Rapid, landscape scale responses in riparian tundra vegetation to exclusion of small and large mammalian herbivores

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Abstract

Productive tundra plant communities composed of a variety of fast growing herbaceous and woody plants are likely to attract mammalian herbivores. Such vegetation is likely to respond to different-sized herbivores more rapidly than currently acknowledged from the tundra. Accentuated by currently changing populations of arctic mammals there is a need to understand impacts of different-sized herbivores on the dynamics of productive tundra plant communities. Here we assess the differential effects of ungulate (reindeer) and small rodent herbivores (voles and lemmings) on high productive tundra vegetation. A spatially extensive exclosure experiment was run for three years on river sediment plains along two river catchments in low-arctic Norway. The river catchments were similar in species pools but differed in species abundance composition of both plants and vertebrate herbivores. Biomass of forbs, deciduous shrubs and silica-poor grasses increased by 40-50 % in response to release from herbivory, whereas biomass of silica-rich grasses decreased by 50-75%. Hence both additive and compensatory effects of small rodents and reindeer exclusion caused these significant changes in abundance composition of the plant communities. Changes were also rapid, evident after only one growing season, and are among the fastest and strongest ever documented in Arctic vegetation. The rate of changes indicate a tight link between the dynamics of productive tundra vegetation and both small and large herbivores. Responses were however not spatially consistent, being highly different between the catchments. We conclude that despite similar species pools, variation in plant species abundance and herbivore species dynamics give different prerequisites for change.

Keywords: plant-herbivore interactions, community dynamics, plant growth forms, *Rangifer tarandus, Lemmus lemmus, Microtus oeconomus, Deschampsia cespitosa,* Varanger Peninsula

Introduction

According to theoretical predictions, mammalian herbivores can strongly impact vegetation in arctic tundra ecosystems, although there are different explanations of the underlying mechanisms (Oksanen & Oksanen 2000; van der Wal 2006; Zimov, Chuprynin, Oreshko, Chapin, Reynolds et al. 1995). These predictions have focused mainly on impact of large mammals. Arctic ecosystems can, however, harbour abundant populations of different-sized mammalian herbivores (Bliss 2000; Ims & Fuglei 2005), which have different forage preference, consumption rates, range use and population dynamics. Thus, studies of herbivore impacts on arctic vegetation need to differentiate between the role of large and small mammals. The potential importance of animal size-dependent impacts is currently accentuated by substantial changes in arctic herbivore populations presumably linked to climatic warming and/or management practices. For instance, lemming population cycles may be vanishing or dampened in tundra ecosystems (Gilg, Sittler, Sabard, Hurstel, Sane et al. 2006; Ims, Henden & Killengreen 2008; Ims, Yoccoz & Killengreen 2011; Kausrud, Mysterud, Steen, Vik, Østbye et al. 2008), while for *Rangifer* (reindeer/caribou) different population trends are found in different parts of the Arctic (CAFF 2001). The ecosystem implications of such changes in key herbivore species are uncertain because our knowledge of the relative importance of different-sized mammalian herbivores to arctic vegetation is still limited.

Previous studies separating effects of different-sized mammalian herbivores in arctic ecosystems have focused on dwarf shrub dominated heath (Grellmann 2002; Olofsson, Hulme, Oksanen & Suominen 2004, 2005; Olofsson, Oksanen, Callaghan, Hulme, Oksanen et al. 2009). Such vegetation is dominated by plants with low productivity (e.g. Bliss 2000), decomposition rates (Cornelissen, van Bodegom, Aerts, Callaghan, van Logtestijn et al. 2007) and palatability (Cornelissen, Quested, Gwynn-Jones, Van Logtestijn, De Beus et al. 2004), and does typically respond slowly to experimental herbivore manipulation (e.g. Olofsson et al. 2009; Virtanen, Henttonen & Laine 1997). Moreover, such low productive vegetation can be expected to be of less importance in providing forage for arctic herbivores than vegetation with faster processrates (cf. Batzli & Jung 1980; White & Trudell 1980). In contrast, productive, fast growing vegetation are more likely to be under strong control by herbivores (Cebrian 1999). The aim of this study is to investigate roles of small and large herbivores across extensive areas of productive tundra vegetation, i.e. in tundra vegetation that potentially represent hot-spots for plant–herbivore interactions (see Bråthen et al 2007).

Fast growing arctic vegetation types are typically found on riparian sediment plains, and in mesic valleys and slopes in tundra (Bliss 2000; Shaver, Laundre, Giblin & Nadelhoffer 1996). Here we focus on riparian sediment plains that can support tall deciduous shrubs (in our study *Salix* spp.) and herbaceous vegetation (cf. Bliss 2000). The herbaceous vegetation typically consists of forbs, grasses, sedges, and deciduous shrubs, whereas evergreen shrubs are less frequent (Pajunen, Kaarlejarvi, Forbes & Virtanen 2010). Hence, such vegetation has a high functional and structural diversity as it harbours the majority of growth forms (sensu Chapin, BretHarte, Hobbie & Zhong 1996) found in low-arctic tundra . Digestibility of growth forms varies from the most digestible forbs to grasses, sedges, deciduous shrubs, and finally to the least digestible evergreen shrubs (Cornelissen et al. 2004). Since such herbaceous vegetation provides important food items for herbivores, it can be expected to attract disproportionally many herbivores as compared to the vegetation in the surrounding landscape (i.e. heaths). At the same time, the effect of intense herbivory on such composite vegetation of different palatability can be expected to be complex. Yet, little is known about the role of different-sized herbivores for the composition of such potentially fast growing tundra vegetation.

Therefore to provide empirical knowledge on the relative roles of large and small arctic herbivores in potentially responsive tundra habitats, we conducted an exclosure experiment on riparian sediment plains along two river catchments of the Varanger Peninsula in north-eastern Norway. Here, herbaceous vegetation with similar species pools but with variable species abundance compositions borders on tall shrub habitats (Ravolainen 2009). By employing a spatially extensive experimental design (see Noda 2004) with many small and spatially well-dispersed experimental plots, much of the existing variation in the composition of the vegetation was included in the study. The focal large herbivore in the study area, present predominantly in the snow-free season, is semi-domesticated reindeer (*Rangifer tarandus*) (see Ravolainen et al. 2010). The focal small herbivores are represented by the three small rodent species grey-sided vole (*Myodes rufocanus*), tundra vole (*Microtus oeconomus*) and Norwegian lemming (*Lemmus lemmus*), of which the voles exhibit a 5-year density cycle and the lemming more irregular outbreaks in the study area (Ims et al. 2011). As the focal herbivores can be expected to show spatiotemporal abundance variation we estimated yearly relative densities of both reindeer and small rodents at the level of river catchment throughout the 3-year study period.

We studied impact on vegetation on the basis of growth forms (sensu Chapin et al. 1996). Growth forms can be interpreted as a functional grouping of plants that captures tundra vegetation responses to herbivory (Bråthen, Ims, Yoccoz, Fauchald, Tveraa et al. 2007). Among the growth forms considered we expected forbs, being palatable (Cornelissen et al. 2004) and generally used as forage by various herbivores (Batzli et al. 1980; Soininen, Valentini, Coissac, Miquel, Gielly et al. 2009; White et al. 1980), to increase in abundance when protected from herbivores (see e.g. Bråthen et al. 2007; Pajunen, Virtanen & Roininen 2008). Change in the abundance of grasses when released from grazing was expected to differ between species with or without silica defenses (see Massey, Ennos & Hartley 2007).

Browsing is known to restrict growth of deciduous shrubs (for review, see Côté, Rooney, Tremblay, Dussault & Waller 2004; den Herder, Virtanen & Roininen 2008; Pajunen 2009) and thus we expected deciduous shrubs to increase in abundance when released from grazing. Responses of other growth forms, as well as community level measures such as total live biomass, cover of standing dead plants, moss cover, species richness, and Simpson diversity were estimated to achieve a comprehensive assessment of herbivore influence on the herbaceous vegetation bordering on tall shrub patches.

Methods

Study area

This study took place over the years 2006-2008 on the Varanger Peninsula (70° N, 30° E) (Fig. 1). The peninsula is formed by a relatively flat plateau having mostly low altitudes (<400 m a.s.l) north of the arctic tree-line in the eastern and northern parts (Moen 1999). Bare block-fields cover a substantial part of the peninsula (Geological Survey of Norway, www.ngu.no), whereas vegetated parts of the plateaus and slopes consist of tundra heath dominated by the unpalatable evergreen shrub *Empetrum nigrum* ssp. *hermaphroditum* (Killengreen, Ims, Yoccoz, Brathen, Henden et al. 2007; Ravolainen, Yoccoz, Bråthen, Ims, Iversen et al. 2010). Rivers descending from the interior of the peninsula towards the coast have created large areas of riparian sediment plains. Our study took place in two river catchments, nearby the two largest rivers on the peninsula; i.e. Komagelva (KO) and Vestre Jakobselv (VJ). The two catchments are approximately 20 km apart and are of similar altitude (110-290 m a.s.l.). Whereas sediment plains in KO are found in one relatively wide and continuous valley, they are narrower and situated along tributaries to the main river in VJ, and thus represent a smaller proportion of the landscape in the latter catchment. Area of the sediment plain of three 2.2 x 2.2 km sections centered on the study areas covers on average

15.6% in KO (range 11.9-21.6%). In VJ, the corresponding coverage of sediment plains is on average 5.2% (range 3.0-8.3%) (Ravolainen et al. unpublished).

System characteristics: vegetation and herbivores

The riparian plains of the river catchments are constituted by a mosaic of two main vegetation types; a herbaceous field layer dominated by a variety of growth forms and woody patches of tall shrubs with distinct edges to the bordering herbaceous vegetation (see Fig. 1). These shrub patches consist of various *Salix* species, including *S. phylicifolia*, *S. glauca*, *S. lanata*, *S. hastata*, and frequently found hybrid specimens. The shrub patches occur in a range of configurations within these sediment (Henden, Ims, Yoccoz, Sorensen & Killengreen 2011), whereas shrub saplings occur scattered within the herbaceous vegetation as small willow ramets on average 17.5 cm tall (range 10-40 cm, measured in unenclosed plots in 2006).

Vascular plant and moss species in the herbaceous vegetation were assigned to seven growth forms; forbs (e.g. *Trollius europaeus*, *Bistorta vivipara*, *Geranium sylvaticum*, *Cerastium* species, *Viola* species), vascular cryptogams (mainly *Equisetum* spp.), deciduous shrubs (mainly ramets of *Salix* spp. still part of the field layer, only small amounts of *Betula nana*), grasses (e.g. *Anthoxanthum odoratum*, *Avenella flexuosa*, *Poa* species, *Calamagrostis* species, *Festuca* species), sedges (e.g. *Carex bigelowii*, *Carex aquatilis* coll., *Juncus filiformis*), silica-rich grasses (mainly *Deschampsia cespitosa*, minor amounts of *Nardus stricta*), and mosses (all combined). While the two river catchments have similar species pools in terms of occurrence of plants, they differ in abundance composition. A more detailed description of the species composition in the herbaceous vegetation can be found in Ravolainen (2009).

On Varanger Peninsula, like in most of the circumpolar arctic tundra biome (cf. Ims and Fuglei 2005), migratory reindeer constitute the dominant large herbivore, whereas rodents such as voles and lemming dominate among the small herbivores (Killengreen et al. 2007). Both focal river catchments were within the same summer grazing reindeer management unit that covers 3, 800 km^2. The reindeer herd counted on average 11500 (range 10532-12841) animals over the three years (Anonymous 2004), which amounts to a density of 3 reindeer km^{-2}. Normally the herd moves into the study area in late April-early May and migrates to the wintering areas further south at the end of October.

In contrast to reindeer, the three small rodent species are present year-round. Among these, the tundra vole is the species normally found in highest densities in riparian tundra herbaceous vegetation (Henden et al. 2011; Tast 1966). An important aspect concerning the impact of small rodents on vegetation is their pronounced density cycles (Ims et al. 2005), which in north-eastern Norway have a 5-year period for the voles. The last cyclic peak before the onset of the present study was in 2002 (Yoccoz & Ims 2004). Thus a new peak year was expected in 2007.

Experimental design

Within the two river catchments experimental grids (n=25) were established on sediment plains along three rivers/tributaries in VJ (n=13) and in three natural sections of the wider sediment plain in KO (n=12). The distance between neighbouring grids within tributaries/sections had a range of 160-900 m in KO and 250-2200 m in VJ, whereas the two most distant grids were 7.7 km apart in KO and 12.5 km apart in VJ. The experimental grids, each sized 15 x 15 m, were located so that one side was aligned with the edge of a willow shrub patch and the grid extending into the herbaceous vegetation (see Fig. 1). Only grids that were covered by less than 30% of stones or mire and with no signs of recent flooding (as judged from the presence of river debris) were selected.

Within each of the grids we located 9 experimental plots (0.25 m^2) for measurement of abundance of plant growth forms and other plant community properties. All plots were centered on an individual willow sapling, subject to a companion study of willow shrub recruitment (Ravolainen et al. unpublished). The saplings were selected so that they were preferentially spatially interspersed within 5 m from the edge, however, clearly not under the tall willow canopy. Three experimental treatments were randomly assigned to the 9 plots per grid (3 replicates/treatment/grid). The treatments were: (1) Exclusion of all vertebrate herbivores by a small-meshed exclosure (iron mesh size approximately 1 x 1 cm), (2) exclusion of large herbivores (mostly reindeer) by a large-meshed exclosure (mesh size approximately 3 x 3 cm) and (3) unenclosed control plots with access for all herbivores. Previous laboratory trials have shown that the two mesh sizes are appropriate for exclusion vs. allowing access to small rodents (Ims unpublished). Since constructing exclosures implies cutting roots, we cut roots at a maximum depth of 20-30 cm around all plot edges, including edges of unenclosed plots. Then exclosures were dug 5-10 cm into the ground. Exclosures finally covered an area of 50 x 50 cm about 60 cm high and constructed with a lid that could be opened for vegetation analyses, (see Fig. 1). For comparison, at the onset of the experiment, height of vegetation was typically less than 30 cm (Ravolainen pers.obs.). All plots were established the first week of July 2006.

Three replicates of each treatment per grid yielded a total of 75 replicates per treatment. However, due to accidental loss of replicates and measurements (incidents that were evenly distributed among the two river catchments and had no systematic cause), 67 unenclosed, 71 large-meshed reindeer exclosures and 63 small-meshed reindeer and small rodent exclosures were used in the analyses. While small rodents a few times managed to enter the exclosures causing omission of data, reindeer had no influence on the exclosures.

Vegetation measurements

Measurements for quantifying the responses of the vegetation to herbivore exclusion were conducted at the peak of the growing season, i.e. the last week of July and first week of August in 2006-2008. Note that in 2006 the measurements were made about one month after the experiment was initiated, and thus the estimated effect size for this year (see Data analysis) must be interpreted in light of a relatively short treatment period. Vegetation analyses were conducted by the point frequency method (Bråthen & Hagberg 2004; Jonasson 1988) using a table with 3 X 3 pins attached at regular intervals of 10 cm across the table. All intercepts of vascular plants to the pins were counted. For mosses and standing dead plant material a maximum of one intercept per pin was recorded. For live vascular plants, point frequency records were converted to biomass per plot using established calibration equations (Ravolainen et al. 2010). Species biomasses were summed to total live vascular plant biomass and to growth form categories prior to data analysis. Biomass hence refers to live aboveground biomass.

Two indices of plant species diversity, namely Simpson diversity and species richness, were estimated. Simpson diversity (D) (Simpson 1949) was calculated as $D = 1 - \Sigma p^2$, where p is the relative biomass of a species in an experimental plot. Simpson diversity has a range of 0-1. Species richness was calculated as the number of species recorded within the plots (within the area of the point frequency table).

Indices of herbivore abundance

Relative population density indices of voles and lemmings were obtained according to the small quadrate method of Myllymäki et al. (1971) in which 12 snap-traps, three in each corner of the grid, were set up in each grid for two nights in mid July (summer) and early September (autumn) every year. This amounts to 288 and 312 trap-nights per season in KO and VJ, respectively.

Similarly, to provide season-specific regional indices of relative densities of reindeer we registered faeces presence in early July and early September in each study year. Eight fixed plots (0.5 m x 0.5 m) were distributed in each experimental grid and presence of faeces were registered and removed. Thus, the faeces found in the autumn represent the relative density of reindeer during the summer. The faeces data are presented as proportion of plots with presence of reindeer faeces per river catchment per season and year (Fig. 2).

Data analyses

Response variables with zero-values, i.e. biomass of plant growth forms, cover of dead vascular plants, cover of mosses and the Simpson index, were transformed by $\log_e$ (x+1), and total biomass and species richness by $\log_e$ (x) to achieve homogeneity of the residual variance. Data were analyzed using linear mixed effects models, package nlme (Pinheiro, Bates, DebRoy, Sarkar Deepyan & R Core 2008) in the R environment (R_Development_Core_Team 2008).The most parsimonious but common model to the analysis of all response variables included treatment, time and catchment as fixed factors with the interaction terms treatment x year + treatment x catchment. To account for the nested design and the repeated measurements over the three years, we included plots nested within experimental grid as the random part.

In the presentation of the results we focus on development of responses to treatment over time, i.e. the model term *treatment x year*. Model estimates for the full model are given as supplementary information (see Appendix Tables 1 and 2). Intercept for all models included catchment ‘KO’, year ‘2006’ and treatment ‘unenclosed’, hence the effects of treatment over time were in contrast to these levels (this contrast, given on logarithmic scale, corresponds to ln response ratio Oksanen, Sammul & Magi 2006, see also caption for Fig. 3). We also assessed whether the additional effect of excluding small rodents was significantly different from only excluding reindeer by contrasting these two different treatments. We focus on effects (i.e. contrasts) being supported by statistical evidence (i.e. 95% CI not overlapping 0). Treatment over time development is given separately for each catchment when there was statistical evidence for catchment-specific response (i.e. the model term *treatment x catchment* had 95% CI not overlapping 0). We provide estimates of effects (on a logarithmic scale) with 95% CI.

Results

Initial vegetation abundance composition

Grasses and deciduous shrubs were the most abundant growth forms in both river catchments (biomasses $1m^{-2}$ given at the base of Fig. 3 A-G). Forbs were more abundant in catchment VJ, whereas catchment KO was characterized by higher abundance of silica rich grasses. Vascular cryptogams and sedges and had generally low abundances in both catchments (Fig. 3 B and E, respectively).

Herbivore densities

The small rodent populations reached a peak during the course of the study. Tundra voles generally reached the highest relative peak densities among the three species (Fig. 2 A and B) and in both river catchments the populations of all small rodent species had crashed before the summer season of 2008. However, there were notable differences between the two focal river catchments in terms of the size of the peak, the timing of the peak and the relative abundance of the different species. The tundra vole attained a much higher abundance in catchment KO than in catchment VJ. Moreover, the Norwegian lemmings, which were almost absent in KO, exhibited a small peak in 2007 in catchment VJ, where the tundra voles at that time already had begun to decline.

Presence of reindeer faeces in the herbaceous vegetation of the tall shrub habitats was relatively stable through the experimental period, apart from high spring-estimates in the river catchment VJ in 2008 (Fig. 2 C). The proportion of plots with reindeer faeces was generally higher in catchment VJ than in catchment KO.

Responses of plant growth forms

Many growth forms exhibited rapid responses to the experimental treatments and several of these were catchment-specific (Fig. 3 A-I, see Appendix Table 1).

Growth forms that increased in response to release from grazing did so most clearly in catchment VJ (Fig. 3 A-C). Deciduous shrubs substantially increased over time due to exclusion of both reindeer and small rodents, with a final doubling of biomass relative to the unenclosed plots at the end of the experiment (Fig. 3 C). The impact of small rodent exclusion in VJ was at this stage significantly larger than exclusion of reindeer only (Fig. 3 C, * indicates effect size and confidence interval [] for contrast between the two exclosure types 0.63 [0.11, 1.16]). Forbs and vascular cryptogams increased when released from reindeer grazing in VJ (Fig. 3 A and B), whereas there was no additional effect due to the exclusion of small rodents in this catchment. In the other river catchment, KO, forb biomass increased when both reindeer and small rodents were excluded, and this increase became statistically significant in the last year of the experiment (Fig. 3 A). In 2008 the impact of small rodent exclusion on forbs became larger than excluding reindeer only (Fig. 3A, * 0.28 [0.00, 0.58]). Grass biomass was similar in all treatment plots across both catchments except for in 2007, when grass biomass was higher in plots where both reindeer and small rodents were excluded as opposed to plots where only reindeer were excluded (Fig. 3 D, * 0.42 [0.12, 0.72]).

Three growth forms exhibited a decrease in biomass in response to the herbivore exclusion. For biomass of silica-rich grasses and cover of mosses (Fig. 3 F and I, respectively) this decrease was catchment-specific. Silica-rich grasses decreased fast and with similar strength of response in both exclosure types in KO, the catchment in which especially *Deschampsia cespitosa* was abundant. The decrease in cover of mosses, which also took place in both exclosure types in KO, was slower. A similar, but weaker and even slower decrease of mosses was evident in VJ. Finally, sedges decreased with herbivore exclusion in both catchments, but only significantly so when herbivores of both sizes had been excluded in first year (Fig. 3 E).

Total biomass and species diversity

There were catchment-dependent and year-dependent effects of herbivore exclusion on total biomass of vascular plants (Fig. 3 G). In KO biomass decreased already in 2006 due to the very fast reduction of abundant silica-rich grasses (Fig. 3 G). This initial decrease was, however, compensated for later in the experiment due to a combined increase in biomass of other growth forms. In the last year of the experiment, biomass in KO was somewhat larger in exclosures excluding both small rodents and reindeer than in the reindeer exclosures (Fig. 3 G, * 0.19 [0.00, 0.37]). In VJ a substantial increase of total live biomass over time reflected the strong response in deciduous shrubs to exclusion of small rodents and the response of forbs to exclusion of reindeer (Fig. 3 G). Cover of standing dead plants showed a clear increase between the years 2007 and 2008 owing to the exclusion from small rodents (Fig. 3 H * in 2007 [95%CI] 0.21 [0.00, 0.42], * in 2008 0.57 [0.36, 0.77]).

None of the two species diversity indices showed clear response to the experimental treatments (see Appendix Table 2).

Species richness (see Appendix Table 2) and total biomass increased strongly from 2006 to 2008 even in the unenclosed plots over the experimental period (Fig. 3 G). Several growth forms appear to have contributed to this increase (see geometric means at the bottom of the panels in Fig. 3).

Discussion

Exclusion of grazers caused rapid and significant changes in plant community composition in herbaceous vegetation of Varanger Peninsula, Norway. Responses were evident after only one growing season. In accordance with our expectations regarding general effects of herbivores, biomass of forbs, deciduous shrubs and silica-poor grasses increased by 40-50% in response to release from herbivory of both reindeer and small rodents, whereas biomass of silica-rich grasses decreased by 50-75%. The rapid change, i.e. from one year to the next, indicates a tight link between the dynamics of productive tundra vegetation and both fluctuating small rodent populations and reindeer. Responses were however not spatially consistent, being highly different between the two catchments despite similar species pools. That is, whereas abundant palatable plants and a population peak of the Norwegian lemming characterized one of the catchments, an abundant unpalatable grass and tundra voles characterized the other. Our catchment-specific results are probably to a large degree reflecting that different vegetation states (Ravolainen 2009) and herbivore dynamics give different prerequisites for change.

Responses of plant community composition to herbivore exclusion in previous tundra studies have typically taken from a few years up to a decade to show (Olofsson et al. 2004; see Olofsson et al. 2009; Virtanen 2000), which is an order of magnitude longer than in our study. This difference is likely due to the fact that previous studies have focused on low-productive tundra heath vegetation dominated by ericoid dwarf shrubs (e.g. Grellmann 2002;

Olofsson et al. 2009; Virtanen 2000). The vegetation we studied largely consists of herbaceous plants and tall willow saplings (still part of the field layer), which are relatively fast growing and productive (Aerts & Chapin 2000; Bliss 2000; Shaver & Chapin 1991). The rapid responses we recorded correspond with a view that productive vegetation represents hot spots to plant-herbivore interactions (cf. Cebrian 1999). Coastal, arctic plant communities can respond to goose grazing (or grubbing) at correspondingly short time scales to those we report (e.g. Abraham, Jefferies & Rockwell 2005; Speed, Woodin, Tommervik, Tamstorf & van der Wal 2009), but these habitats differ fundamentally from our study system in characteristics of the vegetation and of the focal herbivore. Our results demonstrate that tundra plant communities can respond rapidly to changes in mammalian herbivore pressure at much shorter time-scales than previously acknowledged. The rapid responses of the tundra vegetation are comparable to those in temperate grasslands (Howe 2008) and in more southern, alpine vegetation (Austrheim, Mysterud, Hassel, Evju & Okland 2007).

Although both herbivore types affected the plant communities, the different responses among the river catchments suggested a context-dependency that is likely attributed both to varying densities of different small mammal species and to initial vegetation states (see Westoby, Walker & Noy-Meir 1989). For instance, in catchment VJ with high initial abundances of palatable growth forms and a peaking lemming population, (for which forbs are not considered selected forage, see Batzli 1993), forbs biomass was limited by reindeer grazing only (as evident from the similar increase in both exclosure types). Reindeer effect on forbs was, however, negligible in the river catchment KO. Here forb biomass was limited by tundra voles, for which forbs constitute a significant part of the diet (see Soininen et al. 2009), whereas the short-term reduction of grazing pressure had little effect on the other palatable growth forms. In KO the vegetation was dominated by silica-rich grasses, which are unpalatable and well-defended against herbivores (see Massey et al. 2007). Silica-rich grass biomass in KO decreased with reindeer exclusion and was partially replaced by more palatable plants in response to the reduction in grazing pressure. Hence, it seems that the initial vegetation state in KO, dominated by the un-palatable grass *Deschampsia cespitosa*, is maintained by the grazing activities of the large ungulate; reindeer. Similarly, Austrheim et al (2007) found vegetation dominated by a silica-rich grass (*Nardus stricta*) to be maintained by the grazing activities of another large ungulate; sheep. In contrast, the initially palatable vegetation state in VJ seems changed in terms of forb reduction by the presence of reindeer.

The strong increase in deciduous shrubs in small rodent exclosures in the river catchments in VJ can probably be attributed to the presence of lemmings. This functionally important group of small herbivores in tundra ecosystems (Batzli 1993, Ims and Fuglei 2005) can cut down much more vegetation than is actually ingested (Oksanen, Fretwell, Arruda & Niemela 1981). Previous studies have found that vegetation can recover from vole damage during a 3-to-4-year study period (for tundra, see Dahlgren, Oksanen, Olofsson & Oksanen 2009; for grassland, see Howe 2008). The deciduous shrubs we studied responded with significant increase the year after a lemming peak, suggesting even tighter dynamics between small mammals and tundra vegetation. We also found an increase in biomass of deciduous shrubs when released from reindeer browsing, although this finding was not statistically significant. However, reindeer browsing has previously been found to reduce growth of willows in sub-arctic tundra (den Herder et al. 2008; Kitti, Forbes & Oksanen 2009; Pajunen et al. 2008).

While herbaceous vegetation where tall shrub species are present, can act as nuclei for shrub encroachment in low-arctic tundra under climate warming (Tape, Sturm & Racine 2006), simultaneous impact of both herbivory and climate on plant community composition in such habitats is still unknown (cf. Post, Forchhammer, Bret-Harte, Callaghan, Christensen et al. 2009). Based on our results we argue that future studies of tundra vegetation will be more informative if the relative roles of large and small herbivores are specifically considered, in particular because their relative population levels in arctic ecosystems are presently changing (Ims and Fuglei 2005, Ims et al. 2008). Also, on the basis of our results we suggest that vegetation studies should comprise spatial variation in both herbivore and plant community composition. By and large, had we chosen to work in any one of the two river catchments only, our conclusions on the impact of the different-sized herbivores would have become different altogether.

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Appendix A: Spplementary material

The online version of this article contains additional supplementary data. Please visit XXXXX.

Referances

Abraham, K.F., Jefferies, R.L., & Rockwell, R.F. (2005). Goose-induced changes in vegetation and land cover between 1976 and 1997 in an arctic coastal marsh. *Arctic Antarctic and Alpine Research, 37*, 269-275.

Aerts, R., & Chapin, F.S. (2000). The mineral nutrition of wild plants revisited: A re-evaluation of processes and patterns. *Advances in Ecological Research, Vol 30, 30*, 1-67.

Anonymous. (2004). *Ressursregnskapet for reindriftsnæringen.* Reindriftsforvaltningen, Alta, Norway (in Norwegian).

Austrheim, G., Mysterud, A., Hassel, K., Evju, M., & Okland, R.H. (2007). Interactions between sheep, rodents, graminoids, and bryophytes in an oceanic alpine ecosystem of low productivity. *Ecoscience*, *14*, 178-187.

Batzli, G.O. (1993). Food selection by lemmings. In: N.C. Stenseth, & R.A. Ims (Eds.), *The biology of lemmings* (pp. 281-301). London: Academic Press.

Batzli, G.O., & Jung, H.J.G. (1980). Nutritional Ecology of Microtine Rodents - Resource Utilization near Atkasook, Alaska. *Arctic and Alpine Research*, *12*, 483-499.

Bliss, L.C. (2000). Arctic tundra and polar desert biome. In: M.G. Barbour, & W.D. Billings (Eds.), *North American terrestrial vegetation* (pp. XI, 708 s.). Cambridge: Cambridge University Press.

Bråthen, K.A., & Hagberg, O. (2004). More efficient estimation of plant biomass. *Journal of Vegetation Science, 15*, 653-660.

Bråthen, K.A., Ims, R.A., Yoccoz, N.G., Fauchald, P., Tveraa, T., & Hausner, V. (2007). Induced shift in ecosystem productivity? Extensive scale effects of abundant large herbivores. *Ecosystems, 10*, 773:789.

CAFF. (2001). *Arctic flora and fauna : status and conservation.* Helsinki: Conservation of Arctic Flora and Fauna, Edita.

Cebrian, J. (1999). Patterns in the fate of production in plant communities. *American Naturalist, 154*, 449-468.

Chapin, F.S., BretHarte, M.S., Hobbie, S.E., & Zhong, H.L. (1996). Plant functional types as predictors of transient responses of arctic vegetation to global change. *Journal of Vegetation Science*, *7*, 347-358.

Cornelissen, J.H.C., Quested, H.M., Gwynn-Jones, D., Van Logtestijn, R.S.P., De Beus, M.A.H., Kondratchuk, A., Callaghan, T.V., & Aerts, R. (2004). Leaf digestibility and litter decomposability are related in a wide range of subarctic plant species and types. *Functional Ecology, 18*, 779-786.

Cornelissen, J.H.C., van Bodegom, P.M., Aerts, R., Callaghan, T.V., van Logtestijn, R.S.P., Alatalo, J., Chapin, F.S., Gerdol, R., Gudmundsson, J., Gwynn-Jones, D., Hartley, A.E., Hik, D.S., Hofgaard, A., Jonsdottir, I.S., Karlsson, S., Klein, J.A., Laundre, J., Magnusson, B., Michelsen, A., Molau, U., Onipchenko, V.G., Quested, H.M., Sandvik, S.M., Schmidt, I.K., Shaver, G.R., Solheim, B., Soudzilovskaia, N.A., Stenstrom, A., Tolvanen, A., Totland, O., Wada, N., Welker, J.M., Zhao, X.Q., & Team, M.O.L. (2007). Global negative vegetation feedback to climate warming responses of leaf litter decomposition rates in cold biomes. *Ecology Letters, 10*, 619-627.

Côté, S.D., Rooney, T.P., Tremblay, J.P., Dussault, C., & Waller, D.M. (2004). Ecological impacts of deer overabundance. *Annual Review of Ecology Evolution and Systematics, 35*, 113-147.

Dahlgren, J., Oksanen, L., Olofsson, J., & Oksanen, T. (2009). Plant defences at no cost? The recovery of tundra scrubland following heavy grazing by grey-sided voles, Myodes rufocanus. *Evolutionary Ecology Research, 11*, 1205-1216.

den Herder, M., Virtanen, R., & Roininen, H. (2008). Reindeer herbivory reduces willow growth and grouse forage in a forest-tundra ecotone. *Basic and Applied Ecology, 9*, 324-331.

Gilg, O., Sittler, B., Sabard, B., Hurstel, A., Sane, R., Delattre, P., & Hanski, L. (2006). Functional and numerical responses of four lemming predators in high arctic Greenland. *Oikos, 113*, 193-216.

Grellmann, D. (2002). Plant responses to fertilization and exclusion of grazers on an arctic tundra heath. *Oikos, 98*, 190-204.

Henden, J.A., Ims, R.A., Yoccoz, N.G., Sorensen, R., & Killengreen, S.T. (2011). Population dynamics of tundra voles in relation to configuration of willow thickets in southern arctic tundra. *Polar Biology, 34*, 533-540.

Howe, H.F. (2008). Reversal of fortune: plant suppression and recovery after vole herbivory. *Oecologia, 157*, 279-286.

Ims, R.A., & Fuglei, E. (2005). Trophic interaction cycles in tundra ecosystems and the impact of climate change. *Bioscience, 55*, 311-322.

Ims, R.A., Henden, J.A., & Killengreen, S.T. (2008). Collapsing population cycles. *Trends in Ecology & Evolution, 23*, 79-86.

Ims, R.A., Yoccoz, N.G., & Killengreen, S. (2011). Determinants of lemming outbreaks. *Proceedings of the National Academy of Sciences of the United States of America, 108*, 1970-1974.

Jonasson, S. (1988). Evaluation of the Point Intercept Method for the Estimation of Plant Biomass. *Oikos, 52*, 101-106.

Kausrud, K.L., Mysterud, A., Steen, H., Vik, J.O., Østbye, E., Cazelles, B., Framstad, E., Eikeset, A.M., Mysterud, I., Solhøy, T., & Stenseth, N.C. (2008). Linking climate change to lemming cycles. *Nature, 456*, 93-97.

Killengreen, S., Ims, R.A., Yoccoz, N.G., Brathen, K.A., Henden, J.-A., & Schott, T. (2007). Structural characteristics of a low Arctic tundra ecosystem and the retreat of the Arctic fox. *Biological Conservation, 135*, 475-488.

Kitti, H., Forbes, B.C., & Oksanen, J. (2009). Long- and short-term effects of reindeer grazing on tundra wetland vegetation. *Polar Biology, 32*, 253-261.

Massey, F.P., Ennos, A.R., & Hartley, S.E. (2007). Grasses and the resource availability hypothesis: the importance of silica-based defences. *Journal of Ecology, 95*, 414-424.

Noda, T. (2004). Spatial hierarchical approach in community ecology: a way beyond high context-dependency and low predictability in local phenomena. *Population Ecology*, 105-117.

Oksanen, L., Fretwell, S.D., Arruda, J., & Niemela, P. (1981). Exploitation Ecosystems in Gradients of Primary Productivity. *American Naturalist, 118*, 240-261.

Oksanen, L., & Oksanen, T. (2000). The logic and realism of the hypothesis of exploitation ecosystems. *American Naturalist, 155*, 703-723.

Oksanen, L., Sammul, M., & Magi, M. (2006). On the indices of plant-plant competition and their pitfalls. *Oikos, 112*, 149-155.

Olofsson, J., Hulme, P.E., Oksanen, L., & Suominen, O. (2004). Importance of large and small mammalian herbivores for the plant community structure in the forest tundra ecotone. *Oikos, 106*, 324-334.

Olofsson, J., Hulme, P.E., Oksanen, L., & Suominen, O. (2005). Effects of mammalian herbivores on revegetation of disturbed areas in the forest-tundra ecotone in northern Fennoscandia. *Landscape Ecology, 20*, 351-359.

Olofsson, J., Oksanen, L., Callaghan, T., Hulme, P.E., Oksanen, T., & Suominen, O. (2009). Herbivores inhibit climate-driven shrub expansion on the tundra. *Global Change Biology, 15,* 2681-2693.

Pajunen, A., Virtanen, R., & Roininen, H. (2008). The effects of reindeer grazing on the composition and species richness of vegetation in forest-tundra ecotone. *Polar Biology, 31*, 1233-1244.

Pajunen, A.M. (2009). Environmental and biotic determinants of growth and height of Arctic willow shrubs along a latitudinal gradient. *Arctic Antarctic and Alpine Research, 41*, 478-485.

Pajunen, A.M., Kaarlejarvi, E.M., Forbes, B.C., & Virtanen, R. (2010). Compositional differentiation, vegetation-environment relationships and classification of willow-characterised vegetation in the western Eurasian Arctic. *Journal of Vegetation Science, 21*, 107-119.

Pinheiro, J.C., Bates, D.M., DebRoy, S., Sarkar Deepyan, & R Core, t. (2008). nlme: Linear and Nonlinear Mixed Effects Models. *R Package*.

Post, E., Forchhammer, M.C., Bret-Harte, M.S., Callaghan, T.V., Christensen, T.R., Elberling, B., Fox, A.D., Gilg, O., Hik, D.S., Hoye, T.T., Ims, R.A., Jeppesen, E., Klein, D.R., Madsen, J., McGuire, A.D., Rysgaard, S., Schindler, D.E., Stirling, I., Tamstorf, M.P., Tyler, N.J.C., van der Wal, R., Welker, J., Wookey, P.A., Schmidt, N.M., & Aastrup, P. (2009). Ecological dynamics across the Arctic associated with recent climate change. *Science, 325*, 1355-1358.

R_Development_Core_Team. (2008). R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria, URL http://www.R-project.org/.

Ravolainen, V.T. (2009). Tundra plant diversity as influenced by biotic interactions, PhD Thesis. Tromsø: University of Tromsø, Faculty of Biosciences, Fisheries and Economics, Department of Arctic and Marine Biology.

Ravolainen, V.T., Yoccoz, N.G., Bråthen, K.A., Ims, R.A., Iversen, M., & Gonzalez, V.T. (2010). Additive partitioning of diversity reveals no scale-dependent impacts of large ungulates on the structure of tundra plant communities *Ecosystems, 13*, 157-170.

Shaver, G.R., & Chapin, F.S. (1991). Production - Biomass Relationships and Element Cycling in Contrasting Arctic Vegetation Types. *Ecological Monographs, 61*, 1-31.

Shaver, G.R., Laundre, J.A., Giblin, A.E., & Nadelhoffer, K.J. (1996). Changes in live plant biomass, primary production and species composition along a riverside toposequence in Arctic Alaska, USA. *Arctic and Alpine Research, 28*, 363-379.

Simpson, E.H. (1949). Measurement of diversity. *Nature, 163*, 688-688.

Soininen, E., Valentini, A., Coissac, E., Miquel, C., Gielly, L., Brochmann, C., Brysting, A., Sonstebo, J., Ims, R., Yoccoz, N., & Taberlet, P. (2009). Analysing diet of small herbivores: the efficiency of DNA barcoding coupled with high-throughput pyrosequencing for deciphering the composition of complex plant mixtures. *Frontiers in Zoology, 6,* 16.

Speed, J.D.M., Woodin, S.J., Tommervik, H., Tamstorf, M.P., & van der Wal, R. (2009). Predicting Habitat Utilization and Extent of Ecosystem Disturbance by an Increasing Herbivore Population. *Ecosystems, 12*, 349-359.

Tape, K., Sturm, M., & Racine, C. (2006). The evidence for shrub expansion in Northern Alaska and the Pan-Arctic. *Global Change Biology, 12*, 686-702.

Tast, J. (1966). The root vole, *Microtus oeconomus* (Pallas), as an inhabitant of seasonally flooded land. . *Annales Zoologici Fennici, 3*, 127-171.

van der Wal, R. (2006). Do herbivores cause habitat degradation or vegetation state transition? Evidence from the tundra. *Oikos, 114*, 177-186.

Virtanen, R. (2000). Effects of grazing on above-ground biomass on a mountain snowbed, NW Finland. *Oikos, 90,* 295-300.

Virtanen, R., Henttonen, H., & Laine, K. (1997). Lemming grazing and structure of a snowbed plant community - A long-term experiment at Kilpisjarvi, Finnish Lapland. *Oikos, 79,* 155-166.

Westoby, M., Walker, B., & Noy-Meir, I. (1989). Opportunistic Management for Rangelands Not at Equilibrium. *Journal of Range Management, 42*, 266-274.

White, R.G., & Trudell, J. (1980). Habitat Preference and Forage Consumption by Reindeer and Caribou near Atkasook, Alaska. *Arctic and Alpine Research*, *12*, 511-529.

Yoccoz, N.G., & Ims, R.A. (2004). Spatial population dynamics of small mammals: some methodological and practical issues. *Anim Biodivers Conserv, 27*, 427-435.

Zimov, S.A., Chuprynin, V.I., Oreshko, A.P., Chapin, F.S., Reynolds, J.F., & Chapin, M.C. (1995). Steppe-tundra transition - a herbivore-driven biome shift at the end of the Pleistocene. *American Naturalist*, *146*, 765-794.

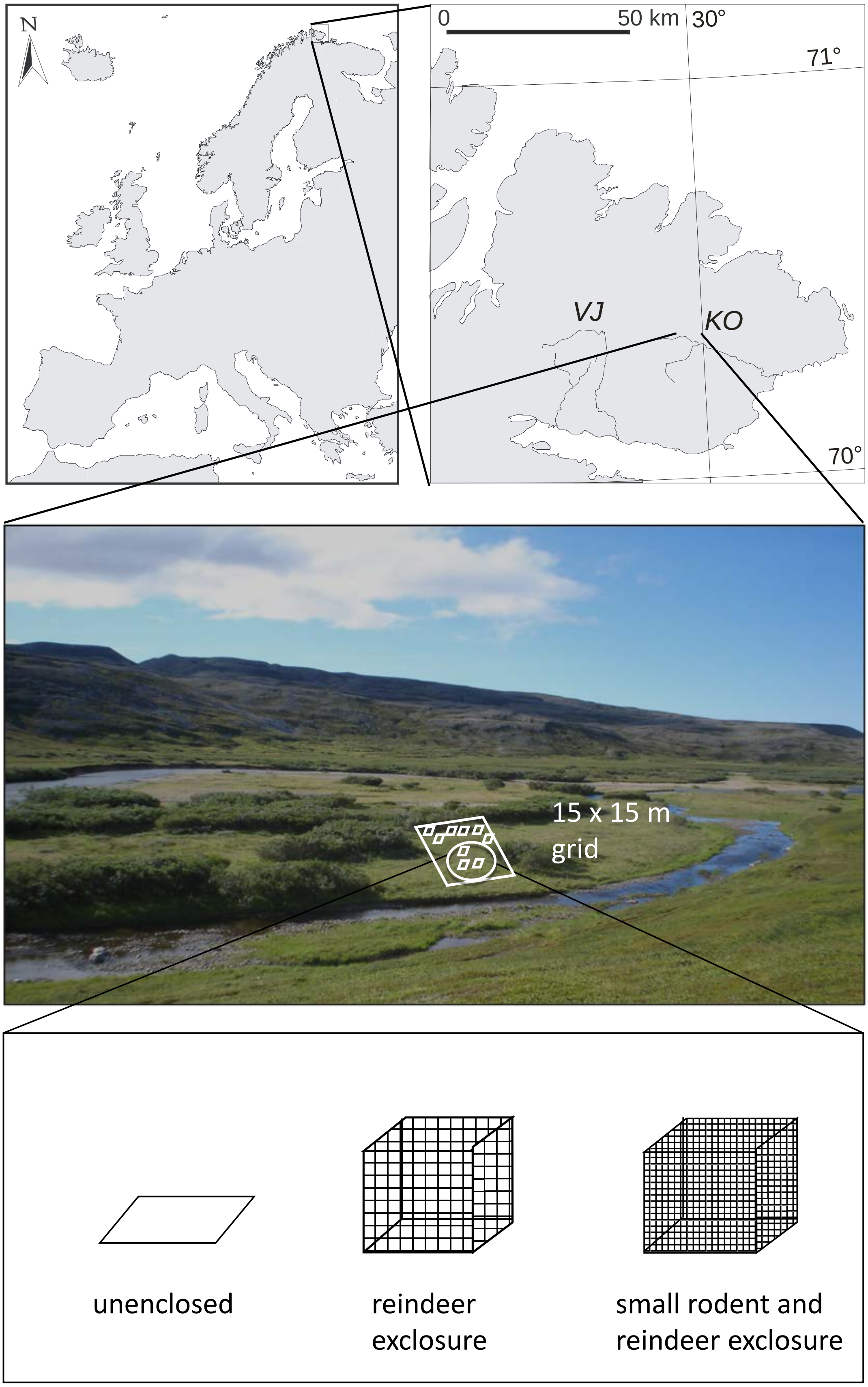
Fig. 1. The experiment was conducted in two separate river catchments Vestre Jakobselv (VJ) and Komagdalen (KO), in north-eastern Norway. Low-arctic riparian habitats can support productive vegetation in a mosaic of tall shrub patches bordered by herbaceous vegetation (photo taken in KO). The experiment was set up in the herbaceous vegetation with a total of 25 15 x 15 m grids distributed across the two river catchments, with three replicates of each treatment per grid. The treatments were: unenclosed control, reindeer exclosure, and exclosure for both reindeer and small mammals.

Fig. 2. Population density of three rodent species (A and B) and frequency of reindeer faeces (C) in the two river catchments (KO and VJ) over the years 2006-2008.

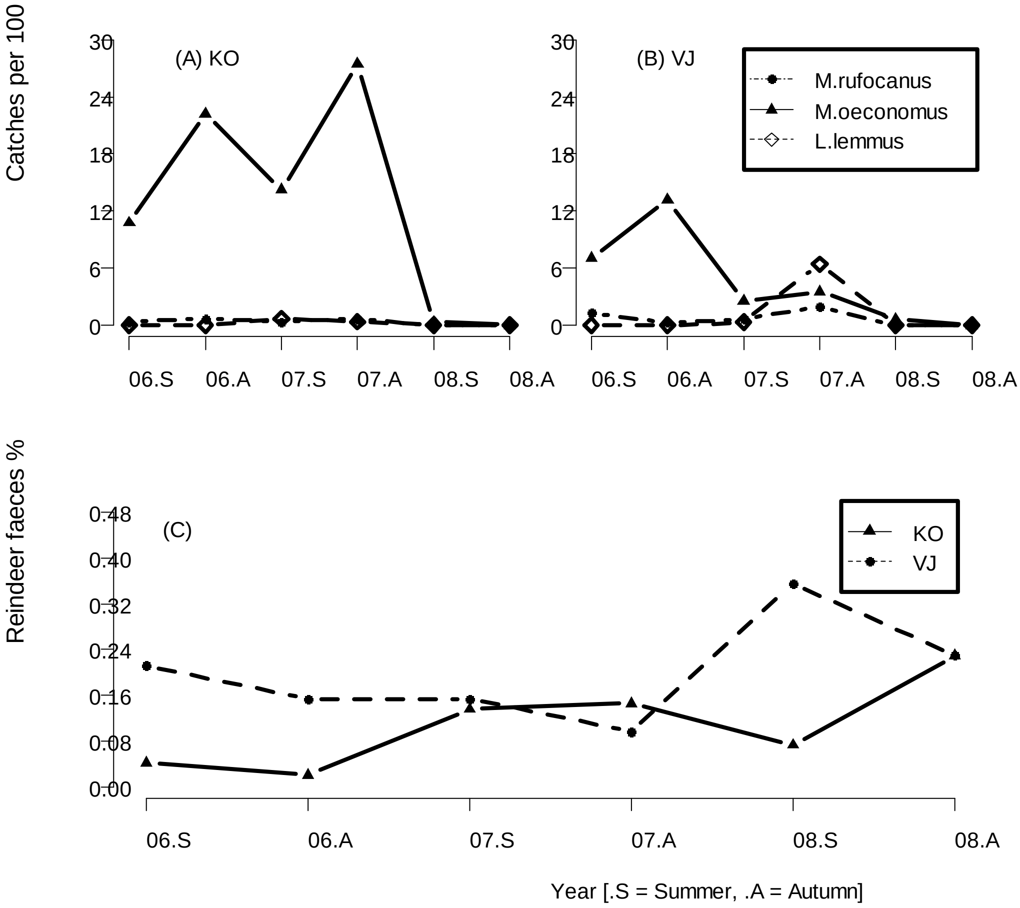
Fig. 3. Effect of mammalian herbivore exclusion from 2006 to 2008 on biomass of different growth forms and total biomass, and on cover of mosses and standing dead plants. Year-specific effect size and 95% confidence interval (model estimates in Appendix Table 1 & 2) are given for reindeer exclosure treatment and small rodent + reindeer exclosures as contrasts to unenclosed plots (i.e. a positive effect size indicates a higher abundance within exclosure than in the unenclosed control plots). Unenclosed plots in catchment KO is used as the reference level and is denoted with the hatched line at 0 effect size. When there were catchment-specific responses the reference level was specific to each of the two river catchments KO and VJ. The sign * indicates that the difference between excluding reindeer only and excluding both reindeer and small rodents was statistically significant. Effect sizes are on a $\log_e(x+1)$ scale and can thus be interpreted as proportional differences in growth form biomass between the different treatments and the unenclosed plots. Abundance estimates for the reference levels are given as geometric means (back-transformed from $\log_e(x+1)$ scale) at

the base of each figure. Units for the biomass are in grams m^{-2}, while cover for standing dead vascular plants and cover of mosses is given as percent cover.

Figure 1.

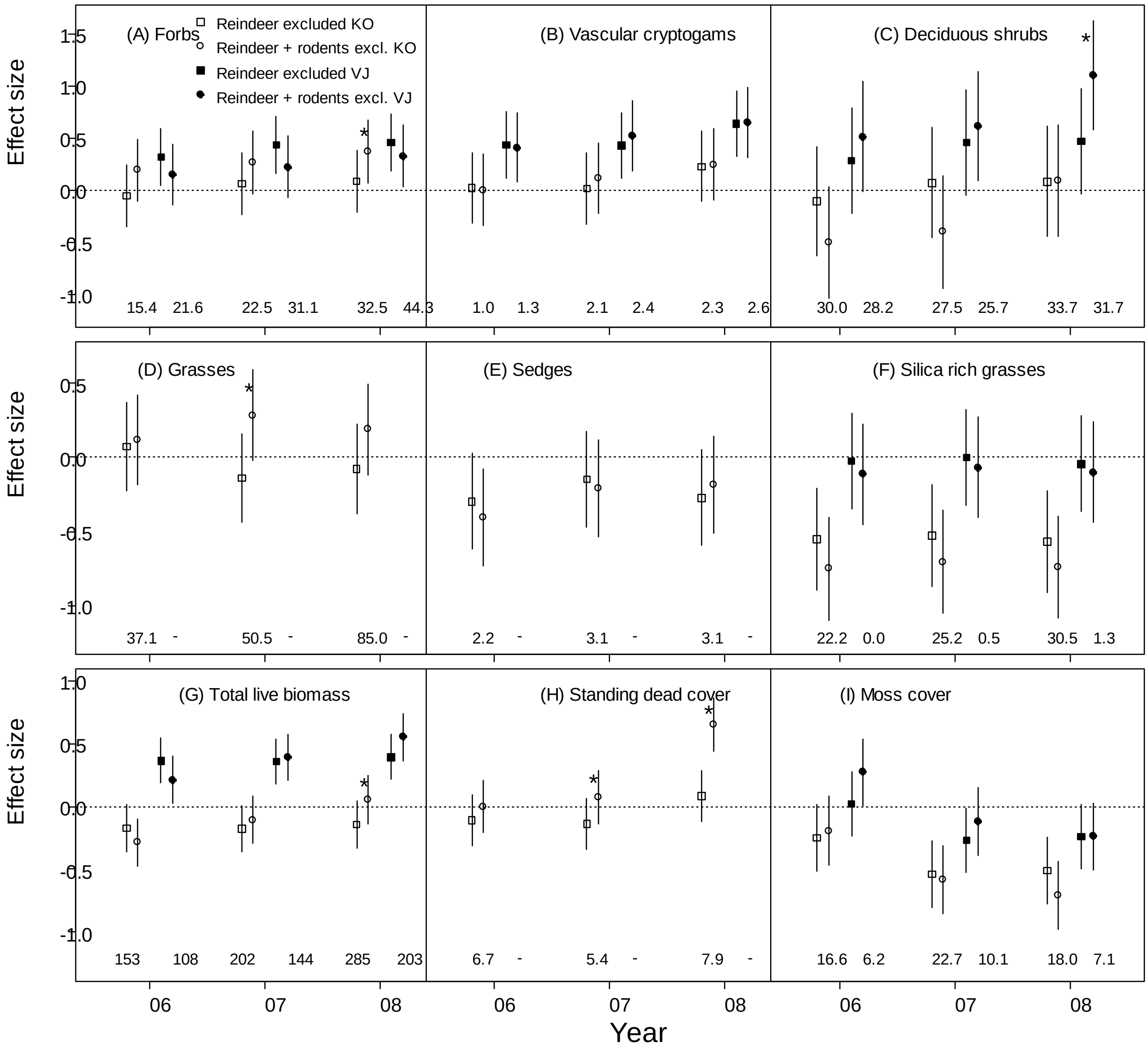

N
0
50 km
30°
71°
70°
VJ
KO
15 x 15 m
grid
unenclosed
reindeer
exclosure
small rodent and
reindeer exclosure

630
Figure 2.



635

Figure 3.



Reindeer excluded KO
Reindeer + rodents excl. KO
Reindeer excluded VJ
Reindeer + rodents excl. VJ
(A) Forbs
(B) Vascular cryptogams
(C) Deciduous shrubs
(D) Grasses
(E) Sedges
(F) Silica rich grasses
(G) Total live biomass
(H) Standing dead cover
(I) Moss cover
Effect size
Year
06
07
08
15.4 21.6 22.5 31.1 32.5 44.3
1.0 1.3 2.1 2.4 2.3 2.6
30.0 28.2 27.5 25.7 33.7 31.7
37.1 - 50.5 - 85.0 -
2.2 - 3.1 - 3.1 -
22.2 0.0 25.2 0.5 30.5 1.3
153 108 202 144 285 203
6.7 - 5.4 - 7.9 -
16.6 6.2 22.7 10.1 18.0 7.1