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The impact of different size herbivores on plant biomass in Yamal (Russia)

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ABSTRACT

Tundra ecosystems are changing environments that are greatly affected by plant-herbivore relationships. Many herbivores of different sizes eat, trample or clip plants. However they can also act as support through nutrient addition by faeces. In this study I look at the impact of three sizes of herbivores (large, medium and small) on ten functional groups of plants (nitrogen-fixing forbs, erect willows, birch bushes, evergreen ericoids, nitrogen-non-fixing forbs, grasses, sedges, deciduous shrubs, semi-evergreen shrubs and toxic plants) in three habitats of differing productivity and importance for herbivores on the Yamal Peninsula in Russia. My research question is: "is the impact of herbivores cumulative on palatable plants and complementary on less palatable plants?". To answer this question, I investigated the first year data from an exclosure experiment that was set up in 2014. There were tendencies suggesting that herbivores do not always have a cumulative impact on palatable plants and that the impact on less palatable plants is not always complementary. However, based on plant traits, herbivores' preferences and previous studies I conclude that the fastest growing plants usually show responses already after a very short time of herbivore exclusion. Further research during the next years will shed light on persistence of these results.

Key words: herbivores, cumulative, complementary, palatability, exclosure experiment, functional groups, point intercept method, Yamal.

The herbivore eats the plant. That is the simplest fact one could ever state on plant-herbivore interactions. This means that animals influence the biomass of plants based on factors like palatability or availability. By consuming plants selectively, they can change the species composition through apparent competition and let some species, which were in minority, become abundant (Holt 1977, Bardgett and Wardle 2003). Inversely, species composition change can make species that were abundant a minority (Crête and Doucet 1998, Den Herder *et al.* 2004). A good example of herbivore-induced change of state is the regulation of shrubification (Ravolainen *et al*. 2014), a climate-driven process (Tape *et* al 2010, Myers-Smith *et al* 2015). Herbivory impacts can be categorized as negative and positive. The most obvious negative effect is consumption (Ravolainen *et al.* 2010; Green and Pickering 2013). This could lead to large shifts in the ecosystem like a reduction in aboveground biomass and a slow recovery (Hansen *et al*. 2006; Olofsson *et al*. 2014). The grubbing of geese is one of the most damaging type of foraging as they grub on young sprouts and, in some cases, leave the grounds dry with an increasing salinity from enhanced erosion and evaporation (Audet *et al.* 2007, Humphries 2012). Along these negative influences on plant biomass, herbivores can have positive effects. Grazing can stimulate plant growth as seen for grasses and shrubs (Ydenberg and Prins 1981, McNaughton 1984, Danell *et al.* 1994, Bardgett and Wardle 2003). A last, but not least, positive impact is that, through the process of decomposition, their urine and faeces become a rich source of nutrient for plants (McNaughton *et al*. 1997, Frank and Groffman 1998, Van der Wal 2006; Zamin and Grogan 2013). Thus, animals have been shown to increase nutrient availability through multiple ways (Bazely and Jefferies 1985, Olofsson *et al*. 2001, Stark and Grellmann 2002). This increased nutrient availability is important for nutrient-poor ecosystems like tundra (Lindwall *et al*. 2013).

Tundra is a term that describes almost all of the dominating vegetation and ecosystem north of the tree line. This very broad region, incorporating the north of Canada, Alaska, Russia, Greenland and Scandinavia can be subdivided in five different subzones extending from the warm and lush subzone E to the cold and barren subzone A (Map 1). Due to a low productivity, the turnover of the ecosystem is slow (Nadelhoffer *et al*. 1997). The tundra vegetation is, for the most part, slow-growing (Doak and Morris 2010) meaning that any disturbance may have a strong impact and that recovery may take a long time. For this reason plant-herbivore relationships are a significant driver of change (Oksanen and Oksanen 2000) and having different size herbivores should add another level of complexity.

In tundra, the main herbivores are mammals along with birds and insects. The vertebrates can be divided into three groups of different sizes in order to look at their impact on plants: the large ones are the ungulates, for instance reindeer (*Rangifer tarandus*) or muskox (*Ovibos moschatus*). The medium ones comprise birds such as ptarmigan (*Lagopus lagopus*) and goose (*Anser* spp), as well as mammals including hares (*Lepus timidus*) or ground squirrel (*Citellus parryi*); and the small ones are the rodents (lemmings (*Dicrostonyx* spp), voles (*Microtus* spp)). They differ, of course, in body size but also in feeding method (grubbing, grazing, browsing), morphology, digestive system, capacity to detoxify a plant and ability to migrate (Davidson 1993, Du Toit and Owen-Smith 1989, Hofmann 1989). Their population characteristics can also be different. For example, reindeer are often semi-domesticated, which make their management important for the health of the ecosystem (Muga 1986, Ektova and Morozova 2015). Lemming exhibits population cycles with peaks and lows that have an effect on the herbivory potential of this category of animals (Johnson *et al.* 2011). Most previous studies have shown a complementary impact of herbivores. An example of complementary impact in time is that small and medium herbivores eat shrubs during winter, and reindeer graze them during summer (Bryant 1987, Ravolainen *et al.* 2014). In addition, because of their different body size, these animals are not supposed to occupy the same ecological niche (Bell 1970 in Belovsky 1997, Illius and Gordon 1992, Belovsky 1997). For example, in winter, small herbivores dig burrows in the snow and feed easily on available plants covered by snow like forbs or grasses (Kalela 1957 in Olofsson *et al.* 2004). These plants are also accessible to larger herbivores, like reindeer, moose or snowshoe hares but to a higher cost so they prefer to eat plants above the snow layer as mentioned by Olofsson *et al.* 2004. However, in summer, they do share the same plants and their impact can become cumulative. Moreover large herbivores could be expected to be generalists, also eating unpalatable plants, but smaller ones might be more selective supporting the growth of palatable plants (Davidson 1993). The impact of small herbivores may be similar to/or greater than the impact of the large ones (Edwards and Crawley 1999, Knapp *et al*. 1999, Kryazhimskii and Danilov 2000, Howe and Brown 2000). However if different animals can have different impact then different types of plant can also have different responses to herbivory.

Plants are preferred by herbivores for different underlying reasons. Preference could be based on palatability: how good a plant taste. It could be depending on habit: if a shrub is erect (tall) or prostrate (short). It could be based on growth form or functional group (forb, graminoid, cyperaceae, shrub) (Diaz *et al.* 2007). Indirectly, regarding palatability, other factors become important such as nutrient content and cycling. Indeed it has been shown that palatability can affect the nutrient content of the soil (Cornelissen *et al.* 2004) and so perhaps determine which species are going to be able to grow next season. The last functional trait is the defence of the plant against herbivory (Cornelissen *et al.* 2004). This includes the production of more or less toxic secondary compounds. In the Arctic many functional groups of plants are found. Erect dwarf shrubs is the most abundant group in the low Arctic. It includes two functional groups: deciduous shrubs and evergreen shrubs. Deciduous shrubs have a high leaf quality. They include *Salix* spp, *Vaccinium uliginosum*, and *Betula nana* and are mostly favoured by hares (Larter 1999), ptarmigans (Thomas 1984) and voles (Soininen *et al* 2013). Evergreen shrubs (e.g. *Empetrum nigrum, Ledum decumbens*) are less palatable but are better at using organic nitrogen from the soil (Chapin *et al.* 1996). Another group liked by herbivores are forbs. They can be separated into two categories, nitrogen fixing forbs (e.g. *Astragalus subpolaris, Hedysarum arcticum, Oxytropis sordida*) and nitrogen non-fixing forbs (e.g. *Bistorta vivipara, Angelica archangelica, Rubus arcticus*). The diet of hares in the summer is mainly composed of the nitrogen-fixing kind (Larter 1999). These species are also found in the diet of reindeer along with some *Salix* (Kazmin *et al.* 2011). However voles even eat ericoids such as *Vaccinium* species (Soininen *et al.* 2013). Grasses and sedges are two fast-growing functional groups of plants appreciated by herbivores. They include *Carex* spp, *Luzula* spp and *Eriphorum* spp. Grasses are more palatable than sedges and have a short turnover (Chapin *et al*. 1996). They include *Poa* spp and *Festuca* spp. All these characteristics or functional traits are important factors in plant-herbivore relationships since they can predict how plants will react to a disturbance in the system, such as herbivory (Bråthen *et* al. 2007, Christie *et al.* 2015).

Shrubification or the increase in biomass, cover and abundance of erect shrubs is a much-discussed response to climate change in the Arctic (Myers-Smith *et al*. 2011). Herbivores can influence the impact of climate change on shrubs and other vegetation (Post and Pedersen 2008, Olofsson *et al*. 2009, Christie *et al.* 2015, Ylänne *et* al. 2015). This creates a need for studies about plants such as shrubs but also plant-herbivore relationships in general. As for now, shrubs, forbs and grasses are perhaps the most studied groups of plants in the context of herbivory in the Arctic, meaning that there could be a need for studies about other groups such as sedges or ericoids. Here, the impact of different sizes of vertebrate herbivores on several functional groups of plants is examined using an exclosure experiment in low Arctic. Studies taking numerous groups of plants in account are quite rare. Similar studies about different size herbivores have been done in many ecosystems. In South Africa, exclosures were used to separate the impact of elephants and nyala from those of small-size herbivores (Lagendijk *et* al. 2012). In Norway and Sweden, an exclosure experiment has been performed to show the impact of reindeer and of voles and lemmings (Olofsson *et al.* 2014). Many of theses studies have focused on one or two groups of herbivores like reindeer and rodents (Ektova and Morozova 2015, Ravolainen *et al.* 2014). The attention given to reindeer is mostly due to the existence of reindeer husbandry and to its well-known important impact on the ecosystem. My study shall introduce another level of separation by including medium-size herbivores (ptarmigan and hares). It will add to the literature about these animals, and especially the medium-sized, in the tundra.

In this study, the simultaneous impact of three size categories of herbivore on ten functional groups of plants is studied in three habitats with different importance to focal herbivores. For this purpose, an exclosure experiment was set up. My main question is to investigate if the impact of different size herbivores is cumulative or complementary. Having a cumulative impact, also called additive effect, means impacts of different herbivores feeding sequentially on a functional group of plants are additive (i.e. it amounts to the sum of the separate effects). Having a complementary impact means that their impacts do not overlap and they are not added to each other (see Fig 1. for more explanations). My main prediction is that most palatable plants are expected to show a cumulative impact as they are favoured by most herbivores. In the same way, herbivores are expected to have a complementary impact on less palatable plants, as they might only eat some plants in each group. Another prediction is that in productive habitats, total biomass should respond more rapidly to herbivore exclusion than in less productive habitats. In addition, I expect the results in reproductive plant parts to be cumulative, due to their high palatability. Moreover, knowing the anatomical differences between large and small herbivores, I expect my results to show signs that large herbivores feed on many different plants and that small herbivores eat only a selection of plants.

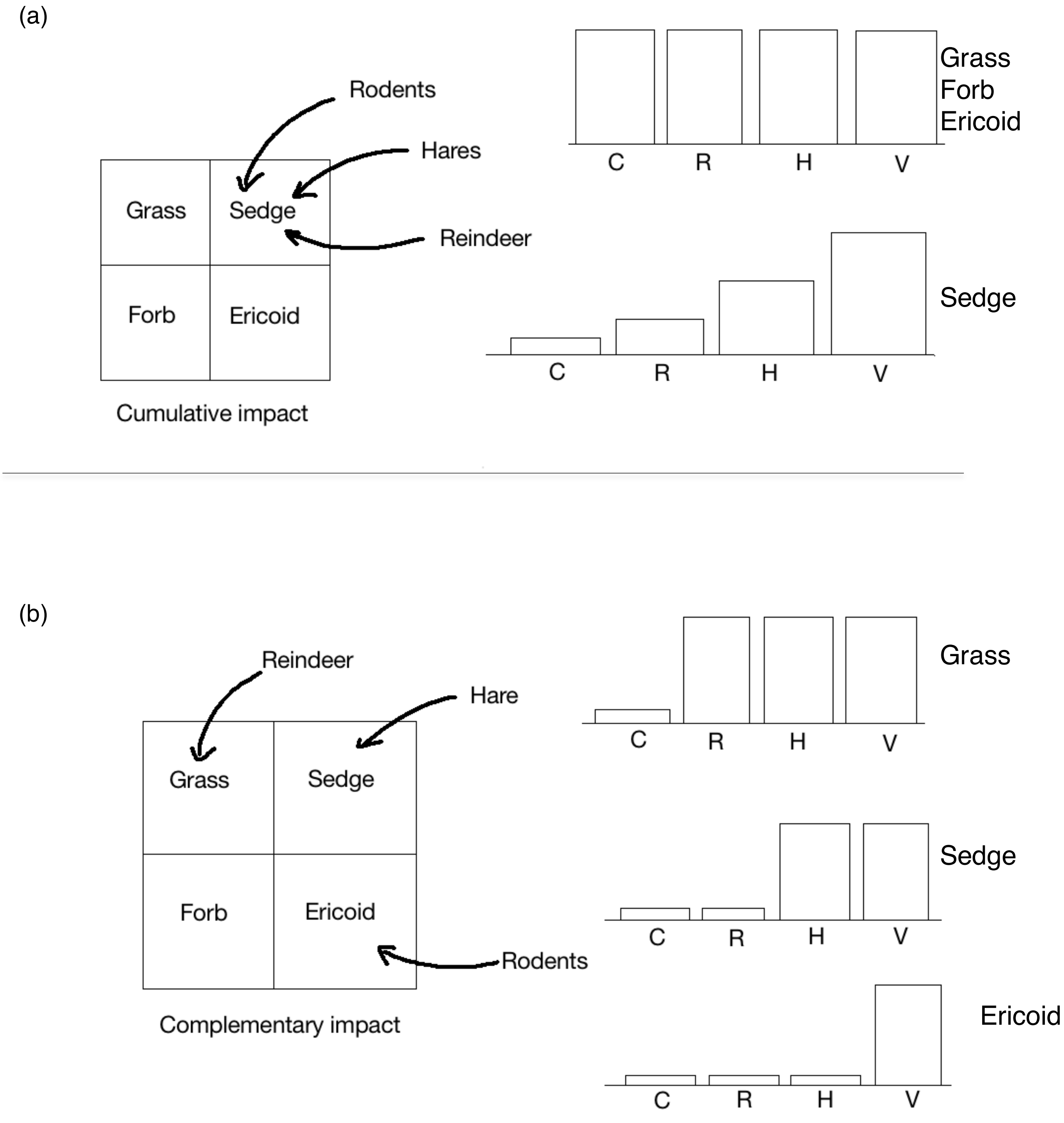
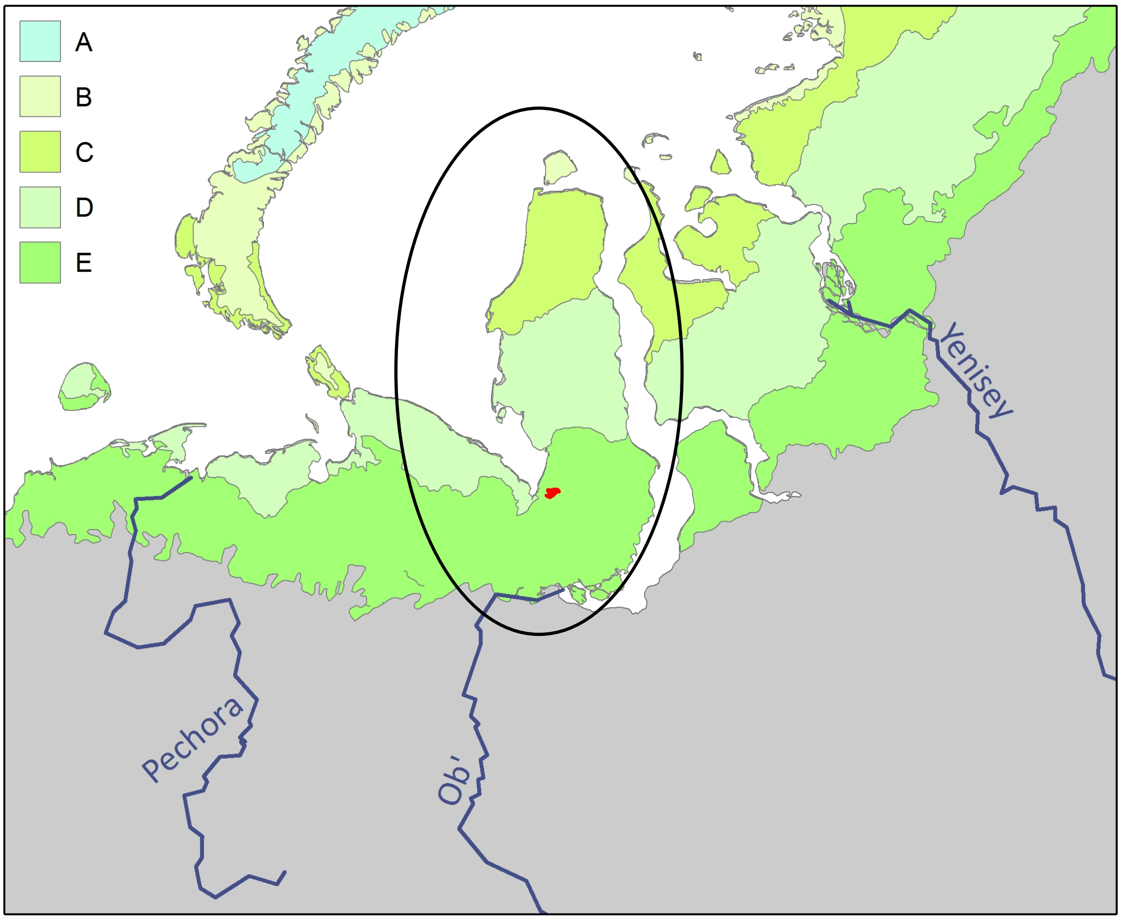


Figure 1: Predicted responses for a cumulative and a complementary impact of three herbivore groups on functional groups of plants in my experimental setup, where an increasing number of herbivores was excluded from the plots. 1a) Predictions of a cumulative impact. C stands for control, R stands for reindeer-excluded plot, H stands for reindeer, ptarmigan and hare-excluded plot, V stands for all-excluded plot, including rodents. In a cumulative impact, rodents, hares and reindeer are feeding on the same group of plant (here, sedges serve as an example). Therefore, in the reindeer-excluded plot, the impact of reindeer on the biomass of sedges will be found. In the reindeer and hare excluded plot, the impact of reindeer plus the impact of hares is shown. In the all-excluded plot, the impact of reindeer, plus the impact of hares plus the impact of rodents is presented. As impacts can be added to one another, this is called a cumulative impact.
1b: Predictions of a complementary impact (treatments are designated as above). In the case of a complementary impact all three herbivores eat a different source of food. As an example, reindeer eat grasses, hares eat sedges and rodents eat ericoids. This means that in the grass graph, only the impact of reindeer exclusion will show as only reindeer eat grasses and not the two other herbivores. In the sedge plot, since only hare eat sedges and not the two other herbivores, an impact will start to show from the reindeer-hare excluded plot. In the ericoid plot, the impact only shows from the all-excluded plot, as rodents are the only one eating ericoids.

METHODS

Study area

This study was carried out in the southern part of the Yamal Peninsula in Russia (68.2°N, 69.2° E). This peninsula encompasses four of the five bioclimatic subzones of the Arctic as described in the Circum-Arctic Vegetation Map (CAVM: Walker *et* al. 2005). It is characterized by gas development, important climate changes and a strong presence of indigenous Nenets (Map 1; Walker *et al*. 2009, Walker *et al.* 2010). My study zone is located in subzone E, the warmest and most vegetated one (Walker *et al.* 2005). In the study area, dominating vegetation types, according to CAVM, are erect dwarf shrub and low shrub tundra (Sokolova 2014). The landscape is mainly composed of continuous shrubland, with shrubs from 50 cm to 2m high. These shrubs can be deciduous or evergreen and be surrounded by graminoids, forbs, true mosses and lichens (Kaplan 2003). The data collection was centred on the Erkuta Tundra Monitoring site, situated close to Payutayakha and Erkutayakha rivers (Sokolov *et al*. 2014). It is defined by flat areas surrounded by sandy hills rising to up to 40 meters (Ehrich *et al.* 2011, Sokolov *et al*. 2012). Many herbivorous animals are present in the area and I am studying the impact of six of them. Large herbivores are represented by reindeer; medium herbivores are willow ptarmigans and mountain hares; small herbivores are Middendorf's voles (*Microtus middendorffii*), narrow-headed voles (*Microtus gregalis*) and collared lemmings (*Dicrostonyx torquatus*) (Sokolov *et al*. 2016).



Map 1: Map of the Yamalo-Nenetsky Autonomous District in Northwest Siberia (Russia). The Yamal peninsula is the one in the circle. The five bioclimatic subzones from Walker 2005 (A-E) are represented with different shades of green. My study area is presented in red.

The first two habitat types are willow meadows (WM) and forb tundra (FT). They were chosen because they are expected to be focal habitats for all studied herbivores. Willow meadows refer to meadows close to willow thickets. Like any meadow, the soil is mainly moist and the vegetation is quite dense. However chosen WM plots were situated in places that are not flooded in spring, such as slopes. The main characteristic is the presence of tall willow shrubs and the primary category of plants is herbaceous. It is home to narrow-sculled voles (Sokolova *et al* 2014). The terrain of this habitat is concave and often has a slope less than 30 degree. Both habitats described are patchy, meaning that vegetation occurs in productive patches, with less productive parts between each patch. Forb tundra is dominated by Fabaceae plants. This habitat is also composed of a large number of graminoids, Caryophyllaceae or Asteraceae, with true mosses and lichens. The vegetation is mostly herbaceous and grows on a sandy substrate. The terrain in this habitat is associated with dry parts of the landscape. It is also often convex and is constituted of patches abundant in plants and patches of lesser abundance of plants. Situated in upper parts of slopes and hills, the snow cover is usually thin and the vegetation remains relatively accessible to herbivores during winter. Hares are active users of this habitat in winter as shown by the large number of hare pellets present in spring. The last habitat is the most common habitat type in this biome called mesic tundra (MT). Mesic tundra is characterized by a slight slope and a diverse vegetation. It is mostly dominated by dwarf shrubs, such as *Betula nana* and *Vaccinium* species. Forbs and graminoids are also found is high numbers (Muc and Bliss 1977, Duclos 2002).

Study design

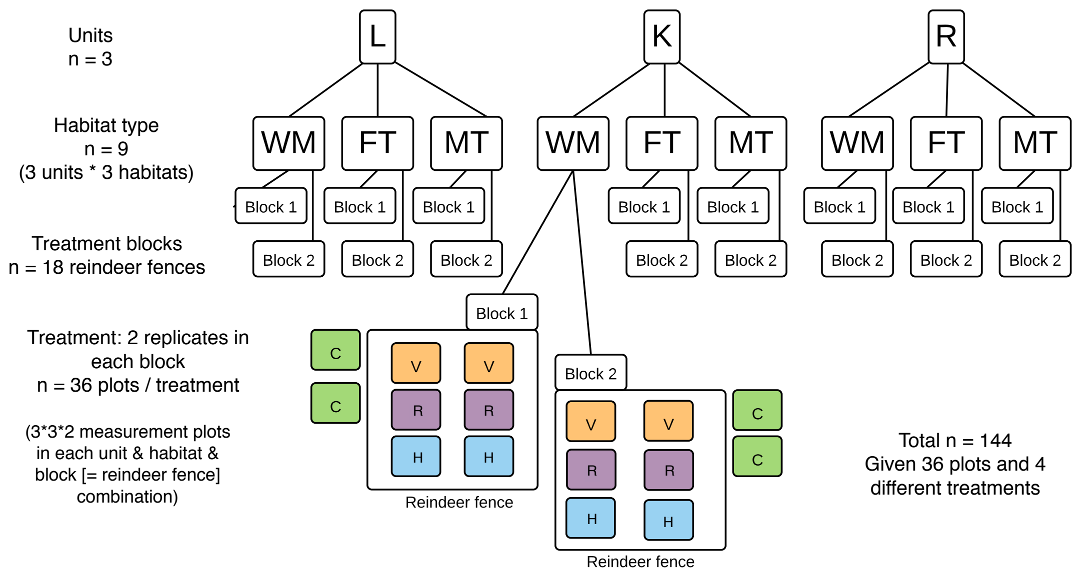


Figure 2: Study design. L, K and R are replicated study units. In each unit are three habitat types: Willow Meadow (WM), Forb Tundra (FT), Mesic Tundra (MT). In each habitat type of each unit are two blocks (1 and 2). Each block has 2 control plots (C), 2 reindeer plots (R), 2 hare plots (H), 2 all-excluded plots (V). The plots are described in the text below.

Picture 1: Photography of an exclosure. The reindeer fence surrounds the small plots. The large mesh exclosures are hare exclosures. The fine mesh exclosures are all-excluded exclosures. Reindeer plots are not marked but are situated between hare plots and all-excluded plots. (Picture from D. Ehrich)

The selection of study plots was done in the field, following a random procedure. Because no vegetation maps or similar information was available over the study area, the whole area encompassed by the study was surveyed during the first field days in 2014. During this survey, GPS coordinates were taken whenever suitable sites for the three categories were found. After having made an initial list of sites (roughly the initial list was 2-3 times larger than the number of final replicated habitats), the ones where exclosures were erected were selected by a random draw. This way selection of study units was guided by terrain form as well as presence of roughly the type of vegetation wanted for the study, but not by the specific characteristics or possible differences between sites. This procedure was chosen based on previous studies that have found the step of selecting study areas for ecological studies possibly influencing the results (Mörsdorf *et al.* 2015; Albert *et al.* 2010).

The general study area at Erkuta is divided into units, termed K, L and R, which are separated by 5 km. For this study, focal habitats were found in all units. Units are similar in topography, having sandy hills with flatter areas and numerous rivers, lakes and peatlands. As explained above, two study sites of at least 5 x 5 m were chosen for each habitat in each unit (Block 1 and Block 2). Each block consisted of an exclosure of 2.5 x 2.5m, built to keep reindeer out. The area within each exclosure was separated into six 0.36m^2 plots: 2 for reindeer exclusion (reindeer plot); 2 for ptarmigan, hare and reindeer exclusion (hare plot); 2 for exclusion of all herbivores (all-excluded plot). Then two control plots (C) were chosen randomly outside of the exclosure by throwing a roll of measuring tape over the shoulder of a person without looking. For each hare and all-excluded plots, a small exclosure was built around the plot, keeping designated animals out (Fig. 2). Hare exclosures had a mesh size of 5 cm, whereas all-excluded exclosures had a mesh size of 1 cm to also keep rodents out. These exclosures were dug 10 cm deep into the soil, to prevent voles from entering under the mesh. In order to treat all plots similarly, a shovel was stuck into the ground to a depth of 10 cm to similarly cut roots around plots of all treatments and controls. Exclosures were built in the summer of 2014.

For each plot the abundance of plants was measured using the point intercept method (Bråthen and Hagberg 2004). A 50 x 50 cm frame with 15 pins was used to record the total number of hits. For erect shrubs (erect *Salix* and *Betula nana*), hits from woody parts were separated from those on vegetative parts. The same principle was also applied to reproductive parts (flowers or seeds) of all plants. For plants that were present in the plot but not touching any pins, a record of 0.1 was written. Then each plot was subdivided into 4 subplots (or quadrats). The presence of shrubs and reproductive parts was recorded in each subplot and recorded as a number between 0 (no reproductive part) and 4 (flowers, fruits or seed in all quadrats). For shrubs, erect *Salix* were separated from *Betula*. For each shrub species, the maximum height was measured. These measurements were done in the summer of 2014, before the exclosures were set up and in the summer (July/ August) of 2015. A total of 90 species of vascular plants were identified during the data collection.

<u>Conversion into biomass</u>

For the conversion into biomass, species were separated into biomass groups. The different groups were narrow-leaved grasses, broad-leaved grasses, cyperaceae, large forbs, medium forbs, small forbs, narrow-leaved ericoids, broad-leaved ericoids, *Betula, Salix, Veratrum* and *Vaccinium vitis-ideae*. This separation is based on the partition done in Ravolainen *et al.* (2010). Species that were not included in the paper by Ravolainen *et al.* (2010) have been placed in different biomass groups based subjectively on their appearance. The complete list of species, following the Panarctic Flora nomenclature, in their corresponding biomass group can be found in Appendix A.

The conversion into biomass is based on the equation presented in Bråthen and Hagberg (2004). First the average number of touches per plot (total number of pins per plot /15) called intercept frequency was calculated. Then it was multiplied by the regression coefficient (b). The regression coefficient for each functional group can be found in Ravolainen *et al.* (2010).

For *Betula nana*, erect *Salix* bushes and *Veratrum lobelianum*, b was calculated from calibrations done in Yamal during the data collection in the summer of 2015. For each species, 30 plots of 50 x 50 cm were chosen based on criteria to get the best widespread distribution: 10 plots with high plants, 10 plots with medium plants, 10 plots with low plants. High, medium and low are subjective size categories. In each category, plots represented the species cover in the plot (0.1, 10%, 20%, 30%, 40%, 50%, 60%, 70%, 80%, 90% and 100%). To count the touches, a 50 x 50 cm frame with 50 pins was used. Counts were separated for wood, leaves and reproductive parts. After counting, the plants were cut to the ground level and conserved in paper bags until drying. Before drying, leaves and reproductive parts of each sample were separated from woody parts. Samples were then dried for 24h at 60°C and weighed. Based on the results found, and following the equations in Bråthen and Hagberg (2004), the regression coefficient b was calculated. In addition, the coefficient of variation (CV) and the variance (SD^2) were calculated. A table with calibration results can be found in Appendix B.

The calculation of b for *Vaccinium vitis-ideae* was done in collaboration with another project (http://herbivory.biology.ualberta.ca/protocol/invertebrate-herbivory-protocol/). Touches were recorded using a 50 x 50 cm frame with 10 pins in 15 plots. The plants were cut, dried in an oven at 70°C during 72h and weighed. CV, b and SD^2 were calculated following the equations in Bråthen and Hagberg (2004).

<u>Analysis</u>

For the analysis, the plant species were separated into ten functional groups: nitrogen-fixing forbs/hemiparasites (N-fix), *Betula*, *Salix*, evergreen ericoids (ericoids), nitrogen-non-fixing forbs (forbs), grasses, sedges, deciduous shrubs, semi-evergreen forbs (evergreen forbs) (Chapin *et al.* 1996) and toxic plants. This last group was created based on the secondary compounds of the plant. If the secondary compound was expected to be harmful enough to make the plant unpalatable then the plant was put in this group (references for secondary compounds found in Appendix A). The list of plant species with their associated functional group can be found in Appendix A.

Functional groups, which were absent in more than 20% of plots, were excluded from the analysis. A list showing which habitats were analysed for each functional group is presented in Appendix C. Both *Salix* and semi-evergreen forbs groups were absent in more than 20% of plots in all habitats. Therefore semi-evergreen forbs were not analysed in this study. However since *Salix* is an important species for herbivores I analysed it in willow meadows, where it was the most abundant.

The results were analysed using one of the three following linear mixed models performed with the function lmer from the lme4 package (R software, Bates 2014). The response variable was log +1 of plant biomass, and explanatory variables were treatment and year (as factor, i.e. 2014: before; 2015: after the construction of exclosures). I used the log of the biomass in order to homogenize the residual variance. I focussed specifically on the interaction of these two variables, as it reflects the effect of the treatment. For plant groups, which could be analysed in several habitats, this first model (no/one habitat model) was compared to a model with an additive effect of habitat (additive model) and a model with a three-way interaction of the two first explanatory variables with habitats (interaction model). Random factors for all models were individual plots and individual blocks. The choice of model was done based on an ANOVA performing a Chi-square test. In addition, diagnostic plots were created. I checked the presence of outliers, the homogeneity of the variance, the normal distribution of the data and the goodness of fit.

Shrub height and presence of reproductive parts was also analysed. Shrub height for *Betula* and *Salix* was analysed the same way as for the biomass. For reproductive parts, a cumulative link model with binomial error was performed with the clm function from the ordinal package (R software, Christensen 2015). Predictors were treatment and year and the response variable was the number of quadrats where reproductive parts are present. Random factors for the models were individual plots and individual blocks. The different models were the same as for the biomass analysis. Results were expressed as odd ratios with confidence intervals

A list of each functional group with their chosen model is shown in Appendix C.

Estimates for each group, for both shrub height and presence of reproductive parts were plotted along with their confidence intervals. For total biomass, all three habitats were plotted.

RESULTS

In 2015, the snowmelt happened about a month earlier than in 2014 and the ice on Erkuta river broke 3 weeks earlier than in 2014, which made the growth and blooming season start earlier (Sokolov and Ehrich, personal communication). Since we did the data collection at the end of July each year, this difference in general growth conditions caused an overall difference in response variables between years. Effect sizes presented in this section are not log transformed as they represent a qualitative difference between treatments and control.

Total biomass

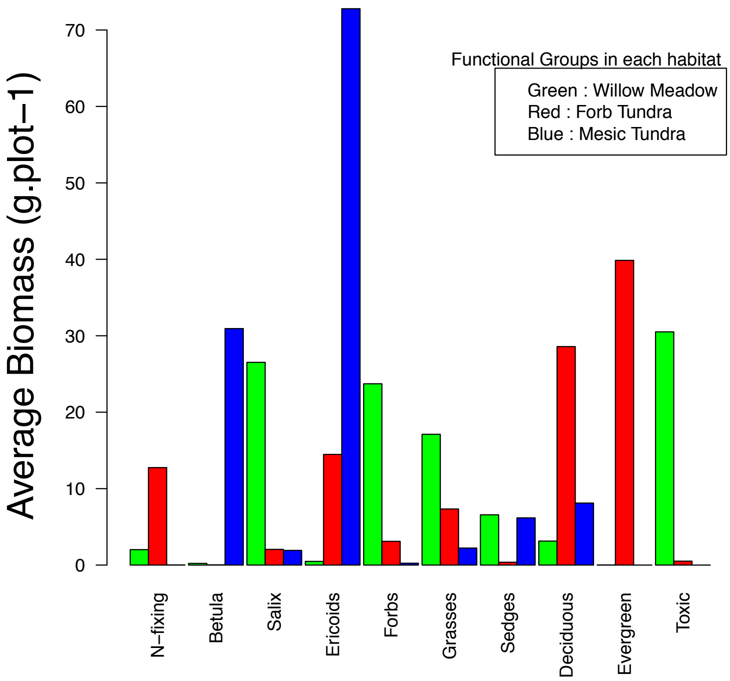
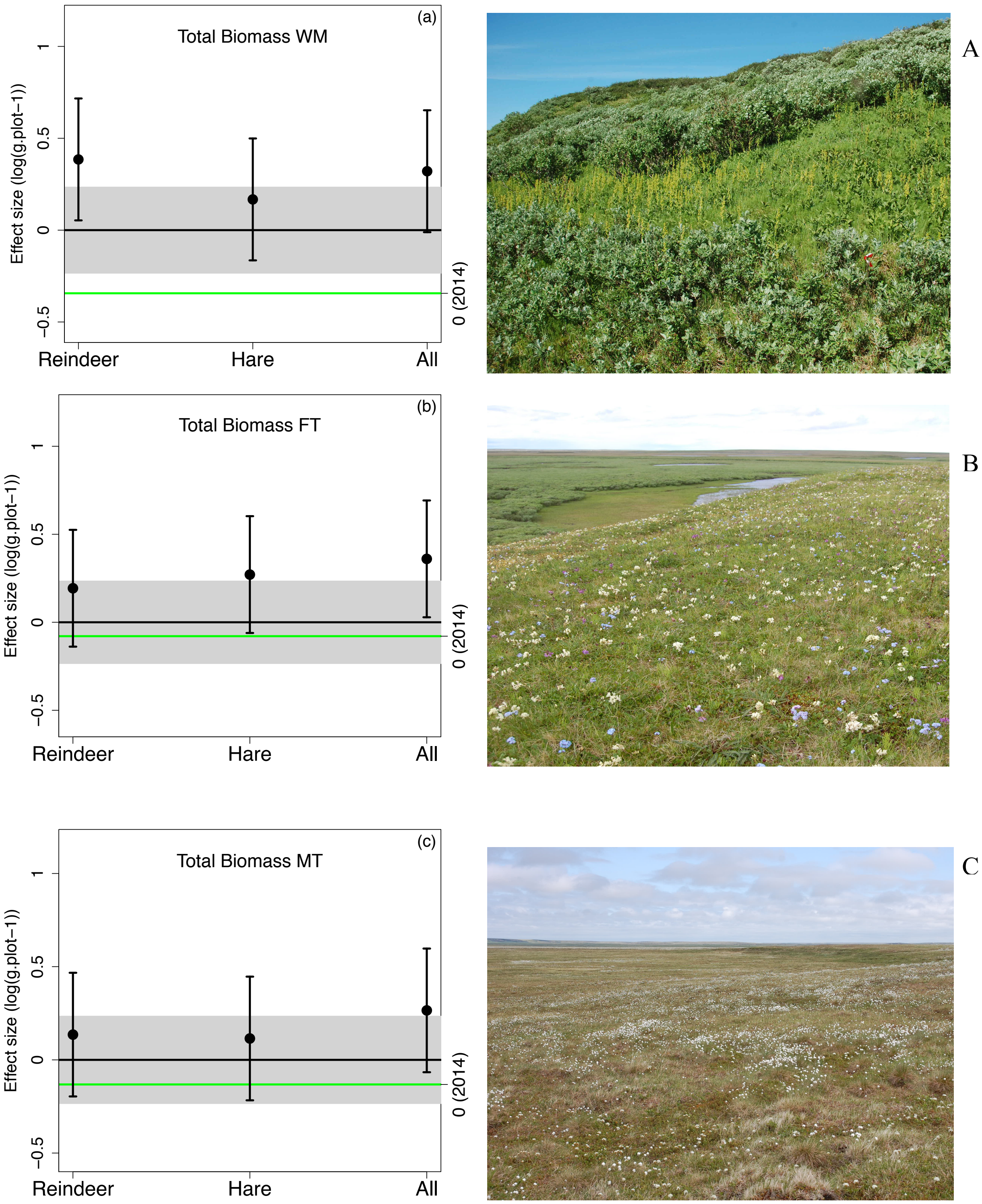


Figure 3: Average biomass (in log(g).plot-1) for each plant functional group in each habitat in 2015. Green bars are for willow meadow, red bars stand for forb tundra and blue bars represent mesic tundra.

In willow meadows, the three largest groups were willows, forbs and toxic plants (Fig. 3). In forb tundra, the two largest groups were deciduous and evergreen shrubs. In mesic tundra, the two largest groups were ericoids and birches.


(a)
Total Biomass WM
Effect size (log(g.plot−1))
1
0.5
0
−0.5
0 (2014)
Reindeer
Hare
All
A
(b)
Total Biomass FT
Effect size (log(g.plot−1))
1
0.5
0
−0.5
0 (2014)
Reindeer
Hare
All
B
(c)
Total Biomass MT
Effect size (log(g.plot−1))
1
0.5
0
−0.5
0 (2014)
Reindeer
Hare
All
C

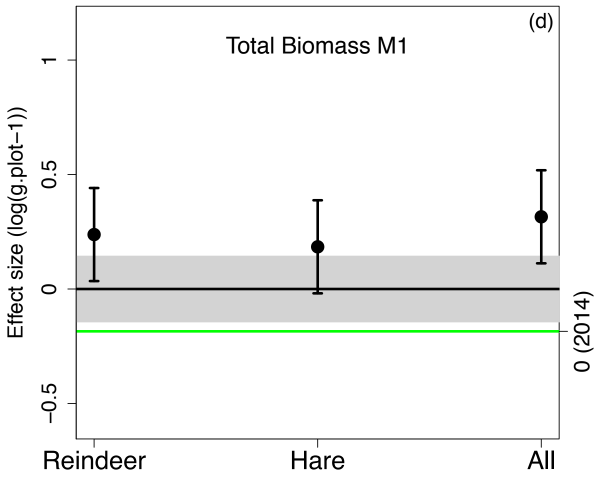


Figure 4: Total Biomass for Willow Meadow habitat (a), Forb Tundra habitat (b) and Mesic Tundra habitat (c) in 2015 from an interaction model. 4d represents the Total Biomass from a no-habitat model. The treatment Reindeer, Hare and All-excluded (All) are represented on the X-axis and the change from the 2015 control (interaction effects treatment x year) is represented on the Y-axis. The black line is the control of 2015 and the green line is the control of 2014. For each value, the confidence interval (95%) is depicted. The confidence interval for the control of 2015 is represented by the grey area.

Picture 2: Photographic examples of willow meadow vegetation (A), forb tundra vegetation (B) and mesic tundra vegetation (C). (Pictures from D. Ehrich)

For total biomass, the model without habitat effect received most support from ANOVA (Appendix C). However to show the different habitats, I also plotted the three habitats with estimates from an interaction model. In the no-habitat model, reindeer and all excluded treatments showed a significant positive interaction between year and treatment, (Fig. 4d) showing that plants grew more in the exclosures than in the control (respective effect sizes: 0.24 and 0.32; p-values: 0.003 and 0.228; a list of effect estimates, with confidence intervals, can be found in Appendix E). The effect was nearly significant for hare exclosures as well.

Figures 4a, 4b and 4c show the results from total biomass analysis using an interaction model to have habitat specific results. First of all, willow meadow habitat (Fig. 4a) had the largest increase from the control compared to other habitats. It also had the most biomass and, when looking at the functional group level (Fig. 3), fast-growing plants, like forbs and grasses, were the most commonly found. In addition, this habitat has the most diversity with nine out of ten functional groups present. The three largest groups are, in decreasing order, toxic plants, *Salix* and forbs. In 2015, only the reindeer treatment led to a significant increase in biomass (effect size (log scale): 0.38; p-value: 0.028). However, the increase in the all-excluded plot was almost significant.

The Forb Tundra habitat results showed the second largest increase of all habitats in control and treatments (Fig. 4b). At the functional group level, FT displayed a high biomass of deciduous shrubs and evergreen ericoids, but quite low biomass for other groups (Fig. 3). In

2015, without large changes, all treatments were increasing from the reindeer excluded to the all excluded. The latter, however, showed a significant increase (effect size: 0.36 p-value: 0.040).

The MT habitat is the least diverse with only 7 functional groups out of 10 represented (Fig. 3). It had also the least biomass of all three habitats (Fig. 4c). Reindeer and hare exclosures had almost the same value and increased as much as the control between 2014 and 2015. However the all excluded plot showed a larger increasing trend from the control.

Biomass per functional group

Nitrogen-non-fixing Forbs

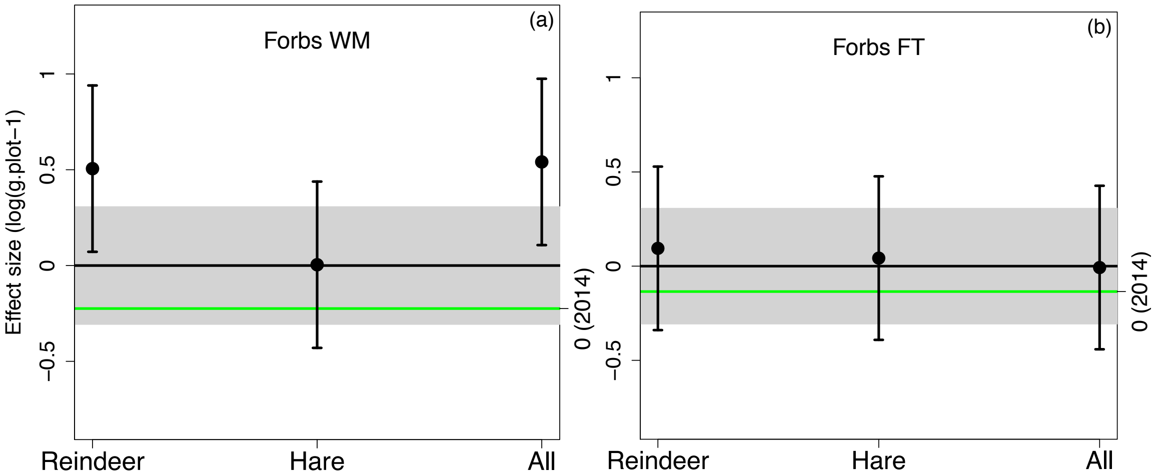


Figure 5: Biomass change (in log(g).plot-1) for the nitrogen-non-fixing forbs from Forb Tundra habitat and Willow Meadow habitat in 2015. The treatment Reindeer, Hare and All-excluded (All) are represented on the X-axis and the changes, estimated from an interaction model, from the 2015 control is represented on the Y-axis. The black line is the control of 2015 and the green line is the control of 2014. For each value, the confidence interval (95%) is depicted. The confidence interval for the control of 2015 is represented by the grey area.

In WM, reindeer and all-excluded treatments had very similar significant effects (effect size of 0.51 and 0.54 respectively, p-values of 0.027 and 0.018 respectively) as shown in Fig. 5a. However the two treatments were not significantly different. Surprisingly, the hare exclosure treatment had nearly no effect.

In FT, no treatment had an effect on the biomass of forbs (Fig. 5b).

Nitrogen-fixing forbs

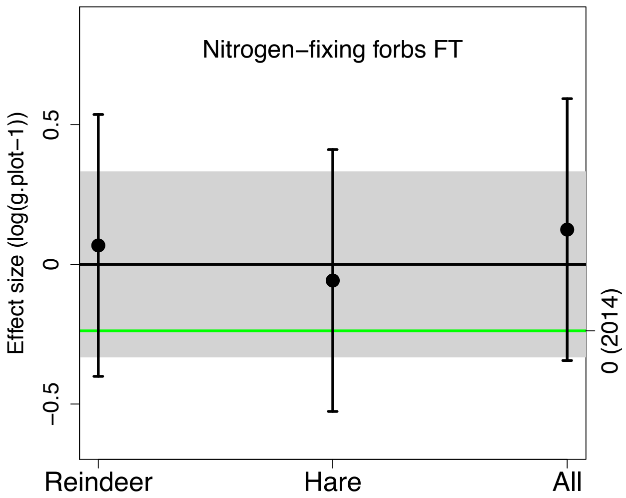


Figure 6: Biomass change (in log(g).plot^{-1}) for the nitrogen-fixing forbs in 2015 in Forb Tundra. The treatment Reindeer, Hare and All-excluded (All) are represented on the X-axis and the changes, estimated from a one habitat model, from the 2015 control is represented on the Y-axis. The black line is the control of 2015 and the green line is the control of 2014. For each value, the confidence interval (95%) is depicted. The confidence interval for the control of 2015 is represented by the grey area.

No treatment had any effect on the biomass of nitrogen fixing forbs in FT (Fig. 6). There was a tendentious overall increase between 2014 and 2015, but it was not significant (Fig. D7 in Appendix D).

Grasses

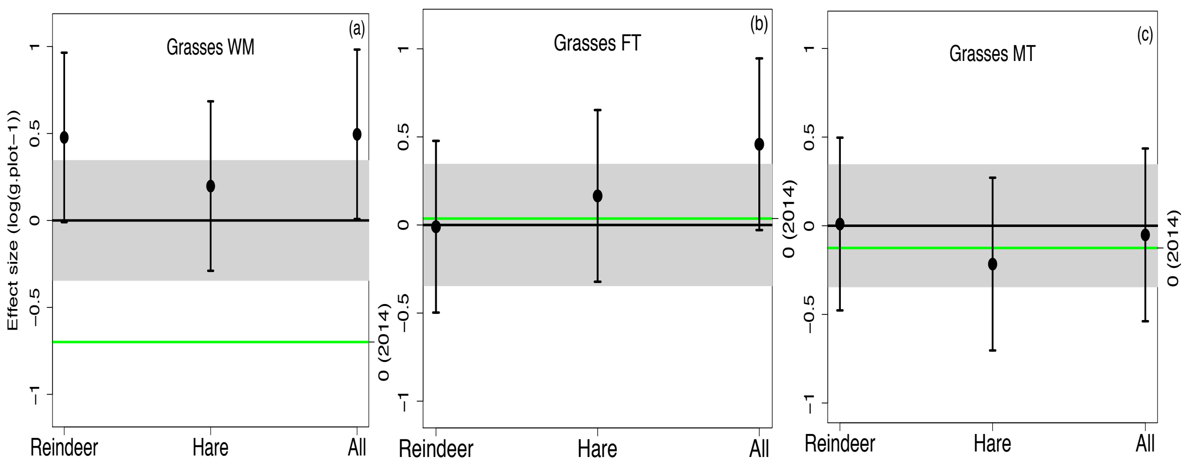


Figure 7: Biomass change (in log(g).plot^{-1}) for the grasses from Willow Meadow habitat, Forb Tundra habitat and Mesic Tundra habitat in 2015. The treatment Reindeer, Hare and All-excluded (All) are represented on the X-axis and the changes, estimated from an interaction model, from the 2015 control is represented on the Y-axis. The black line is the control of 2015 and the green line is the control of 2014. For each value, the confidence interval (95%) is depicted. The confidence interval for the control of 2015 is represented by the grey area.

For grasses in willow meadows, reindeer and all-excluded treatments had similar effect (Fig. 7a). However the two treatments were not significantly different. They had a higher value than the hare exclosure. They were also close to significance (respective effect sizes: 0.48 and 0.50; p-values: 0.064 and 0.055). For the hare exclosure, there was almost no effect.

In FT, changes from the control were small but the all-excluded plot showed an increase that was almost significant (effect size: 0.46; p-value: 0.076) (Fig. 7b). The reindeer treatment did not have any effect. However the two treatments were not significantly different. A small increase was seen in the hare exclosure and when all herbivores were excluded, there was a tendentious increase.

In MT, all treatments had less effect than in other habitats (Fig. 7c). Both reindeer and all-excluded treatments did not have any effect. Only the hare exclosure showed a small decrease.

Sedges

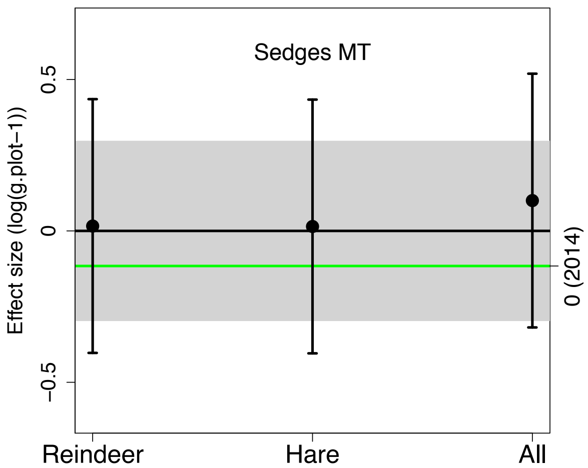


Figure 8: Biomass change (in log(g).plot^{-1}) for the sedges in 2015 in Mesic Tundra. The treatment Reindeer, Hare and All-excluded (All) are represented on the X-axis and the changes, estimated from a no habitat model, from the 2015 control is represented on the Y-axis. The black line is the control of 2015 and the green line is the control of 2014. For each value, the confidence interval (95%) is depicted. The confidence interval for the control of 2015 is represented by the grey area.

The all-excluded exclosure had a slight non-significant increase. However, in overall, treatments did not have an effect on the biomass of sedges (Fig. 8).

Erect willows

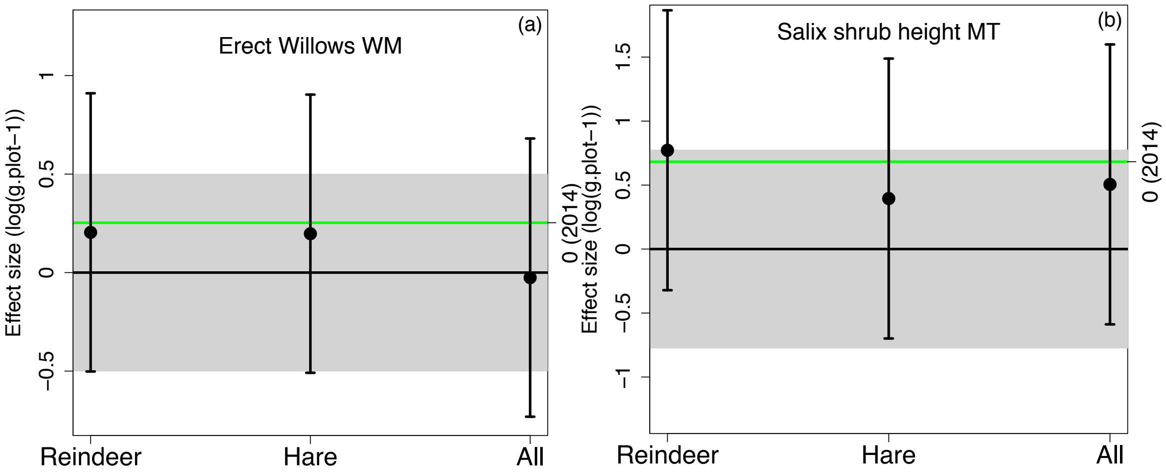


Figure 9a (left): Biomass change (in log(g).plot^{-1}) for the *Salix* bushes in 2015 in Willow Meadows. The treatment Reindeer, Hare and All-excluded (All) are represented on the X-axis and the changes, estimated from a one habitat model, from the 2015 control is represented on the Y-axis. The black line is the control of 2015 and the green line is the control of 2014. For each value, the confidence interval (95%) is depicted. The confidence interval for the control of 2015 is represented by the grey area.

Figure 9b (right): Maximum shrub height change (in cm.plot^{-1}) for the *Salix* bushes in 2015 in Willow Meadows. The treatment Reindeer, Hare and All-excluded (All) are represented on the X-axis and the changes, estimated from a one habitat model, from the 2015 control is represented on the Y-axis. The black line is the control of 2015 and the green line is the control of 2014. For each value, the confidence interval (95%) is depicted. The confidence interval for the control of 2015 is represented by the grey area.

Reindeer and hare treatments had the same effect and revealed a slight but clearly not significant increase (Fig. 9a) (respective effect sizes: 0.197 and 0.204). Contrary to that, there was nearly no effect of the all-excluded treatment.

Regarding shrub height, all treatments were above the control but none of them were significant (Fig. 9b). The reindeer treatment led to the largest increase but the hare and the all-excluded treatments had similar effects.

Deciduous shrubs

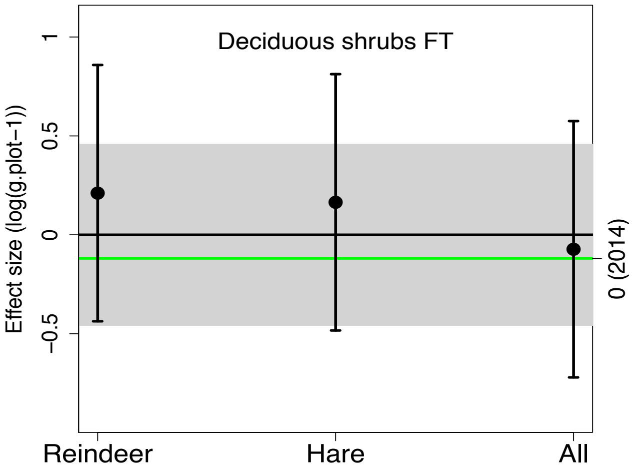


Figure 10: Biomass change (in log(g).plot^{-1}) for the deciduous shrubs in 2015 in Forb Tundra. The treatment Reindeer, Hare and All-excluded (All) are represented on the X-axis and the change, estimated from a no-habitat model, from the 2015 control is represented on the Y-axis. The black line is the control of 2015 and the green line is the control of 2014. For each value, the confidence interval (95%) is depicted. The confidence interval for the control of 2015 is represented by the grey area.

The reindeer and the hare exclosure had a slight non-significant increase. Nevertheless, all treatments did not have an interpretable effect on the biomass of deciduous shrubs (Fig. 10).

Birch (*Betula nana*)

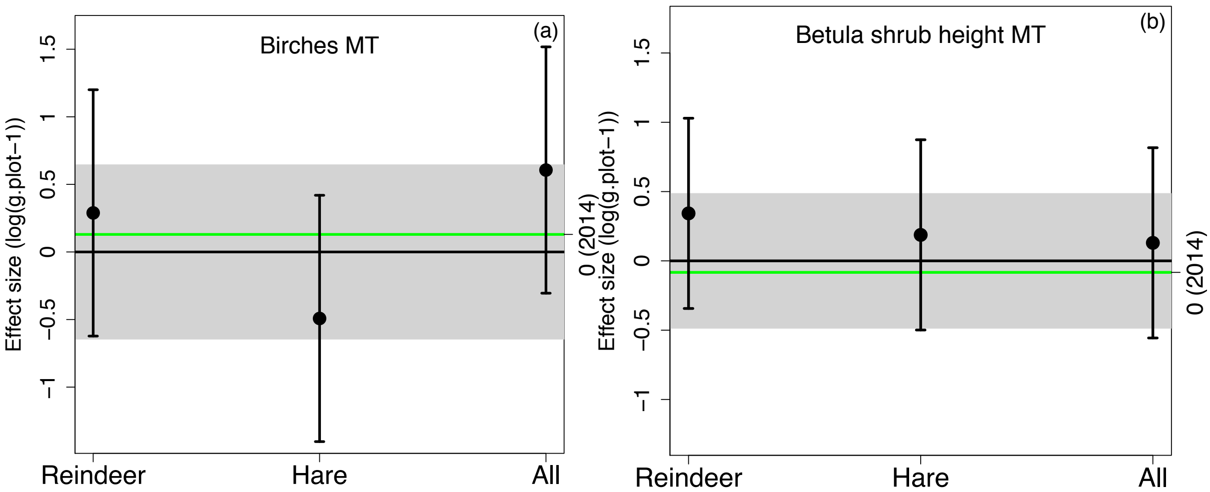


Figure 11a: Biomass change (in log(g).plot^{-1}) for *Betula nana* in 2015 in Mesic Tundra. The treatment Reindeer, Hare and All-excluded (All) are represented on the X-axis and the change, estimated from a one habitat model, from the 2015 control is represented on the Y-axis. The black line is the control of 2015 and the green line is the control of 2014. For each value, the confidence interval (95%) is depicted. The confidence interval for the control of 2015 is represented by the grey area.

Figure 11b: Maximum shrub height change (in cm.plot^{-1}) for *Betula nana* in 2015 in Mesic Tundra. The treatment Reindeer, Hare and All-excluded (All) are represented on the X-axis and the change, estimated from a one habitat model, from the 2015 control is represented on the Y-axis. The black line is the control of 2015 and the green line is the control of 2014. For each value, the confidence interval (95%) is depicted. The confidence interval for the control of 2015 is represented by the grey area.

Both reindeer and all-excluded treatments resulted in a non-significant increasing trend in biomass (Fig. 11a) (respective effect sizes: 0.29 and 0.61). This increase was larger in the all-excluded plot. However these two treatments were not significantly different. When hares and reindeer were excluded there is a decrease in biomass (effect size: -0.49). Confidence intervals for this group are large, which could impact the clarity of this interpretation.

Concerning maximum shrub height, all treatments had a non-significant effect (Fig. 11b). The largest increase in biomass was seen when only reindeer were excluded. Hare and all-excluded treatments had almost no effect.

Evergreen ericoids

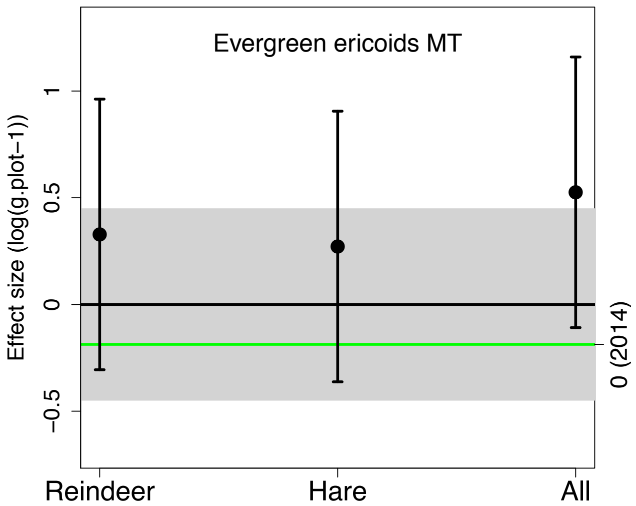


Figure 12: Biomass change (in log(g).plot^{-1}) for the evergreen ericoid in 2015 from Forb Tundra. The treatment Reindeer, Hare and All-excluded (All) are represented on the X-axis and the changes, estimated from a no-habitat model, from the 2015 control is represented on the Y-axis. The black line is the control of 2015 and the green line is the control of 2014. For each value, the confidence interval (95%) is depicted. The confidence interval for the control of 2015 is represented by the grey area.

All treatments had a weak positive effect, but none was significant (Fig. 12). Reindeer and hare treatments had similar effects (respective effect size: 0.33 and 0.27). However these two treatments were not significantly different. The all-excluded exclosure presented a somewhat larger increase in biomass (effect size: 0.53).

Toxic plants

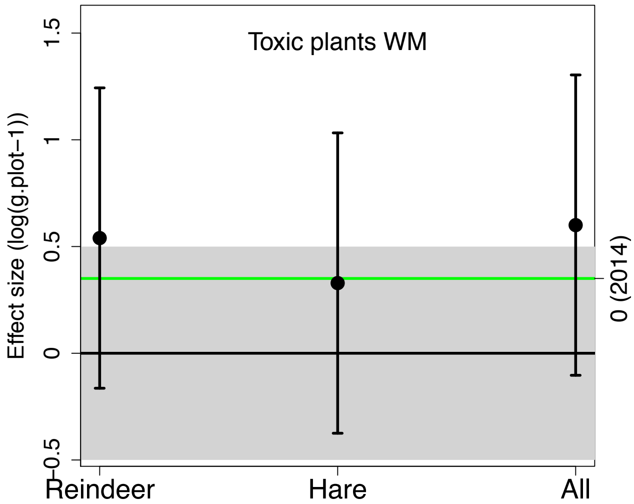


Figure 13: Biomass change (in log(g).plot^{-1}) for the toxic plants in 2015 in Willow Meadows. The treatment Reindeer, Hare and All-excluded (All) are represented on the X-axis and the changes, estimated from a no habitat model, from the 2015 control is represented on the Y-axis. The black line is the control of 2015 and the green line is the control of 2014. For each value, the confidence interval (95%) is depicted. The confidence interval for the control of 2015 is represented by the grey area.

All-excluded and reindeer treatments displayed similar tendencies for increased biomass (respective effect sizes: 0.60 and 0.54; p-values: 0.10 and 0.14) (Fig. 13). However these two treatments were not significantly different. The hare treatment had a smaller effect than other treatments.

Reproductive parts

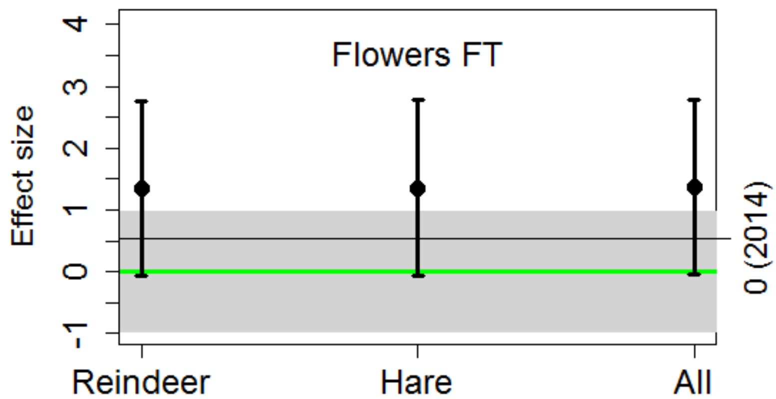


Figure 14: Reproductive parts count change for all species in 2015 in Forb Tundra. The treatment Reindeer, Hare and All-excluded (All) are represented on the X-axis and the changes, estimated from an additive model, from the 2015 control is represented on the Y-axis. The control is not quantitative and serves as a qualitative mark. It is represented by a black line. The blue dots stand for Willow Meadows, the black dots represent Forb Tundra and the blue dots are for Mesic Tundra.

The selected model by ANOVA for this group was the model with habitat as an additive factor. This means that the effect was similar in all habitats. The habitat shown for reproductive plant parts is forb tundra because it had the largest number of quadrats with reproductive parts (see Picture 2B). All treatments had the same effect on reproductive parts counts (Fig. 14). The odd ratio between FT/WM was higher than the one between FT and MT (ratio: 0.031 // CI up: 0.006 // CI down: 0.162). The odd ratio FT/MT was quite low (ratio: 0.013// CI up: 0.002 // CI down: 0.075).

DISCUSSION

Cumulative or complementary?

Large herbivores show a generalist type of effect as they dispatch their impact on multiple species. Indeed my results show that they have a more or less significant effect on forbs, grasses, willows, birches, reproductive parts, ericoids and toxic plants. The first five groups are palatable plants and it has been shown that high reindeer densities decrease the biomass of palatable plants (Bråthen *et al.* 2007). The next two groups could have mostly been trampled by reindeer. Reindeer density is quite high in the studied area (2 reindeers.km^{-2}), which corroborates our results (Ehrich, personal communication). Because of this generalist behaviour, I could not see any complementary effect. The impact of medium-sized herbivores has been shown to occasionally be lower than that of reindeer. This surprising result could be due to either the "hungry-rodents hypothesis" or an unplanned effect of the experiment (see below). This result is even more curious when considering that, according to faeces counts, hares are abundant in Yamal compared to other places in the low Arctic (Ehrich *et al*. 2012). Indeed in birches and willows, a cumulative impact to the large and medium herbivores was expected but it was muffled by an experimental effect. In forbs, grasses, ericoids and toxic plants, small herbivores had a weak cumulative impact to the reindeer. The low abundance of rodents measured in the study area could be an explanation to such small effects. Indeed it is lower than other arctic places, like Varanger, and has been declining during the last decade (Appendix F) (Sokolova *et al.* unpublished, Sokolova *et al.* 2014).

In the following paragraphs, I will go into a detailed interpretation of the results. The plants are subjectively ranked based on their palatability from the most palatable to the least: nitrogen-non-fixing forbs, nitrogen-fixing forbs, grasses, sedges, erect willows, deciduous shrubs, birch, evergreen ericoids, toxic plants.

Cumulative impact

There are five groups that show indications for a cumulative impact for at least two types of herbivores. The first one is forbs in willow meadows. As fast growing plants, forbs are expected to respond quickly to a release from herbivory (Bråthen *et al.* 2007). Indeed in other exclosure experiments, a fast increase in forb biomass has often been seen (Shaver and Chapin 1991, Ravolainen *et al.* 2011). When reindeer were excluded there was a significant increase in forb biomass (Fig. 5a). This is congruent with the fact that reindeer are known for eating plenty of forbs (Skogland 1980, White and Trudell 1980) and reducing their cover (Myllymäki 1959 in Hansson 1977, Olofsson 2001). When large, medium and small herbivores were excluded this increase was larger and also significant. Therefore rodents had a small cumulative impact to the impact of reindeer on forb biomass but hares and ptarmigans did not have a noticeable impact on the biomass of forbs.

On one hand, for grasses in willow meadows, all treatments had an almost-significant effect (Fig. 7a). When reindeer were excluded, the biomass of grasses increased. When all herbivores were excluded, the increase in biomass was somewhat larger than in the reindeer exclosure. This means that both large and small herbivores had an impact and the all-excluded plot showed the cumulative impact of both animals. This is corroborated by the fact that reindeer are known to consume grasses (White *et al*. 1975, Skogland 1980, White 1983, Klein 1990) and that rodents also prefer grasses (Soininen *et al*. 2013). On the other hand, in forb tundra, the exclusion of reindeer did not have any effect (Fig. 7b). The other two treatments, though, showed the same increases as in willow meadows. This can be explained by the fact that FT has a lower grass biomass than WM (Fig. 3), due to a lower productivity. In a less productive habitat, the effect of reindeer should be attenuated, as they would graze less.

For birches, I did not expect many changes since it can take decades for these plants to recover after a disturbance (Crête and Doucet 1998, Olofsson *et al*. 2009). It is known that reindeer can consume large amounts of birch bushes, supporting the non-significant increase found in my results (Fig. 11a) (Bråthen and Oksanen 2001, Eskelinen and Oksanen 2006, Bergerud 1972, Manseau *et al*. 1996). In the contrary, rodents are not large consumers of *Betula nana* (Soininen *et al*. 2013). Therefore the reindeer plot showed the tendentious increase of reindeer and the all-excluded plot presented the impact of reindeer plus the weak impact of rodents. It is logical to conclude that the impact of rodents is cumulative to those of reindeer. However, if the biomass is impacted by small herbivores, these animals and their small size did not affect the maximum shrub height of birch (Fig. 11b). Reindeer, per contra, are tall animals that are able to reduce the size of *Betula* by cutting buds, breaking new branches and removing the bark (Ihl and Klein 2001, Tape *et al.* 2010). This would explain the slight increase in height when reindeers are excluded.

The small increase in biomass of ericoids in the reindeer plot (Fig. 12) was expected since large herbivores eat ericoids in small amounts (Warenberg *et al*. 1997). The increase was smaller in the hare treatment than in the reindeer treatment. However since medium-size herbivores are not primarily consumers of ericoids (Willson 1986 in Norment and Fuller 1997), this leads me to believe that the increase in the hare plot reflects the impact of reindeer. In the all-excluded plot, there was a larger non-significant increase than in the other two treatments. It represents the cumulative impact of reindeer, hares and ptarmigans and rodents. For the latter, ericoids are an important part of their diets (Soininen *et al*. 2013). Indeed even though ericoids contain numerous defensive secondary compounds, they have palatable berries, which makes them attractive for rodents (Pajunen *et al*. 2008, Iversen *et al*. 2009, Dahlgren *et al*. 2009).

The last group is toxic plants. The toxic plant group was the most surprising functional group. It was created to categorize plants that had toxic compounds that could make them unpalatable. Therefore the main prediction was that their biomass would remain the same as the control, showing that herbivores are not eating them. The non-significant increase in the reindeer plot went against my predictions (Fig. 13). *Veratrum lobelianum* is part of the toxic plants and is present in large numbers in willow meadows. Therefore they make up for a large part of the biomass of toxic plants. This plant is quite sensitive to trampling and so when the reindeer is excluded, the absence of trampling may have lead to an increase in biomass. This was seen is all three plots with a weak cumulative impact of small herbivores. In conclusion, absence of trampling by reindeer may be the main reason for the increase in biomass of toxic plants.

Erect willows

Willows show that only reindeer had a non-significant impact on the biomass. Contrary to my expectations for these palatable plants, which are preferred by many herbivores, the exclosure treatments had little effect on the biomass of erect willows (Fig. 9a). This could be explained by the fact that willows can take a few years to respond to changes (den Herder *et al*. 2004). Reindeer eat large amounts of *Salix* in summer (Manseau *et al.* 1996, Kazmin *et al*. 2011). Hares, however, consume *Salix* only in small quantities during summer (Pulliainen and Tunkkari 1987) and in average quantities during winter (Larter 1999). In addition, ptarmigans are primarily consumers of *Salix* during winter, focusing mostly on buds and less on leaves (Thomas 1984). Since my data collection method is based on leaves count and does not take in account feeding on buds, the impact of medium-size herbivores is small. Therefore the increase in reindeer plots corresponds to the impact of reindeer and the similar increase in the hare plot shows the impact of reindeer plus the absence of impact of medium herbivores. This effect within the functional group is supported by the results of maximum shrub height (Fig. 9b). Indeed all three results had the same value meaning that only reindeer influence the size of *Salix* bushes (Bryant 1987, den Herder *et al*. 2004, Tape *et al*. 2010) (Fig. 1b). Once again ptarmigans and hares were expected to influence the size by eating buds and young shoots but that lack of results here might be explained by them mainly eating *Salix* as part of their winter diet.

Unexpected results

There are many unexpected results. The first one is that even though literature supports hares feeding on forbs (Soininen *et al.* 2013) and on grasses (Bakker *et al*. 2009), results showed a weak effect (Fig. 5a and 7a). This could be due to the "hungry-rodents hypothesis". The basis for this hypothesis is that willow meadows are the main habitat for *Microtus gregalis*; therefore they are present in large numbers (Sokolova *et* al. 2014). Rodents might prefer to eat in hare cages since there is no competition with hares. Therefore plants that are liberated by the release from hare/ptarmigan herbivory are eaten by rodents leading to a large decrease in biomass. This theory is congruent with the fact that in another study rodents preferred to eat in exclosures that have not been grazed (Bakker *et al.* 2009). Indeed with a lack of competition, these plots are more attractive to rodents. In addition, according to my results, an absence of reindeer does not attract them; only an absence of hares and ptarmigans can make them graze more.

The second special case is the tendencies for decreasing biomass observed in hare treatment (for *Betula,* Fig.11a) and in all-excluded treatment (in *Salix*, Fig. 9a and in deciduous shrubs, Fig. 10). They could be resulting from an experimental effect. When exclosures were set up in 2014, some bushes had to be cut, branches and roots included. Bushes where this effect is encountered (willows, birches and deciduous) are relatively slow-growing and they take more than a year to recover from these cuts (Aerts and Chapin 2000). Thus our results could be due to the non-recovery of these bushes. This theory also applies in term of height as it can explain the decrease seen in hare and all-excluded plots in the results of the *Betula* shrub height (Fig. 11b). For willows, these plants react faster to changes (Ravolainen *et al*. 2011) in terms of height. To a lesser extend, this is the case for my study as there is decrease in *Salix* shrub height (Fig. 9b). Another experimental effect could be that hares do not enter the cages. If hares are absent in reindeer exclosures then their effect is, of course, null. This could contribute to explaining the decreases in the hare and the all-excluded plot previously described.

Absence of effect

There are five groups, where treatments did not have any effect on biomass. The first group is nitrogen-fixing forbs. The absence of effect (Fig. 6) in these forbs is curious as I was expecting strong results. Indeed nitrogen-fixing forbs should be preferred by herbivores since they are an important source of nitrogen (Quested *et al*. 2003). Nitrogen-fixing forbs encompass both nitrogen-fixers and hemiparasitic plants, as their value for herbivores is equivalent. These plants gather nitrogen in their leaves, (Marvier 1998) which could have lead to herbivores consuming them. However, several Fabaceae (e.g. *Astragalus* spp., *Hedysarum* spp.) can concentrate toxic compounds (Coburn Williams and Gomez-Sosa 1986), but for species present in my study system I was not able to find evidence of such toxic content in the literature. The presence of these compounds could explain these weak effects. In conclusion, it is not clear why nitrogen-fixing forbs do not show any effect.

The second group is sedges (Fig. 8). All exclosure treatments did not have any effect on the biomass of sedges, which corroborates the fact that herbivores do not eat sedges that much even though they are quite palatable (Bakker *et al*. 2009, Soininen *et al*. 2013, Kazmin *et al.* 2011).

The third group is deciduous shrubs. Deciduous shrubs are not the first choice for any of the animals but they are still a food source for all herbivores (Pulliainen and Tunkkari 1987, Dahlgren *et al*. 2009, Soininen *et al*. 2013). Therefore, I was expecting larger results. Their absence (Fig. 10) could be due to the fact that I am looking at the first year of results, and that dwarf shrubs are slow-growing plants (Crête and Doucet 1998, Olofsson *et al*. 2009).

The fourth group is grasses in mesic tundra. All exclosure treatments did not have any impact (Fig. 7c). In this habitat, grasses are scarce while ericoids are common (Fig. 3). Since ericoids are important for rodents (Soininen *et al*. 2013), these results might indicate that ericoids are better competitors than grasses and they keep them from growing. Another explanation could be that since mesic tundra is supposedly not a focal habitat for these herbivores, they will graze less in this habitat. This would perhaps lead to a weaker effect of the herbivores' exclusion.

The last group is forbs in forb tundra. All exclosure treatments did not have an impact in forb tundra (Fig. 5b). The difference between WM and FT could be explained by the fact that the humidity of these places is different: WM is a moist place while FT is a dry area (Kaplan *et al.* 2003, Framstad and Stenseth 1993). More water in the soil means a more productive spot and a more rapid response (Johnson *et al*. 2011). The effect of the difference in moisture is seen in fast-growing plants such as forbs or grasses. The biomass of these plants is expected to be lower in less productive sites, like FT.

Presence of reproductive parts

The results regarding frequency of reproductive plant parts in the experimental plots were expected to be increasing through the treatments (Control < Reindeer < Hare < All-excluded). Reproductive parts are preferred by all herbivores (Klein 1990, den Herder *et al*. 2004) due to their high nutrient content and low fibre content (Demment and Van Soest 1985, Audet *et al*. 2007). My results do not match these predictions as the same value was found for all treatments (Fig. 14). This could mean that either only reindeer have an impact on flowers, fruits and seeds or that hares and ptarmigans did not enter and graze the reindeer exclosure.

Total Biomass

Total biomass was analysed in order to see if the experiment worked and to look at differences between habitats. On one hand, I chose two focal habitats (willow meadows and forb tundra) that are expected to be attractive to herbivores and so to yield a higher biomass when herbivores are excluded. On the other hand, a common and less preferred by herbivores habitat (mesic tundra) should generate a lower biomass when herbivores are excluded than the other two habitats.

The large increase of biomass found in willow meadow (Fig. 4a) was following my predictions. This habitat, moist during summer, is mostly composed of fast-growing plants, such as grasses or forbs. It also has a relatively faster nutrient turnover than other habitats. In this habitat there was a significant effect of the reindeer exclusion, which can be explained by the fact that the most dominant functional groups of this habitat are *Salix* and forbs (Fig. 3). These groups are liked by reindeer (White and Trudell 1980) and therefore excluding the reindeer could be expected to increase their biomass (Pajunen *et al*. 2008, Ravolainen *et al*. 2011). This is corroborated by the fact that the reindeer exclusion generates also a significant increase in forbs.

In forb tundra, there is an increase of biomass as shown by trends in Fig. 4b. The increase found in this habitat is less large than in the meadows as expected by the fact that forb tundra is a drier habitat (Kaplan *et al*. 2003), which makes it less productive. This is also supported by the strong presence of fast growing deciduous shrubs and slow-growing evergreen shrubs (Chapin *et al*. 1996). There is, in this habitat, a significant increase when all herbivores are excluded. This can be explained by the fact that *Dryas octopetala*, an evergreen shrub, has a few strong increases of biomass in the all-excluded plot. Finally, as mentioned in the methods, evergreen shrubs are absent in most plots, making it hard to allow a clear interpretation of the results.

Mesic tundra shows a weak increase in biomass (Fig. 4c). This is in accordance to my predictions as it is not a focal habitat for herbivores.

The model with no habitat effect, fitting the data better, shows that reindeer have an impact on total biomass, hares and ptarmigans have no impact and that rodents have a small impact. Indeed the increase, where reindeer only are excluded, is congruent with this conclusion (Fig. 4d). Since this increase is the same when both medium and large herbivores are excluded, hares and ptarmigans have no effect on total biomass. When all herbivores are excluded, the increase is larger, meaning that the small impact of rodents is added to the large impact of reindeer. However I can say that release from herbivory during only one year had a great impact on the biomass (true increase of biomass of 0.47 for reindeer plot, 0.44 for hare plot and 0.51 for the -excluded plot).

Signs of generalist or specialist grazing?

From the results generated by the analysis, it seems that there is no clear relation between size and feeding style. It seems as if large herbivores have a generalist feeding behaviour as they have an impact on seven out of ten groups of plant presented (forbs, grasses, willows, birches, ericoids, toxic, reproductive parts). Indeed with a high metabolic rate and a large mouth, they may favour the quantity and not the quality of food. They can eat plants with low nutrient content and a high amount of fibres. However they would need to eat large amounts (Hofmann 1989, Olff and Ritchie 1998). Because the results from exclosures did no show a significant effect on any group of plant, I think that medium herbivores are either selective or they are not present in the exclosure, as previously explained. However it was suggested that they do not have the capacity of larger herbivores to tolerate secondary compounds but can handle high amounts of fibres due to microbial fermentation in their caecum (Davidson 1993, Olofsson *et al.* 2004). In addition, they eat a variety of winter foods, which should characterize them as quite generalist herbivores (Rodgers and Sinclair 1997). Finally it looks like small herbivores are selective feeders since they have an impact on five of the presented groups (forbs, grasses, birches, ericoids, toxic plants). Such diversity of plants has been also seen in Soininen *et al.* (2013). However, in theory, plants chosen by rodents have a high nutrient content, a low amount of secondary compounds and a low fibre content making it easy to digest (Davidson 1993, Liu *et al*. 2015). In addition, with such high-quality plants they should eat less (Demment and Van Soest 1985).

In conclusion, this first year of results partly fit with my predictions. A cumulative impact has been found in forbs, grasses and *Salix*, which are palatable plants but also in *Betula*, ericoids and toxic plants, which are less palatable plants. In addition, nitrogen-fixing forbs, sedges and deciduous shrubs ranking at different places on my palatability scale did not show any effect. Lastly, reindeer seem to have a generalist impact on the rest of functional groups. Therefore palatability does not seem to be the main reason for the emergence of cumulative or complementary impact of herbivores. The type of impact may also depend on the functional traits of plants and the associated preferences of the animals. Moreover, several studied herbivores impact the biomass of bushes that are involved in climate-driven shrubification, leading me to the assumption that they could regulate this ecosystem shift, as suggested in several previous studies. Another note is that considering the diversity of plant eaten by reindeer, semi-domesticated reindeer management is quite important for the ecosystem. Continuing with results, the total biomass results show that the experimental design seems to be working and that chosen habitats experience different impacts of herbivory. An important habitat for herbivores (willow meadow or forb tundra) yields more biomass than a habitat less important for them (mesic tundra). In addition a productive habitat (willow meadow) will generate more biomass than a less productive habitat (forb tundra). However the presence of an experimental effect hypothetically impeding the results of shrubs and medium herbivores could hint that the experiment design needs improvements. As for the type of grazing, both large and small herbivores show signs of generalist grazing while hares and ptarmigans show signs of selective grazing. However one should not forget that I am looking at the first year of results. Indeed, most palatable plants are also fast-growing, meaning that they are expected to show results from the first year. Less palatable plants often had results that were not easily interpretable. These are slow-growing and may take more than a year to show a response. Therefore, the next years of the experiment should give more accurate results on the impact of different size herbivores in the tundra.

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APPENDIX A

Species	Biomass group	Functional group
Betula_nana	Betula	Betula
Salix_arctica	Broad leaved ericoids	Deciduous shrubs
Salix_nummularia	Broad leaved ericoids	Deciduous shrubs
Salix_reticulata	Broad leaved ericoids	Deciduous shrubs
Vaccinium_uliginosum	Broad leaved ericoids	Deciduous shrubs
Arctous_alpina	Broad leaved ericoids	Evergeen ericoids
Empetrum_nigrum	Narrow leaved ericoids	Evergeen ericoids
Rhododendron_subarticum	Broad leaved ericoids	Evergeen ericoids
Vaccinium_vitis_idaea	Vaccinium vitis-ideae	Evergeen ericoids
Adoxa_moschatellina *	Narrow leaved grasses	Forbs
Angelica_archangelica	Large forbs	Forbs
Antennaria_villifera	Small forbs	Forbs
Armeria_maritima *	Narrow leaved grasses	Forbs
Artemisia_telesii	Small forbs	Forbs
Bistorta_officinalis	Small forbs	Forbs
Bistorta_vivipara	Small forbs	Forbs
Campanula_rotundifolia	Small forbs	Forbs
Caryophyllaceae	Small forbs	Forbs
Cerastium_sp	Small forbs	Forbs
Comarum_palustre	Small forbs	Forbs
Equisetum_arvense *	Narrow leaved grasses	Forbs
Silene_involucrata	Small forbs	Forbs
Huperzia_arctica *	Narrow leaved ericoids	Forbs
Lagotis_minor	Medium forms	Forbs
Lycopodium_dubium *	Narrow leaved ericoids	Forbs
Minuartia_verna	Small forbs	Forbs
Myosotis_asiatica	Small forbs	Forbs
Pachypleurum_alpinum	Small forbs	Forbs
Parnassia_palustris	Small forbs	Forbs
Petasites_frigidus	Small forbs	Forbs
Polemonium_acutiflorum	Small forbs	Forbs
Polemonium_boreale	Small forbs	Forbs
Rubus_arcticus	Small forbs	Forbs
Rubus_chamaemorus	Small forbs	Forbs
Stellaria_longifolia	Small forbs	Forbs
Stellaria_peduncularis	Small forbs	Forbs
Tanacetum_bipinnatum	Small forbs	Forbs
Viola_biflora	Small forbs	Forbs
Viola_epipsiloides	Small forbs	Forbs
Viola_sp	Small forbs	Forbs
Alopecurus_alpinus	Narrow leaved grasses	Grasses

Arctagrostis_latifolia	Narrow leaved grasses	Grasses
Calamagrostis_purpurea	Broad leaved grasses	Grasses
Calamagrostis_neglecta	Broad leaved grasses	Grasses
Deschampsia_borealis	Broad leaved grasses	Grasses
Festuca_ovina	Narrow leaved grasses	Grasses
Festuca_richardsonii	Broad leaved grasses	Grasses
Festuca_rubra	Broad leaved grasses	Grasses
Grass_1	Narrow leaved grasses	Grasses
Hierochloe_alpina	Broad leaved grasses	Grasses
Poa_alpigena	Broad leaved grasses	Grasses
Poa_alpina	Broad leaved grasses	Grasses
Poa_arctica	Broad leaved grasses	Grasses
Poaceae	Broad leaved grasses	Grasses
Tripleurosperum_maritimus	Narrow leaved grasses	Grasses
Trisetum_spicatum	Narrow leaved grasses	Grasses
Astragalus_alpinus	Medium forbs	Nitrogen-fixing forbs
Castilleja_arctica	Medium forbs	Nitrogen-fixing forbs
Euphrasia_frigida	Medium forbs	Nitrogen-fixing forbs
Hedysarum_hedysaroides	Medium forbs	Nitrogen-fixing forbs
Oxytropis_sordida	Medium forbs	Nitrogen-fixing forbs
Pedicularis_antemipholia	Medium forbs	Nitrogen-fixing forbs
Pedicularis_labradorica	Medium forbs	Nitrogen-fixing forbs
Pedicularis_oederi	Medium forbs	Nitrogen-fixing forbs
Pedicularis_sp	Medium forbs	Nitrogen-fixing forbs
Veronica_longifolia	Medium forbs	Nitrogen-fixing forbs
Corallorhiza trifida	Small forbs	Toxic plants
Gagea_serotina	Small forbs	Toxic plants
Ranunculus_borealis	Small forbs	Toxic plants
Tofieldia_coccinea	Small forbs	Toxic plants
Trollius_asiaticus	Large forbs	Toxic plants
Valeriana_capitata	Narrow leaved grasses	Toxic plants
Veratrum_lobelianum	Veratrum	Toxic plants
Salix_glauca	Salix	Erect Salix
Salix_hastata	Salix	Erect Salix
Salix_lanata	Salix	Erect Salix
Salix_phylicifolia	Salix	Erect Salix
Carex_bigelowii	Cyperaceae	Sedges
Carex_chordorrhiza	Cyperaceae	Sedges
Carex_rariflora	Cyperaceae	Sedges
Carex_small	Cyperaceae	Sedges
Carex_stans	Cyperaceae	Sedges
Eriophorum_scheuchzeri	Cyperaceae	Sedges
Eriophorum_vaginatum	Cyperaceae	Sedges
Luzula_confusa	Cyperaceae	Sedges
Luzula_multiflora	Cyperaceae	Sedges

Luzula_parviflora	Cyperaceae	Sedges
Luzula_sp_1	Cyperaceae	Sedges
Dryas_octopetala	Narrow leaved ericoids	Semi_evergreen shrubs
Pyrola_minor	Medium forbs	Semi_evergreen shrubs

Table A1: Species list following the Panarctic Flora nomenclature. In a few cases plants could not be identified to the species level, for instance because they were not flowering. They were designated with the smallest certain taxonomic unit. The biomass group is the group that was used for the biomass conversion. The separation was done based on the groups made in Ravolainen *et al* (2010). If the species was not included in the paper, it was place in a group subjectively based on its appearance. The functional group is the group used for analyses. For most species the biomass group and the functional group are the same. For species marked by * , their appearance placed them in either grasses or ericoids. The functional group is based on key characteristics such as woodiness, ability to survive a disturbance, secondary metabolites (Chapin *et al.* 1996). The toxic plant group is based on the presence of possibly harmful secondary metabolites. Information about secondary metabolites was retrieved from in the following references: Jung *et al*. 1979, Salasoo 1987, Jensen and Doncaster 1999, Aerts and Chapin 2000, Dinan *et al.* 2001, Van de Staaij *et al*. 2002, Albach *et al*. 2003, Mamedov *et al*. 2005, Crozier *et al*. ed. 2006, Hukkanen *et al* 2008, Ivanova *et al*. 2011, Markovskaya and Sergienko 2013, Vysochina and Voronkova 2013, European Commission CORDIS 2014, Jankovic *et al*. 2014, Zitterl-Eglseer *et al*. 2015.

APPENDIX B

Type	***Betula* Wood**	***Betula* Leaves**	***Salix* Wood**	***Salix* Leaves**	***Veratrum* Leaves**
b	126.9828	15.11911	216.9286	25.3898	52.93476
SD^2	0.0975667	0.03169931	0.02865975	0.08007821	0.06943706
CV	0.07982967	0.08890306	0.1265725	0.07745029	0.1176982
n	32	32	32	30	33

Table B1: Table of results from the calibration for *Betula nana, Veratrum lobelianum* and erect *Salix*. SD^2 is the variance, b is the regression coefficient, CV is the coefficient of variation and n is the number of plot for each category.

The regression coefficient represents the relation between the intercept frequency, or the number of touches per plot divided by the total number of pins (in this study, 15 pins), and the weighed biomass (in log(g).plot-1), gathered from the dried cuts in each plot. Using this coefficient, one can determine the weighed biomass of any number of touches. Leaves and woody parts have been separated in this correlation since the biomass of wood and of leaves is different. A touch of wood will represent more biomass than a touch of leaf.

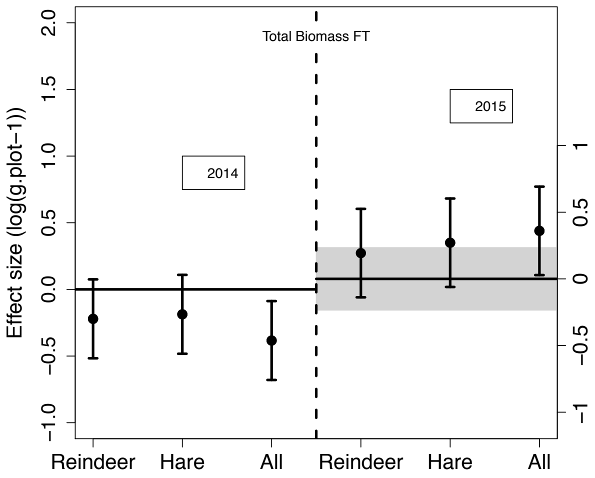
APPENDIX C

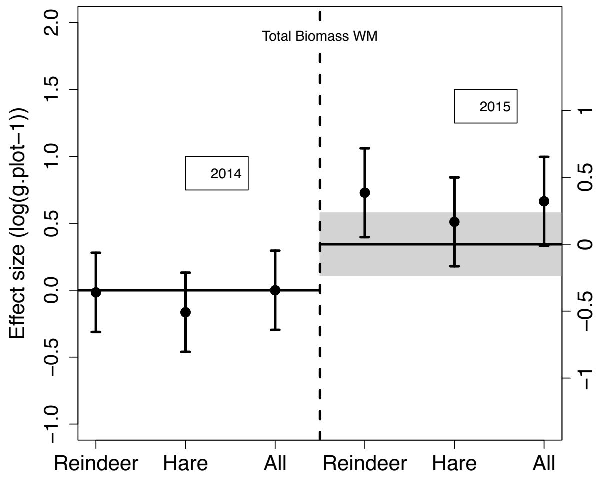
Functional Group	Habitat analysed	Model chosen
Nitrogen-fixing forbs	FT	One habitat model (M1)
Betula	MT	One habitat model (M1)
Erect *Salix*	WM (exception)	One habitat model (M1)
Evergreen ericoids	MT	One habitat model (M1)
Forbs	FT / WM	Interaction model (M3)
Grasses	FT / MT / WM	Interaction model (M3)
Sedges	MT	One habitat model (M1)
Deciduous shrubs	FT	One habitat model (M1)
Semi-evergreen shrubs	Excluded from analysis	Non Applicable
Toxic plants	WM	No habitat model (M1)
Total biomass	FT / MT / WM	No habitat model (M1)
Shrub height *Betula*	MT	One habitat model (M1)
Shrub height *Salix*	WM	One habitat model (M1)
Reproductive parts	FT	Additive model (M2)

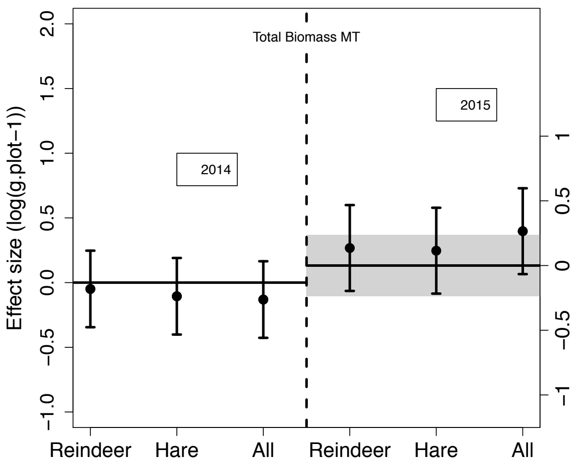
Table C1: Table of the functional groups with the habitat(s) analysed and model that fitted best to each of them.

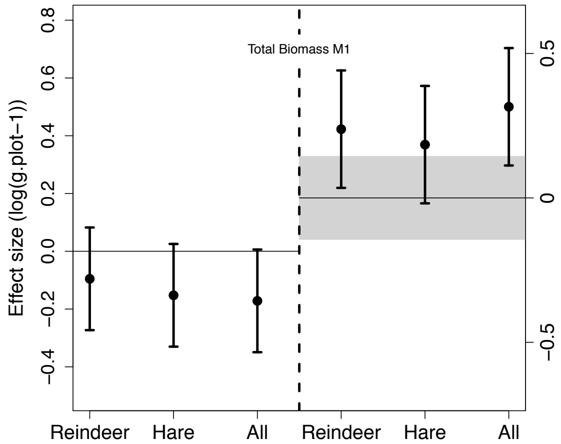
APPENDIX D

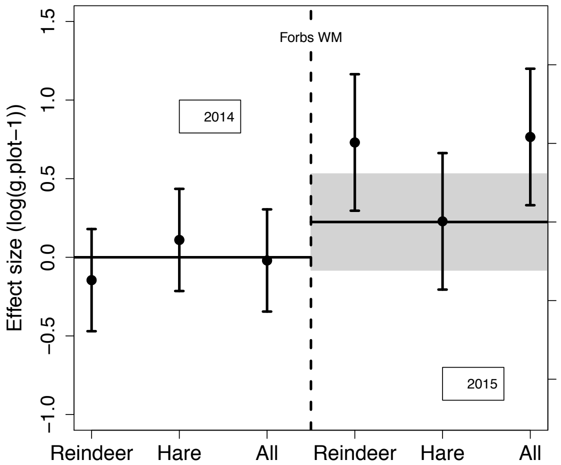
Description of the 2014 baseline

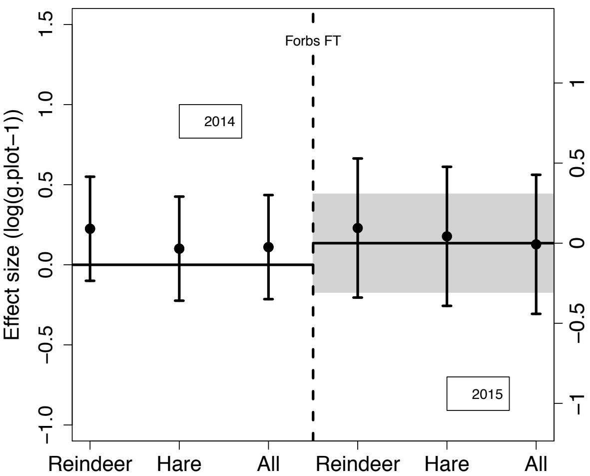


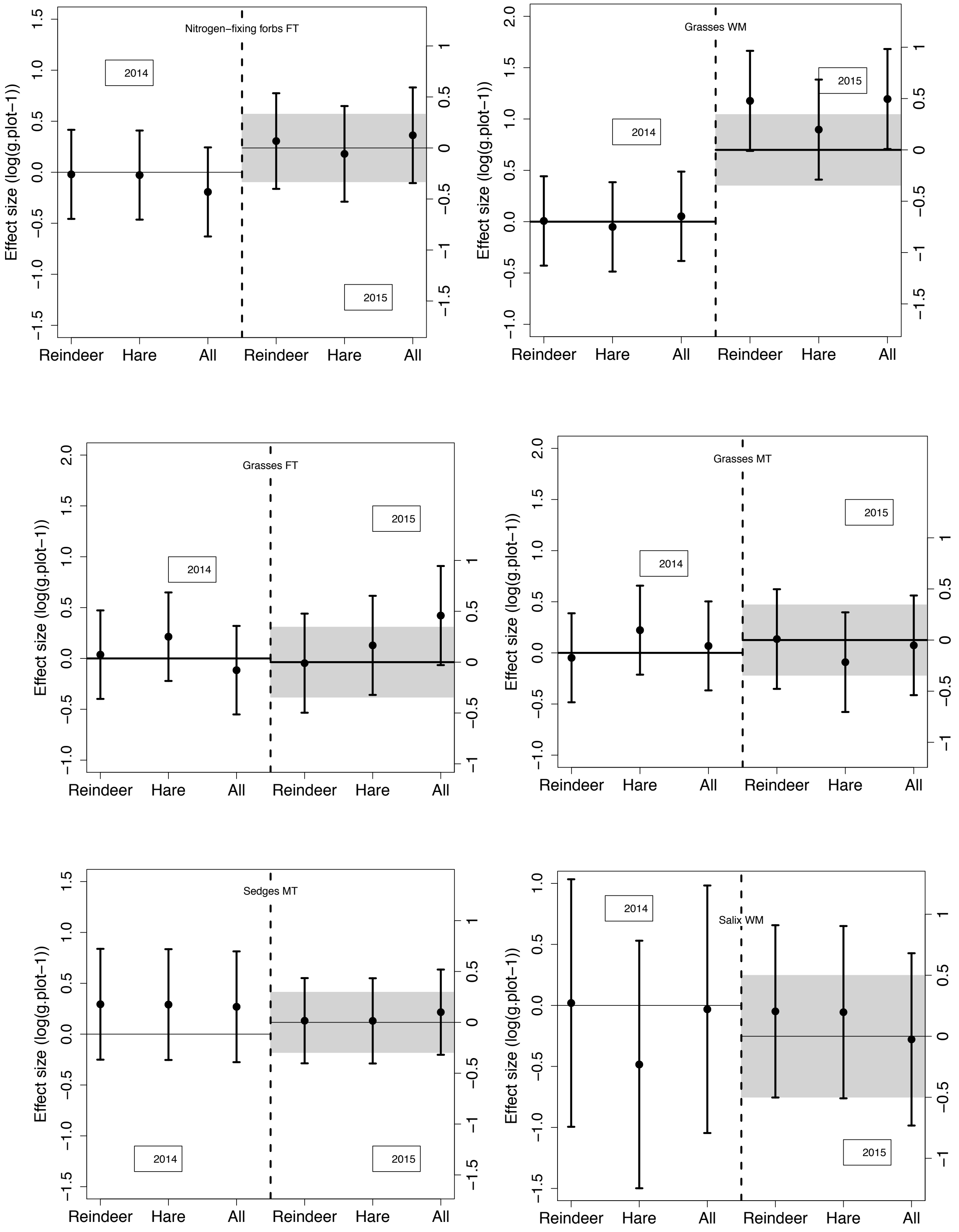




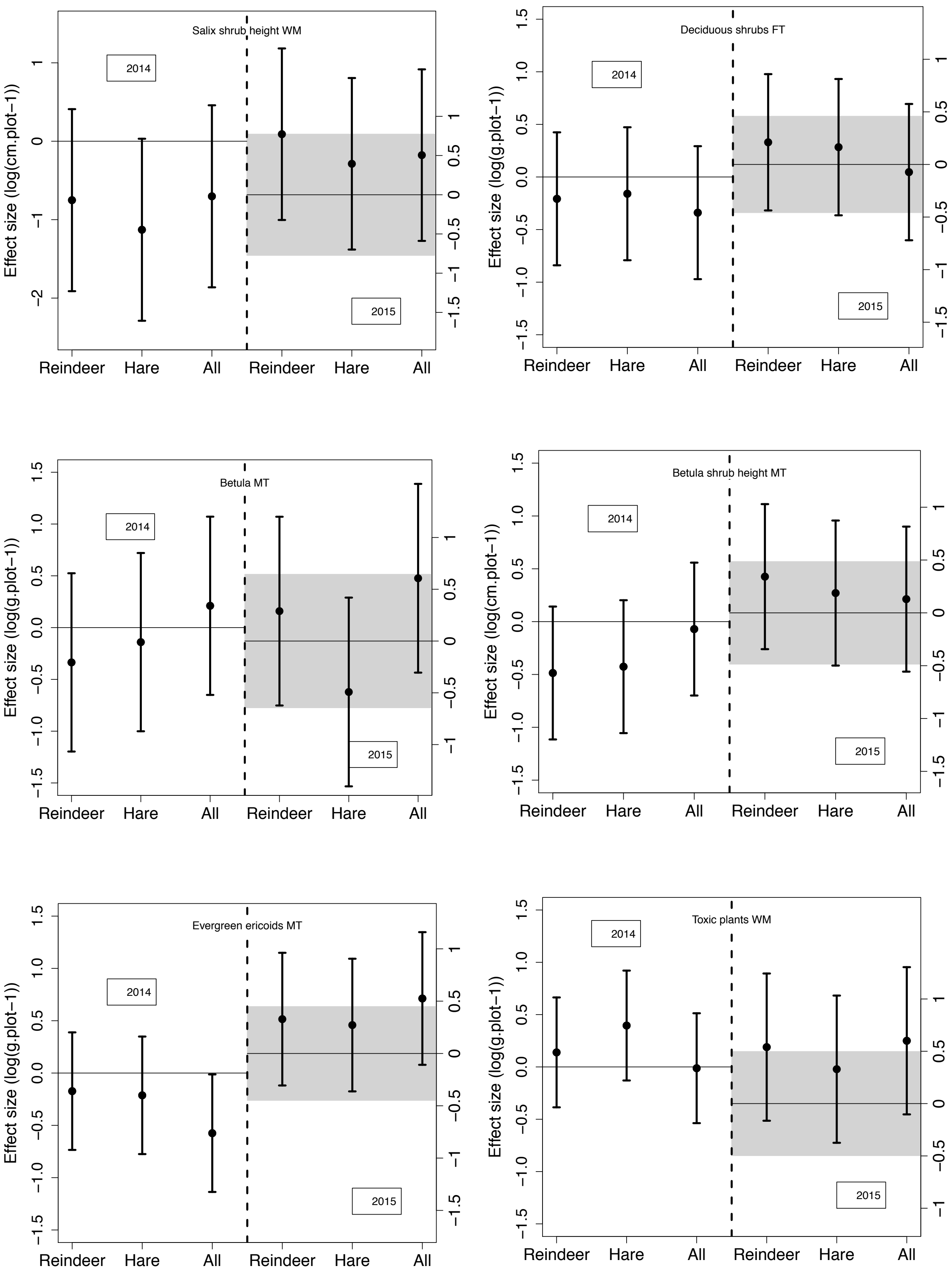








Nitrogen−fixing forbs FT
2014
2015
Grasses WM
2014
2015
Grasses FT
2014
2015
Grasses MT
2014
2015
Sedges MT
2014
2015
Salix WM
2014
2015
Effect size (log(g.plot−1))
Reindeer
Hare
All


Salix shrub height WM
2014
2015
Effect size (log(cm.plot−1))
Reindeer
Hare
All
Reindeer
Hare
All
Deciduous shrubs FT
2014
2015
Effect size (log(g.plot−1))
Reindeer
Hare
All
Reindeer
Hare
All
Betula MT
2014
2015
Effect size (log(g.plot−1))
Reindeer
Hare
All
Reindeer
Hare
All
Betula shrub height MT
2014
2015
Effect size (log(cm.plot−1))
Reindeer
Hare
All
Reindeer
Hare
All
Evergreen ericoids MT
2014
2015
Effect size (log(g.plot−1))
Reindeer
Hare
All
Reindeer
Hare
All
Toxic plants WM
2014
2015
Effect size (log(g.plot−1))
Reindeer
Hare
All
Reindeer
Hare
All

Page 1	
D1	D2
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Page 3	
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D15	D16
D17	D18

Figures D1, D2, D3, D4, D5, D6, D7, D8, D9, D10, D11, D13, D15, D16, D17, D18: Biomass change (in log(g).plot-1) for the designated functional group in 2015. The treatments Reindeer, Hare and All-excluded (All) are represented on the X-axis and the change from the 2014 control on the left and from the control of 2015 on the right is represented on the Y-axis. The black line on the left side is the control of 2014 and the black line on the right side is the control of 2015. For each value, the confidence interval (95%) is depicted. The confidence interval for the control of 2015 is represented by the grey area.

Figures D12, D14: Maximum shrub height change (in cm.plot^{-1}) for the designated functional group in 2015. The treatment Reindeer, Hare and All-excluded (All) are represented on the X-axis and the change from the 2014 control on the left and from the control of 2015 on the right is represented on the Y-axis. The black line on the left side is the control of 2014 and the black line on the right side is the control of 2015. For each value, the confidence interval (95%) is depicted. The confidence interval for the control of 2015 is represented by the grey area

There was no significant difference between treatments in 2014 as they were assigned at random, except in the total biomass of forb tundra and in the evergreen ericoids group.

APPENDIX E

Total Biomass WM	Estimate	Std Error	T value	P value	2.5 %	97.5 %
Control 2014	3.73	0.22	16.88	0.000	3.32	4.14
Hare/Ptarmigan	-0.16	0.16	-1.05	0.290	-0.46	0.13
Reindeer	-0.02	0.16	-0.10	0.920	-0.31	0.28
All-excluded	0.00	0.16	0.00	1.000	-0.30	0.30
Control 2015	0.34	0.12	2.77	0.010	0.11	0.58
Hare/Ptarmigan : 2015	0.17	0.18	0.95	0.340	-0.16	0.50
Reindeer : 2015	0.38	0.18	2.19	0.030	0.05	0.72
All-excluded : 2015	0.32	0.18	1.83	0.070	-0.01	0.65
Plot var: 0.054; Block ID var: 0.219						
Total Biomass FT	Estimate	Std Error	T value	P value	2.5 %	97.5 %
Control 2014	4.44	0.22	20.1	0.000	4.03	4.86
Hare/Ptarmigan	-0.19	0.16	-1.20	0.230	-0.48	0.11
Reindeer	-0.22	0.16	-1.41	0.160	-0.52	0.08
All-excluded	-0.38	0.16	-2.45	0.010	-0.68	-0.09
Control 2015	0.08	0.12	0.64	0.520	-0.16	0.31
Hare/Ptarmigan : 2015	0.27	0.18	1.54	0.120	-0.06	0.6
Reindeer : 2015	0.19	0.18	1.10	0.270	-0.14	0.53
All-excluded : 2015	0.36	0.18	2.05	0.040	0.03	0.69
Plot var: 0.054; BlockID var: 0.219						
Total Biomass MT	Estimate	Std Error	T value	P value	2.5 %	97.5 %
Control 2014	4.54	0.22	20.56	0.000	4.03	4.86
Hare/Ptarmigan	-0.11	0.16	-0.68	0.500	-0.48	0.11
Reindeer	-0.05	0.16	-0.31	0.750	-0.52	0.08
All-excluded	-0.13	0.16	-0.84	0.400	-0.68	-0.09
Control 2015	0.13	0.12	1.06	0.290	-0.16	0.31
Hare/Ptarmigan : 2015	0.11	0.18	0.65	0.510	-0.06	0.6
Reindeer : 2015	0.14	0.18	0.77	0.440	-0.14	0.53
All-excluded : 2015	0.27	0.18	1.51	0.130	0.03	0.69
Plot var: 0.054; BlockID var: 0.219						

Total Biomass M1	Estimate	Std Error	T value	P value	2.5 %	97.5 %
Control 2014	4.24	0.14	30.7	0.00	3.97	4.51
Hare/Ptarmigan	-0.15	0.09	-1.67	0.10	-0.33	0.03
Reindeer	-0.10	0.09	-1.04	0.30	-0.27	0.08
All-excluded	-0.17	0.09	-1.88	0.06	-0.35	0.01
Control 2015	0.18	0.07	2.50	0.01	0.04	0.33
Hare/Ptarmigan : 2015	0.18	0.10	1.76	0.08	-0.02	0.39
Reindeer : 2015	0.24	0.10	2.28	0.02	0.03	0.44
All-excluded : 2015	0.32	0.10	3.02	0.00	0.11	0.52
Plot var: 0.052; BlockID var: 0.267						

N-non-fixing forbs WM	Estimate	Std Error	T value	P value	2.5 %	97.5 %
Control 2014	2.47	0.28	8.80	0.000	1.94	3.01
Hare/Ptarmigan	0.11	0.17	0.64	0.520	-0.21	0.44

Reindeer	-0.15	0.17	-0.85	0.397	-0.47	0.18
All-excluded	-0.02	0.17	-0.12	0.906	-0.35	0.30
Control 2015	0.22	0.16	1.39	0.166	-0.08	0.53
Hare/Ptarmigan : 2015	0.004	0.23	0.02	0.985	-0.43	0.44
Reindeer : 2015	0.51	0.23	2.21	0.027	0.07	0.94
All-excluded : 2015	0.54	0.23	2.36	0.018	0.11	0.97
Plot var: 0.019; BlockID var: 0.386						
N-non-fixing forbs FT	Estimate	Std Error	T value	P value	2.5 %	97.5 %
Control 2014	0.91	0.28	3.23	0.000	0.37	1.45
Hare/Ptarmigan	0.10	0.17	0.59	0.560	-0.22	0.43
Reindeer	0.22	0.17	1.31	0.190	-0.10	0.55
All-excluded	0.11	0.17	0.64	0.520	-0.21	0.44
Control 2015	0.13	0.16	0.83	0.400	-0.17	0.44
Hare/Ptarmigan : 2015	0.04	0.23	0.19	0.850	-0.39	0.48
Reindeer : 2015	0.09	0.23	0.41	0.680	-0.34	0.53
All-excluded : 2015	-0.01	0.23	-0.03	0.970	-0.44	0.43
Plot var: 0.019; BlockID var: 0.386						

N-fixing forbs	Estimate	Std Error	T value	P value	2.50%	97.50%
Control 2014	2.26	0.20	11.39	0.000	1.88	2.64
Hare/Ptarmigan	-0.03	0.23	-0.12	0.904	-0.46	0.41
Reindeer	-0.02	0.23	-0.09	0.928	-0.46	0.42
All-excluded	-0.19	0.23	-0.84	0.398	-0.63	0.24
Control 2015	0.24	0.17	1.38	0.169	-0.09	0.57
Hare/Ptarmigan : 2015	-0.06	0.24	-0.24	0.813	-0.53	0.41
Reindeer : 2015	0.07	0.24	0.28	0.782	-0.40	0.54
All-excluded : 2015	0.12	0.24	0.51	0.611	-0.34	0.59
Plot var: 0.133; BlockID: 0.079						

Grasses WM	Estimate	Std Error	T value	P value	2.5 %	97.5 %
Control 2014	1.63	0.25	6.58	0.000	1.16	2.09
Hare/Ptarmigan	-0.05	0.23	-0.22	0.825	-0.49	0.38
Reindeer	0.01	0.23	0.03	0.976	-0.43	0.44
All-excluded	0.05	0.23	0.23	0.820	-0.38	0.49
Control 2015	0.70	0.18	3.83	0.000	0.35	1.04
Hare/Ptarmigan : 2015	0.20	0.26	0.77	0.444	-0.29	0.68
Reindeer : 2015	0.48	0.26	1.85	0.064	-0.01	0.96
All-excluded : 2015	0.50	0.26	1.92	0.055	0.01	0.98
Plot var: 0.118; BlockID var: 0.208						
Grasses FT	Estimate	Std Error	T value	P value	2.5 %	97.5 %
Control 2014	1.80	0.25	7.29	0.000	1.34	2.26
Hare/Ptarmigan	0.21	0.23	0.93	0.353	-0.22	0.65
Reindeer	0.04	0.23	0.16	0.872	-0.40	0.47
All-excluded	-0.12	0.23	-0.50	0.615	-0.55	0.32
Control 2015	-0.04	0.18	-0.20	0.841	-0.38	0.31
Hare/Ptarmigan : 2015	0.17	0.26	0.64	0.522	-0.32	0.65
Reindeer : 2015	-0.01	0.26	-0.04	0.969	-0.50	0.48

All-excluded : 2015	0.46	0.26	1.78	0.076	-0.03	0.95
Plot var: 0.118; BlockID var: 0.208						
Grasses MT	Estimate	Std Error	T value	P value	2.5 %	97.5 %
Control 2014	0.75	0.25	3.02	0.003	0.28	1.21
Hare/Ptarmigan	0.22	0.23	0.97	0.334	-0.21	0.66
Reindeer	-0.05	0.23	-0.21	0.834	-0.48	0.39
All-excluded	0.07	0.23	0.30	0.767	-0.37	0.50
Control 2015	0.13	0.18	0.69	0.492	-0.22	0.47
Hare/Ptarmigan : 2015	-0.22	0.26	-0.84	0.402	-0.70	0.27
Reindeer : 2015	0.01	0.26	0.04	0.970	-0.48	0.50
All-excluded : 2015	-0.05	0.26	-0.20	0.841	-0.54	0.44
Plot var: 0.118; BlockID var: 0.208						

Sedges	Estimate	Std Error	T value	P value	2.50%	97.50%
Control 2014	1.32	0.25	5.25	0.000	0.84	1.81
Hare/Ptarmigan	0.29	0.28	1.02	0.306	-0.25	0.84
Reindeer	0.29	0.28	1.04	0.300	-0.25	0.84
All-excluded	0.27	0.28	0.95	0.343	-0.28	0.81
Control 2015	0.12	0.15	0.75	0.454	-0.18	0.41
Hare/Ptarmigan : 2015	0.01	0.22	0.07	0.947	-0.40	0.43
Reindeer : 2015	0.02	0.22	0.07	0.941	-0.40	0.44
All-excluded : 2015	0.10	0.22	0.46	0.647	-0.32	0.52
Plot var: 0.339; BlockID var: 0.140						

Salix	Estimate	Std Error	T value	P value	2.50%	97.50%
Control 2014	1.65	0.75	2.21	0.027	0.13	3.18
Hare/Ptarmigan	-0.48	0.53	-0.92	0.359	-1.50	0.53
Reindeer	0.02	0.53	0.04	0.971	-0.99	1.03
All-excluded	-0.03	0.53	-0.06	0.952	-1.05	0.98
Control 2015	-0.25	0.26	-0.97	0.332	-0.75	0.25
Hare/Ptarmigan : 2015	0.20	0.37	0.53	0.593	-0.51	0.90
Reindeer : 2015	0.20	0.37	0.55	0.580	-0.50	0.91
All-excluded : 2015	-0.03	0.37	-0.07	0.945	-0.73	0.68
Plot var: 1.263; BlockID var: 2.529						
Salix max shrub height	Estimate	Std Error	T value	P value	2.50%	97.50%
Control 2014	2.13	0.51	4.18	0.000	1.16	3.11
Hare/Ptarmigan	-1.13	0.61	-1.86	0.063	-2.29	0.03
Reindeer	-0.75	0.61	-1.24	0.215	-1.91	0.41
All-excluded	-0.70	0.61	-1.16	0.247	-1.86	0.46
Control 2015	-0.68	0.40	-1.69	0.091	-1.46	0.09
Hare/Ptarmigan : 2015	0.39	0.57	0.69	0.489	-0.70	1.49
Reindeer : 2015	0.77	0.57	1.35	0.176	-0.32	1.87
All-excluded : 2015	0.51	0.57	0.88	0.376	-0.59	1.60
Plot var: 1.226; BlockID: 0.466						

Deciduous shrubs	Estimate	Std Error	T value	P value	2.50%	97.50%
Control 2014	3.00	0.44	6.89	0.000	2.12	3.88

Hare/Ptarmigan	-0.16	0.33	-0.48	0.630	-0.79	0.47
Reindeer	-0.21	0.33	-0.63	0.530	-0.84	0.42
All-excluded	-0.34	0.33	-1.03	0.305	-0.97	0.29
Control 2015	0.12	0.24	0.50	0.618	-0.34	0.58
Hare/Ptarmigan : 2015	0.16	0.34	0.49	0.627	-0.48	0.81
Reindeer : 2015	0.21	0.34	0.62	0.534	-0.44	0.86
All-excluded : 2015	-0.07	0.34	-0.22	0.829	-0.72	0.57
Plot var: 0.312; BlockID var: 0.814						

Betula	Estimate	Std Error	T value	P value	2.50%	97.50%
Control 2014	2.91	0.43	6.80	0.000	2.08	3.75
Hare/Ptarmigan	-0.14	0.45	-0.31	0.755	-1.00	0.72
Reindeer	-0.34	0.45	-0.75	0.455	-1.20	0.52
All-excluded	0.21	0.45	0.47	0.640	-0.65	1.07
Control 2015	-0.13	0.34	-0.39	0.700	-0.77	0.51
Hare/Ptarmigan : 2015	-0.49	0.48	-1.03	0.301	-1.40	0.42
Reindeer : 2015	0.29	0.48	0.61	0.544	-0.62	1.20
All-excluded : 2015	0.61	0.48	1.27	0.203	-0.31	1.52
Plot var: 0.537; BlockID var: 0.493						
Betula max shrub height	Estimate	Std Error	T value	P value	2.50%	97.50%
Control 2014	2.00	0.30	6.62	0.000	1.41	2.58
Hare/Ptarmigan	-0.43	0.33	-1.29	0.195	-1.06	0.20
Reindeer	-0.49	0.33	-1.48	0.140	-1.11	0.14
All-excluded	-0.07	0.33	-0.21	0.830	-0.70	0.56
Control 2015	0.08	0.25	0.33	0.743	-0.40	0.57
Hare/Ptarmigan : 2015	0.19	0.36	0.52	0.601	-0.50	0.87
Reindeer : 2015	0.34	0.36	0.96	0.339	-0.34	1.03
All-excluded : 2015	0.13	0.36	0.36	0.717	-0.56	0.82
Plot var: 0.265; BlockID var: 0.222						

Evergreen ericoids	Estimate	Std Error	T value	P value	2.5 %	97.5 %
Control 2014	3.85	0.33	11.64	0.000	3.20	4.51
Hare/Ptarmigan	-0.21	0.29	-0.72	0.469	-0.77	0.35
Reindeer	-0.17	0.29	-0.59	0.556	-0.73	0.39
All-excluded	-0.58	0.29	-1.95	0.051	-1.14	-0.01
Control 2015	0.19	0.23	0.80	0.425	-0.26	0.64
Hare/Ptarmigan : 2015	0.27	0.33	0.82	0.412	-0.36	0.91
Reindeer : 2015	0.33	0.33	0.99	0.322	-0.31	0.96
All-excluded : 2015	0.53	0.33	1.59	0.112	-0.11	1.16
Plot var: 0.190; BlockID var: 0.397						

Toxic plants	Estimate	Std Error	T value	P value	2.5 %	97.5 %
Control 2014	2.91	0.45	6.51	0.000	2.00	3.82
Hare/Ptarmigan	0.40	0.28	1.43	0.151	-0.13	0.92
Reindeer	0.14	0.28	0.50	0.614	-0.39	0.66
All-excluded	-0.01	0.28	-0.04	0.965	-0.54	0.51
Control 2015	-0.35	0.26	-1.35	0.178	-0.85	0.15

Hare/Ptarmigan : 2015	0.33	0.37	0.89	0.371	-0.37	1.03
Reindeer : 2015	0.54	0.37	1.47	0.142	-0.16	1.24
All-excluded : 2015	0.60	0.37	1.63	0.102	-0.10	1.30
Plot var: 0.051; BlockID var: 0.970						

Flowers FT	Estimate	2.5 %	97.5 %
Control 2015	-0.54	-1.51	0.44
Hare/Ptarmigan	-0.39	-1.38	0.60
Reindeer	-0.48	-1.47	0.51
All-excluded	-0.15	-1.13	0.84
Plot var: 0.2381; Block ID var: 1.0974			

Table E: Table of the estimates, the standard error, the t-value, the p-value, the confidence intervals and the random effect variances (plot var and blockID var) from the chosen model of each functional group

APPENDIX F

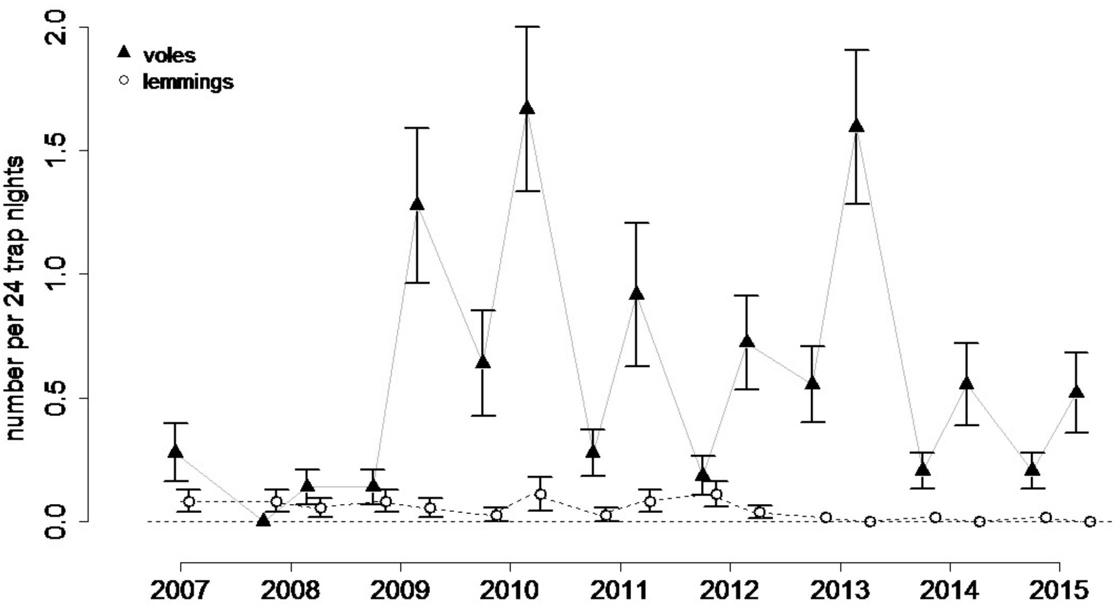

Figure F1: Mean number of voles and lemmings trapped per session and trapping plot (24 trapping nights) at the Erkuta Tundra Monitoring Site. The error bars represent the standard error of the mean. Figure and trapping methods can be found in Sokolova *et al*. 2014.

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