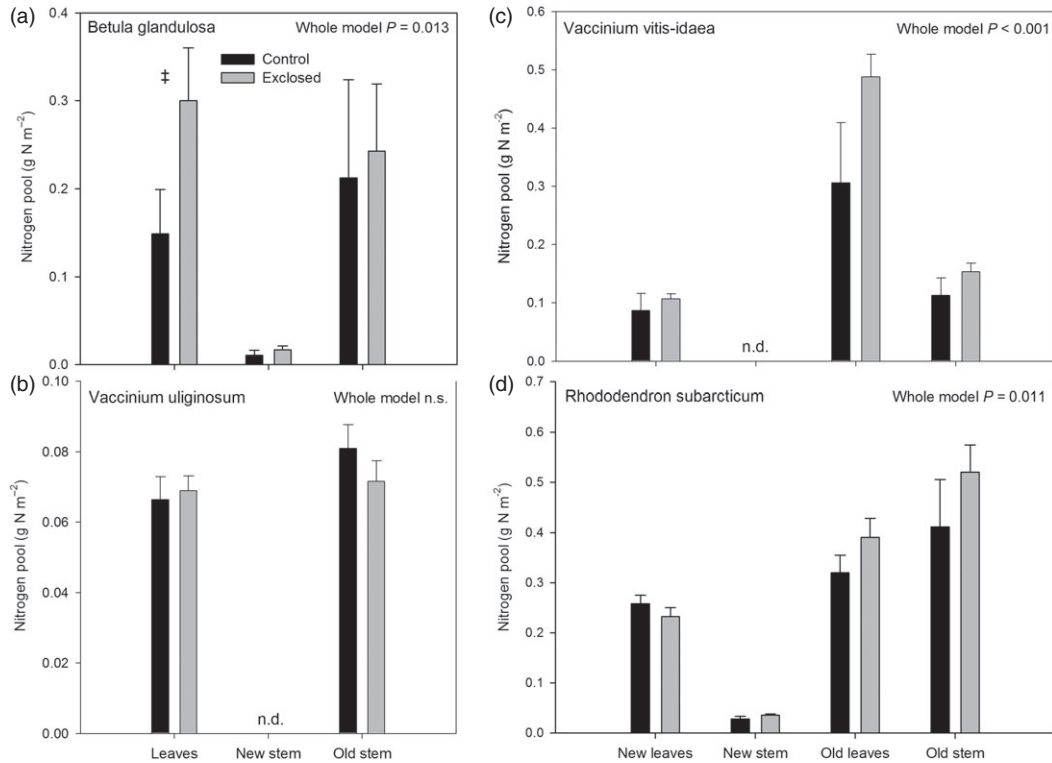
Fig. 4. Above-ground N pools of the four major shrub species in control and caribou-excluded plots ($n = 5$; bars= standard errors). MANOVA whole model effects listed in top right corner, with individual tissue effects: $^{\ddagger}P < 0.10$.
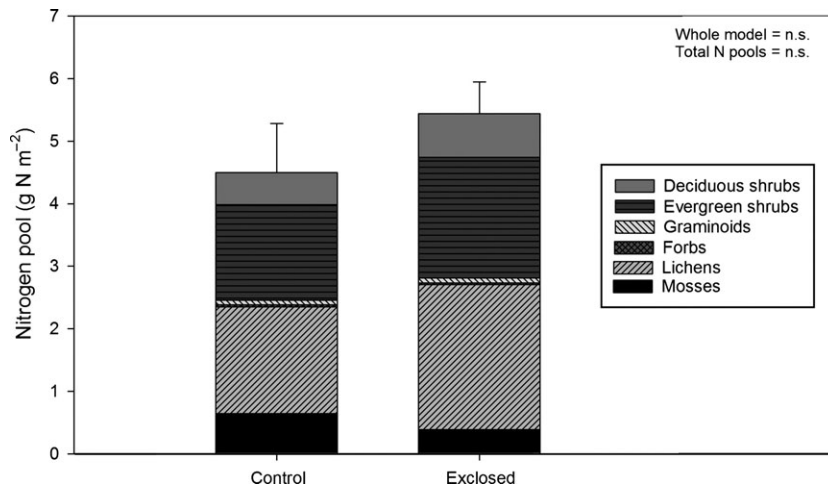

Fig. 5. Above-ground N pools of each plant functional group in control and caribou-excluded plots ($n = 5$, bars = standard errors).

biomass response led to the corresponding lack to response for the deciduous shrub group.

EVERGREEN SHRUB SPECIES GROWTH INCREASES WITH CARIBOU EXCLUSION

The increases in biomass of *V. vitis-idaea* and *R. subarcticum* with exclosure treatment, both across the whole models and specifically on old leaves, contradicted Hypothesis 1 and was unexpected since that these two evergreen species tend to be a marginal part of summer diets (e.g. 1–8%; Bergerud 1972;

Boertje 1984; Crête, Huot & Gauthier 1990). There may be several mechanisms contributing to these effects. First, direct consumption of evergreen leaves in the control plots may drive these effects. Whilst occasional summer consumption of *V. vitis-idaea* has been observed in both the Rivière Georges and Rivière aux Feuilles herds in Quebec (Crête, Huot & Gauthier 1990), evergreens are known to be heavily consumed in the spring prior to the appearance of deciduous growth (Bergerud 1972), or in the autumn when leaves of deciduous plants are unavailable (Bergerud 1972; Boertje 1984). At our research site, the Bathurst herd migrates

through in the spring on their way to the calving grounds, but more importantly, spends several months in the region in late summer and autumn, from mid-July through to mid-October (CARMA 2008). As deciduous shrubs senesce in late August to early September at this site (T. Zamin, unpublished data), autumn browsing of either *V. vitis-idaea* or *R. subarcticum* may be important. Although uncommon, increased biomass of *V. vitis-idaea* and *R. subarcticum* with long-term *Rangifer* exclusion or in naturally ungrazed or lightly grazed sites has been previously reported in Fennoscandia and northern Quebec (Manseau, Huot & Crete 1996; Olofsson 2006; Olofsson, Moen & Ostlund 2010).

Secondly, a legacy effect may have caused the comparatively lower *V. vitis-idaea* and *R. subarcticum* biomass in the browsed plots, whereby browsing on the measured individuals within the past 5 years has either decreased growth or decreased allocation to above-ground growth (Holland, Cheng & Crossley 1996; Crête & Doucet 1998). Similarly to *B. glandulosa*, whilst the lack of statistically significant changes to the newly grown tissues indicates that this mechanism is not strong, the consistent increases in growth across all four tissues that led to significant whole model effects suggest that this cumulative process may be slowly occurring. Meanwhile, the strong effects on old leaves indicate a legacy from browsing in earlier years of the study when the herd had been larger.

The remaining two mechanisms we consider for exclosure effects on evergreen shrub biomass do not require that the species were browsed. Altered soil properties could have caused the observed patterns, whereby shrub leaf and stem biomass were comparatively lower in the control plots because browsing activity in the valley over the past 5 years altered soil physical and chemical parameters in a way that restricted productivity. In Fennoscandia, reindeer browsing has been shown to alter soil respiration, microbial biomass C and N, soil nutrient availability and cycling rates, bulk density, and soil moisture (Väre, Ohtonen & Mikkola 1996; Stark & Grellmann 2002; Stark *et al.* 2003; Olofsson, Moen & Ostlund 2010; Stark, Mannisto & Smolander 2010). Nonetheless, we did not find clear evidence for an exclosure effect in our soil measurements, and yet, it is possible that this was a function of sampling frequency and date (Frank & Groffman 1998; Stark, Mannisto & Smolander 2010). In our case, we sampled soils only once and in mid-August, and so, it is possible that the higher nutrient uptake by the increased shrub biomass in the exclosures may have removed any early-season differences in soil nutrient pools. Nonetheless, with the present data, we tentatively conclude that total soil nutrient availability was not affected by the exclosure treatment and therefore that this process did not contribute to the observed responses.

Lastly, the increased evergreen biomass in the exclosures may be due to alleviation from caribou trampling and not from consumption. *Vaccinium vitis-idaea* may be more vulnerable to trampling than *R. subarcticum* and *B. glandulosa*, given its relatively large areal cover near the ground surface. Trampling can decrease the depth of the moss layer and increase soil temperatures (van der Wal & Brooker 2004; Olofsson 2009), which has been shown to increase graminoid biomass at certain temperature differentials (van der Wal & Brooker 2004) and decrease total root biomass (Olofsson 2009), yet not affect total above-ground plant biomass or cover (van der Wal & Brooker 2004; Olofsson 2009). However, since we did not see a difference in soil bulk density in the control and exclosed plots, or in lichen or moss biomass, it seems unlikely that trampling was an important process in this system.

In summary, we conclude that the most likely explanation for the exclosure effects on evergreens is that late-season browsing on these species in the control plots significantly reduced shoot biomass in following years. Strong browsing impacts to evergreens may have been under-represented in past studies because of responses being measured at the less-sensitive functional group level (Gough *et al.* 2008), studies focused specifically on the summer ranges (Manseau, Huot & Crete 1996; Crête & Doucet 1998; Kitti, Forbes & Oksanen 2009; Ravolainen *et al.* 2011) or studies on the spring or autumn range where evergreens comprise a small proportion of the vascular plant biomass relative to that of our site (e.g. 17–37% vs. 72% at our site; Grellmann 2002; Olofsson, Moen & Oksanen 2002; Olofsson *et al.* 2009), with the notable exception of dominance by *Empetrum spp.* at several sites (Olofsson, Stark & Oksanen 2004b; Olofsson *et al.* 2004a, 2009; Olofsson 2006). Nonetheless, as this functional group has been increasing with warming over the past several decades (Elmendorf *et al.* 2012) and is the dominant vascular functional group in tussock tundra and heath sites (Shaver & Chapin 1991; Jonasson *et al.* 1999; Gough, Wookey & Shaver 2002; Hudson & Henry 2009), our results demonstrate the importance of including *Rangifer* browsing as a potential constraint on evergreen shrub growth in projections of Arctic vegetation change.

DECREASED GROWTH OF *VACCINIUM ULIGINOSUM* IN THE EXCLOSURES

The reduced *V. uliginosum* growth across multiple tissues, and most notably new stem, in response to caribou exclusion was unexpected and did not support Hypothesis 1. These results suggest that this species was a relatively small component of the caribou diet at our site, and that decreased competition from *B. glandulosa*, *V. vitis-idaea* and *R. subarcticum* as a result of preferential browsing of these species, favours its growth. Whilst heavy consumption of *V. uliginosum* in the spring or summer has been documented in several herds across North America (Bergerud 1972; Boertje 1984; Crête, Huot & Gauthier 1990), it has also been entirely absent from the diet of other herds (Crête, Huot & Gauthier 1990). Similar variability has been seen in browsing impacts, with *V. uliginosum* biomass lower in a grazed site relative to a naturally ungrazed dwarf shrub tundra site in Quebec (Manseau, Huot & Crete 1996), but unaffected by grazing in other sites (Olofsson *et al.* 2009; Olofsson, Moen & Ostlund 2010). Increased plant growth or abundance in the presence of caribou is well documented for graminoid species (Olofsson *et al.* 2001, 2004a; Olofsson, Stark & Oksanen 2004b; Olofsson 2006; Kitti, Forbes & Oksanen 2009) and in certain cases for

bryophytes (Manseau, Huot & Crete 1996; Olofsson, Moen & Oksanen 2002; Olofsson 2006), but has rarely been found with shrubs, except for the evergreen *Loiseleuria procumbens* (Olofsson 2006). Altogether, the greater abundances of *V. uliginosum* and the other less common species (*L. procumbens*, *A. polifolia*, and *E. nigrum*) contributed to the higher vascular plant alpha (α) diversity in the presence of caribou browsing, which has been previously observed in some sites (Pajunen, Virtanen & Roininen 2012), but not others (Olofsson & Oksanen 2005; Ravolainen *et al.* 2010).

Effects of caribou exclusion on tissue chemistry were only found in *V. uliginosum*, contradicting Hypothesis 2, yet these effects may be a function of the unexpected increased growth of this species in the control plots. Increased growth in *V. uliginosum* may have led to its decreased old stem N concentration by diluting of tissue N, which would occur if C assimilation and growth exceeded N uptake (Chapin 1980; Shaver & Chapin 1980). The absence of this tissue nitrogen dilution in *B. glandulosa*, *R. subarcticum* and *V. vitis-idaea* with their enhanced growth in the exclosures suggests that these three species were able to take up additional soil N or reallocate internally, thereby maintaining stable tissue N concentrations (Chapin, Johnson & McKendrick 1980; Andresen & Michelsen 2005). In addition, the increased growth of *V. uliginosum* in the control plots may explain the comparatively lower old stem phenolic concentrations if the plant had sufficient N to prioritize growth over defence and allocated phenylalanine towards protein synthesis rather than phenolic synthesis (Bryant, Chapin & Klein 1983; Herms & Mattson 1992; Jones & Hartley 1999).

LICHEN BIOMASS UNAFFECTED BY 5 YEARS OF CARIBOU EXCLUSION

The lack of an exclosure effect on lichen biomass contradicts Hypothesis 1 and is likely due to the short duration of the study, as this affects both browsing intensity in the control plots and recovery the exclosures. Whilst lichen consumption may range from 8 to 25% of summer diets (Bergerud 1972; Boertje 1984; Crête, Huot & Gauthier 1990), browsing pressure on the lichens may have been particularly low at our site. Additionally, recovery of lichen communities after browsing alleviation may be particularly slow, ranging from 10 to over 20 years (Klein 1987; Eskelinen & Oksanen 2006; Hansen *et al.* 2007). Whilst increased lichen abundance has been generally documented in exclosures > 30 years old (Väre, Ohtonen & Mikkola 1996; Olofsson, Moen & Ostlund 2010), it has been observed that the abundance of *Cladina mitis* can be comparatively higher in exclosures after only 4 years (Olofsson, Stark & Oksanen 2004b; Olofsson *et al.* 2004a). Nonetheless, the tendency for common, abundant lichens such as *Cetraria cucullata*, *Cetraria nivalis*, *Cladina mitis* and *Cladonia gracilis* to be positively associated with exclusion in the PCA and for moss to be negatively associated with exclusion is in agreement with the hypothesis that tundra vegetation shifts from being moss-dominated to lichen-dominated as grazing pressure decreases (van der Wal 2006).

CARIBOU EXCLUSION REDISTRIBUTES BIOMASS AND NITROGEN RATHER THAN A NET CHANGE

Excluding the Bathurst caribou herd from browsing during a severe population low did not lead to a net change in the total vegetation community biomass or total above-ground N pools as predicted by Hypothesis 3, but rather to a redistribution. The consistent increase in N pools across multiple tissues of *B. glandulosa*, *V. vitis-idaea* and *R. subarcticum* were driven by the changes in biomass, since tissue N concentrations were not significantly affected, and yet, variation in N pools within tissue replicates tended to be higher than that of biomass, decreasing the statistical significance of some effects. Nonetheless, the increased growth in these three species in the exclosures must have been met by increased N uptake or internal reallocation for the tissue N concentrations to have remained stable (Chapin, Johnson & McKendrick 1980; Andresen & Michelsen 2005). Caribou browsing may then restrict the growth of these three species both by removing photosynthetic tissue and by decreasing plant N pools, the latter of which leads to reduced capacity for mobilization of internal N reserves (Chapin, Johnson & McKendrick 1980) and an increased reliance on new N uptake from the soil in future years.

Leaf removal by caribou may constitute a significant nitrogen loss to the plant not only in terms of potential retranslocation at the end of the season, but also in terms of N cycled back to the plant via its own litterfall. The decreases in leaf biomass and N pools of *B. glandulosa* in the control plots relative to the exclosures may be disproportionately important for nutrient return, as this species' leaves are relatively high quality at 1.8% N, compared with 0.8% N and 1.2% N of *V. vitis-idaea* and *R. subarcticum* respectively, and its annual leaf litter production is around 35% and 11% higher than *V. vitis-idaea* and *R. subarcticum*. More specifically, *B. glandulosa* leaf N pools were 0.15 g N m^{-2} lower in the control plots relative to the exclosures, which is nearly 100% of the total annual N requirement for apical growth for this species alone and 12% of the total vascular plant community annual N requirement for apical growth (1.25 g N m^{-2}; as measured by the sum of all new shoot N pools in the unbrowsed plots). The impacts of browsing on *B. glandulosa* may then have a particularly strong effect on litter N inputs to the immediate soil, lowering N availability to that species in subsequent years. Furthermore, the substantial decrease in total shrub leaf biomass in the browsed plots relative to the exclosures led to a difference of 0.40 g m^{-2} N, which is 32% of vascular plant community annual N requirement for apical growth. Since N availability is a fundamental constraint on tundra plant growth (Haag 1974; Shaver & Chapin 1980; Baddeley, Woodin & Alexander 1994), our results suggest that *Rangifer* browsing strongly affects local spatial heterogeneity in a critical resource. At the larger spatial scale, the N inputs associated with caribou urine and foecal deposition may enhance fertility locally elsewhere (Hobbs 1996; Pastor, Cohen & Hobbs 2006), also leading to greater spatial heterogeneity in soil nutrient availability.

THESE RESULTS IN THE CONTEXT OF OTHER RANGIFER BROWSING WORK

Important parameters that vary considerably between this study and past *Rangifer* exclosure studies are the duration over which browsing impacts are measured and the caribou population density. Previous long-term research using 30-year-old exclosures or natural browsing intensity gradients have demonstrated substantial *Rangifer* browsing impacts on shrub biomass (Manseau, Huot & Crete 1996; Väre, Ohtonen & Mikkola 1996; Olofsson *et al.* 2001; Olofsson 2006; Kitti, Forbes & Oksanen 2009). However, few short-term investigations have documented significant *Rangifer* impacts on tundra shrub biomass (Wegener & Odasz-Albrigtsen 1998; Olofsson, Stark & Oksanen 2004b; Olofsson *et al.* 2004a), with the exception of the preferred *Salix* (Grellmann 2002; den Herder, Virtanen & Roininen 2004, 2008).

Secondly, our results are particularly noteworthy because the population size of the caribou herd at our site was especially low over the study period, both in relation to its own mean size and in comparison with Fennoscandian herds for which browsing impacts to plants and soils have been measured (Wegener & Odasz-Albrigtsen 1998; Bråthen *et al.* 2007; den Herder, Virtanen & Roininen 2008; Adamczewski *et al.* 2009; Kitti, Forbes & Oksanen 2009; Ravolainen *et al.* 2011). Whilst the Bathurst herd population peaked at $472\,000 \pm 72\,900$ individuals in 1986 and averaged $233\,000 \pm 32\,400$ individuals at each sampling date from 1970 to 2009, the population during our study period ranged from an estimated 166 000 in 2004 to $31\,900 \pm 10\,900$ in 2009 (Adamczewski *et al.* 2009). Although range contraction may occur during times of population decline (Bergerud, Luttich & Camps 2008), it is highly likely that animal density and browsing intensity have decreased to some extent with such dramatic declines. Range use is non-random in accordance with both biotic and abiotic habitat parameters (Post & Klein 1996; Skarin *et al.* 2008; Sharma, Couturier & Côté 2009), and therefore, local browsing intensities will differ from densities expressed per square kilometre. Nonetheless, since we do not have a measure of browsing intensity specific to the research site, we instead use the latter for comparison between other studies. The Bathurst population sizes from 2004 to 2009 translate to an average density of around 0.25–1.3 animals km^{-2} on the summer range (Bruno Croft and Adrian D'Hont, Government of the Northwest Territories, unpublished data), which is substantially lower than those reported for summer in northern Finland (10–12 individuals km^{-2}; Kitti, Forbes & Oksanen 2009) and Svalbard (3.7–5.4 individuals km^{-2}; Wegener & Odasz-Albrigtsen 1998), or yearly averaged densities in northern Finland (3–5 individuals km^{-2}; den Herder, Virtanen & Roininen 2008; Ravolainen *et al.* 2011) or northern Norway (2–18 individuals km^{-2}; Bråthen *et al.* 2007). Despite local scale variation in range use, it can still be concluded that *Rangifer* population densities in Fennoscandian studies are generally higher than those at our site during the study period.

This study contributes two important conclusions to projections of Arctic vegetation change. First, *B. glandulosa,* *V. vitis-idaea* and *R. subarcticum* are highly responsive to changes in caribou browsing pressure over short time scales, as alleviation from browsing led to substantial increases in leaf biomass within only 5 years. Both the short time scale of response within a mesic tundra system (e.g. nonriparian or wet sedge) and the response of evergreen species that are abundant across the low Arctic are new and important findings. Secondly, this study demonstrates that browsing pressure on this landscape is sufficiently strong, even when the herd is at a population low, to cause substantial biomass and nitrogen losses from the dominant shrub species. Caribou browsing may then be a more important influence on Arctic tundra vegetation composition than previously realized and therefore, despite uncertainty in herd recovery, should be incorporated into projections of vegetation change.

Acknowledgements

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Map of plots used in this study; Daring Lake Tundra Ecosystem Research Station, NWT, Canada.

Figure S2. Above-ground biomass of each plant functional group in control and caribou-excluded plots ($n = 5$, bars = standard errors).

Table S1. Linear regression parameters used for the hits: biomass calibration.

Table S2. Statistical test results for browsing impacts on shrub species biomass investigated at three levels of tissue-type resolution.

Table S3. MANOVA results for shrub species N pools, tissue N concentrations and phenolics concentrations.

Table S4. Age- and tissue-type-differentiated C concentration, N concentration and total phenolics concentrations for all species and functional groups in control and exclosed plots.

Table S5. Organic soil chemical and physical properties in control and exclosed plots.