Norwegian University of Life Sciences
Faculty of Environmental Sciences and
Natural Resource Management)

Philosophiae Doctor (PhD)
Thesis 2018:66

Ecological impacts of red deer browsing in boreal forest

Økologiske effekter av hjortebeiting i boreal skog

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Ås (2018)

Thesis number 2018:66
ISSN 1894-6402
ISBN 978-82-575-1534-8

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Contents

1 Summary

The populations of wild ungulates are increasing in the northern hemisphere, and in many areas, their populations have developed from critically low to historically high numbers within the last century. There are multiple causes for this increase, which differ between species and areas. In general, however, changing forestry techniques, reduced free-ranging livestock herbivory, and milder climate have increased food plant availability and thereby stimulated the wild ungulate population growth. This, in combination with hunting regulations that favor increased productivity and the reduction or removal of large predators, has been central for the ungulate population growth. Because large herbivores affect their ecosystems via various mechanisms in such as selective feeding on plants, trampling, defecation, and urination, they are considered as potential ecosystem engineers. Hence, the dramatic increase in population densities has become an ecological concern. Populations without substantial natural predation may risk to reach overabundance. Wild ungulates may, however, already have severe impacts on their ecosystem long before reaching overabundance. Knowledge about the ecological role of how different ungulate densities can shape and impact their ecosystems, is therefore central for determining appropriate population management goals, and to prevent irreversible effects on the ecosystem.

In Scandinavia, cervids were relatively rare around 1900. In recent decades, the populations have shown an exponential increase in population size. In Norway, the red deer (*Cervus elaphus*) population has increased approximately 150-fold since 1900, and passed the moose (*Alces alces*) as the most hunted ungulate around 2010. This development has been applauded by hunters, but creates concern among foresters and nature management authorities, regarding forest regeneration, loss of biodiversity, and potential trophic cascades. However, many aspects of how variation in red deer population densities can affect ecological dynamics in the boreal forest remain unclear.

The main objective of this thesis was to identify how red deer, and variation in their densities, may structure the boreal forest and affect dynamics, composition and diversity of ecological communities. I investigated how historically high densities of red deer affect the understory plant and insect communities. Such changes can alter food and habitat availability for, for example, forest dwelling birds and mammals, and implies that red deer

may induce trophic cascades. I used a long-term, paired exclosure vs. deer-access research design to reach my objectives. The exclosures were established in December 2000 within old-growth pine-bilberry (*Pinus sylvestris*-*Vaccinium myrtillus*) forest at the Svanøy island in Western Norway, as part of a long-term research project to assess how red deer affect ecological dynamics in general (the EcoDynDeer project). Specifically, I investigated the role of red deer browsing on the structure, abundance, and diversity of plant (paper I and II) and insect communities (III). In addition, I studied whether red deer may induce trophic cascades by modifying interactions between the key boreal plant, bilberry, and the ecological important insect group of herbivorous Lepidoptera and Symphyta (paper IV).

We found that intermediate red deer browsing intensities resulted in the most species rich understory plant communities (Paper I). We found that growth-form determined much of the plants responses to browsing. In general, early succession and prostrate growing species benefited (Paper I), whereas there was a reduction of woody species when exposed to red deer browsing (Paper I & II). This dichotomy between growth forms was reflected in a positive relationship between temporal heterogeneity and red deer browsing, as higher plant species turnover rates occurred at higher browsing intensities (Paper II). Red deer browsing had a homogenizing effect on the spatial distribution of plant species, and thus made the plant communities more similar across sites than would be expected based on the variation in abiotic factors (Paper II).

The ground-dwelling beetle community responded differently to red deer browsing compared to plants. The overall beetle species richness did not relate to red deer browsing (Paper III). Although, as for the plants, measured in abundance, there were more beetle species benefitting from red deer browsing than those that decreased (Paper III). The species in disadvantage of browsing were functionally related to plant cover and detritus or arthropod predation (Paper III). Red deer browsing structured the ground-dwelling beetle community. Contrary to the effect on the plant community, red deer browsing increased the ground-dwelling beetle heterogeneity (beta diversity, Paper III). Thus the beetle assemblages showed higher local variation between plots where red deer had access than in exclosures. Finally, we showed that red deer also affected other primary consumers. The abundance of herbivorous larvae was halved by red deer browsing (Paper IV). The main mechanism behind this response appeared to be the removal of biomass (Paper IV). Interestingly, our results also indicated that red deer browsing alters the nutritional quality of shared food plants (Paper IV). The larvae selected the highly browsed bilberry ramets much stronger than ramets subjected to both lower, and extremely heavy, browsing intensity. The reductions in larvae numbers are likely to affect forest vegetation-dwelling bird species of which their reproductive success depends on insect larvae densities. Hence, our results suggest that red deer has the potential for inducing trophic cascades.

2 List of papers

Paper I

Hegland, S. J., Lilleeng, M. S. and Moe, S. R. (2013). Old-growth forest floor richness increases with red deer herbivory intensity. Forest Ecology and Management **310**: 267-274. https://doi.org/10.1016/j.foreco.2013.08.031

Paper II

Lilleeng, M. S., Hegland, S. J., Rydgren, K., and Moe, S. R. (2016). Red deer mediate spatial and temporal plant heterogeneity in boreal forests. Ecological Research **31**: 441-448. https://doi.org/10.1007/s11284-016-1391-6

Paper III

Lilleeng, M. S., Rydgren, K., Halvorsen, R., Moe, S. R., and Hegland, S. J. (2018). Red deer structure the ground-dwelling beetle community in boreal forest. Biodiversity and Conservation **27**: 2507-2525. https://doi.org/10.1007/s10531-018-1550-x

Paper IV

Lilleeng, M. S., Hegland, S. J., Rydgren, K., and Moe, S. R. Red deer limit the number of herbivorous larvae on bilberry in a boreal forest. Submitted June 2018

3 Introduction

The populations of wild ungulates have reached historically high densities in the northern hemisphere, and in many areas, their populations have developed from critically low to historically high numbers within the last century (Fuller and Gill 2001, Côté et al. 2004, Milner et al. 2006). There are multiple causes for this increase, which differ between species and areas. In general, the main causes for the population growth relate to intensification of agriculture and forestry (Mysterud et al. 2002), supplementary feeding (Putman and Staines 2004), hunting regulations that favour population growth (Langvatn and Loison 1999, Solberg et al. 1999, Milner et al. 2006, Milner et al. 2011), the reduction or total removal of large predators (Beschta and Ripple 2009), and milder climate (Gaillard et al. 1998, Mysterud et al. 2001). Such profound changes in population numbers and densities concern managers and conservationists.

Large herbivores can structure entire ecosystems (Danell and Bergström 2002, Côté et al. 2004), and are considered as ecosystem engineers (Jones et al. 1994). Selective herbivory is considered as a primary mechanism by which large herbivores can affect their environment (Augustine and McNaughton 1998, Diaz et al. 2007), in addition to, for example, trampling (Cumming and Cumming 2003), nutrient redistribution by urinating and defecating (Hobbs 1996), or plant seed dispersal (Olff and Ritchie 1998, Albert et al. 2015). The effects of herbivory may vary on a wide scale, from temporary effects within a plant (Nykänen and Koricheva 2004, Moe et al. 2018), to long-term changes in the ecological state on the landscape scale (Côté et al. 2004, Nuttle et al. 2014). By influencing abiotic factors and primary production, large herbivores may affect third parties, such as arthropods and birds (Allombert et al. 2005a, Allombert et al. 2005b, van Klink et al. 2015, Chollet et al. 2016, Jirinec et al. 2017). Because of their great potential for inducing ecological change, the dramatic increase in population densities has become an ecological concern. Populations without substantial natural predation can become overabundant (Côté et al. 2004), but severe impacts on their ecosystem can arise already long before reaching such a state (Mysterud 2006). Knowledge on how large herbivores modify their ecosystems is paramount for predicting ecological outcomes of their population dynamics and distributions, as well as for determining appropriate population management goals.

Large herbivores can affect their ecosystems both directly and indirectly, as direct effects on vegetation and soil biogeochemistry often lead to effects on third parties. Selective herbivory directly affects the abundance and biomass of preferred species (Speed et al. 2013), can induce plant defence mechanisms or change their nutritional value (Danell and Huss-Danell 1985, Karban 2011), and can eventually affect population dynamics of specific species (Evju et al. 2010). Other direct effects include; trampling, which can compress soil, damage vegetation, and create gaps of bare soil (Cumming and Cumming 2003). Bare soil can function as 'recruitment windows of opportunity' for seedling establishment. Such windows may be essential for the generative reproduction of the clonal dwarf-shrub species that dominate the boreal forest floor (Eriksson and Fröborg 1996). Furthermore, urination and defecation may increase nitrogen input in the upper soil layer (Hobbs 1996), and ungulates contribute to seed dispersal by both endo- and ectozoochory (Howe and Smallwood 1982, Albert et al. 2015).

Indirectly, large herbivores can affect sympatric organisms via changes in the vegetation and environment (van Klink et al. 2015), which can even induce trophic cascades that flow throughout food webs (Vandegehuchte et al. 2017). Herbivory is selective, and occurs on specific plant species and plant parts. This implies that herbivory can alter the plant species composition by, for example, facilitating growth of avoided or browsing tolerant species (Augustine and McNaughton 1998), and thereby potentially alter intra- and inter-specific competition in the vegetation community (Hester et al. 2006). Changes in plant species richness affects the herbivores associated with the specific plant species, and reduction in available plant biomass can result in direct competition for food resources (van Klink et al. 2015).

Plants have several strategies to resist herbivory, which can be separated into avoidance or tolerance strategies (Strauss and Agrawal 1999, Hester et al. 2006). Avoidance strategies include physical (e.g. thorns) and chemical defense (e.g. reduced palatability). Tolerant species can for example respond with increased branching e.g. after removal of apical dominance (Danell and Huss-Danell 1985). Such regrowth tissue often contains less chemical defense than older shoots (du Toit et al. 1990), and therefore often experience re-browsing by ungulates (Mathisen et al. 2017) or herbivorous insects (Moe et al. 2018). Increases in large herbivore densities may therefore feedback to large herbivores themselves, but also to the herbivores with whom they share their food plants, for example, defoliating insect larvae. Most herbivorous larvae feed on only one or few different plant species (Danell and Bergström 2002), and are therefore sensitive to changes in the abundance or the quality of their food species. Despite their small body size, herbivorous insect larvae can have tremendous ecological significance. For example, herbivorous insect larvae have been estimated to remove more plant biomass than the mammalian browsers on a South African savannah (Danell and Bergström 2002); or, since they are protein rich and often occur in high numbers, they play an important role in many ecosystems as food, for example for insectivorous birds (Picozzi et al. 1999).

Vegetation structure and composition of growth forms are also affected by large herbivores. Changes in vegetation structure may moderate the abiotic conditions, for example creating warmer and dryer microclimate, and removal of shelter vegetation may increase predation risk for, for example, prey insects (van Klink et al. 2015). The combination of changes in abiotic conditions, resources and predation risk are likely to have cascading effects on vegetation- and ground-dwelling arthropods, mammals, and birds (Thomas et al. 1986, Foster et al. 2014, van Klink et al. 2015). Furthermore, the ecological impacts of herbivory are highly dependent of ecosystem productivity (Proulx and Mazumder 1998, Bakker et al. 2006), herbivore densities (Danell and Bergström 2002, Foster et al. 2014), as well as animal size and behavior (Creel et al. 2005, Bakker et al. 2006), food selectivity (Augustine and McNaughton 1998) and interactions with other herbivores (Adler et al. 2001). Because ecological impacts of ungulates on their environment are strongly context-dependent, there is a need for improving our species-, area-, and ecosystem-specific knowledge.

In Scandinavia, cervids were relatively rare around 1900. Carl von Linné (Linneaus), the Swedish founder of modern taxonomy, even never saw a wild moose, and he assigned '*Alces alces*' as its scientific name based on observations in a zoo (Schwartz et al. 2003). In recent decades, the populations have shown an exponential increase in population size. In Norway, the total cervid biomass increased by approximately 280% from 1949 to 1999 (Austrheim et al. 2011), and the red deer (*Cervus elaphus*) population has increased approximately 150-fold since 1900, and passed the moose as the most hunted ungulate around 2010 (Statistics Norway 2018) (Fig. 1). This development has been applauded by hunters, but creates concern among foresters and nature management authorities, regarding forest regeneration, loss of biodiversity, and trophic cascades (Côté et al. 2004).

However, many aspects of how variation in red deer population densities can affect ecological dynamics in the boreal forest remain unclear.

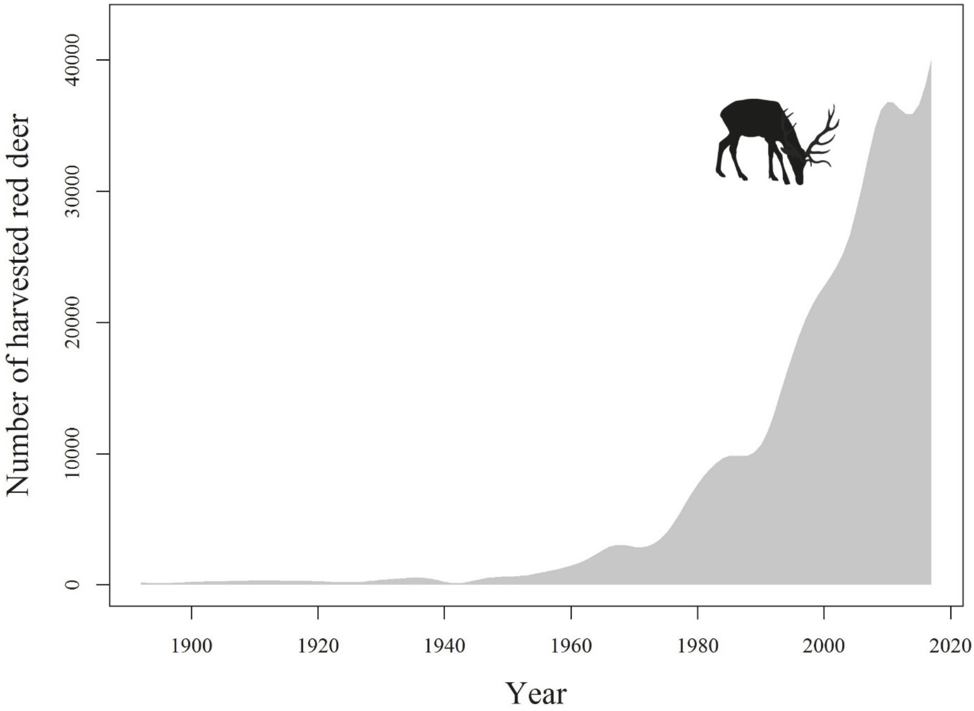

Figure 1. The number of hunted red deer in Norway from 1892–2017. Hunting statistics are probably the best estimates available to reflect trends in population numbers. In the first 20 years of the time series, the average number of red deer hunted was approximately 200 per year. During the last 20 years, on average about 31 000 animals have been hunted per year. Data from Statistics Norway (2018).

How herbivory affects ecosystems is a central question in ecology, and has been intensively studied (review in e.g. Hester et al. 2006, Foster et al. 2014). Yet, several knowledge gaps remain in the basic biological understanding of the impacts of large herbivores on biodiversity (Foster et al. 2014): (1) investigation of nonlinear responses of organisms to herbivore pressure, (2) how ecological responses differ between herbivore species, (3) spatial and (4) temporal variation of responses, (5) interactions between herbivores and land use, and (6) cascading effects of ecological responses. The goal of my thesis was to improve our knowledge on how red deer browsing affects the boreal forest. I have investigated how red deer affect different aspects of diversity measures for plants and ground-dwelling beetle communities, and if these responses vary over a deer-browsing intensity gradient. Furthermore, I investigated how red deer browsing can affect third parties, the herbivorous insect larvae with whom they share food plants.

4 Objectives

The main objective of this thesis was to identify how variation in red deer density may structure vegetation, and affects dynamics, composition, and diversity of ecological communities in the boreal forest. Specifically, I investigated how variation in red deer densities affects understory plant and insect communities, and addressed the following questions:

1. How does variation in red deer browsing intensity relate to a) plant species richness in general and b) plant species richness within functional groups (bryophytes, dwarf-shrubs, trees, forbs, ferns, and graminoids)? (Paper I)
2. How does variation in red deer browsing intensity affect plant species heterogeneity in space and time? (Paper II)
3. How and to what extent does red deer browsing affect a) the abundance of specific beetle species and b) the diversity of the ground-dwelling beetle community? (Paper III)
4. Do red deer browsing limit the abundance of herbivorous larvae on a shared food plant? In case such a mechanism arises, to what extent can the limitation be attributed by a) biomass removal, or b) browsing-induced changes in food quality of the food plant? (Paper IV)

5 Study system

5.1 Red deer

Red deer (Fig. 2) is a forest-dwelling intermediate feeder (Hofmann 1989) with a wide native distribution in Europe and Asia (Milner et al. 2006). It has been introduced to several other regions, such as New Zealand (Tanentzap et al. 2009) and South America (Flueck 2010). Red deer has an important economic value as a game species (Milner et al. 2006), but is also a risk factor and cost for society, when involved in vehicle collisions (Hegland and Hamre 2018), and crop or forest damage (Arnold et al. 2018). Red deer feed on a wide range of plant species depending on their availability and deer population density, with grasses (*Poaceae* spp.), sedges (*Cyperaceae* spp.), trees, and forbs as major part of their diet (e.g. Fløjgaard et al. 2017). During winter, red deer browse selectively (i.e. higher use compared to availability) on *Sorbus, Populus*, and *Salix* species, whereas bilberry and birch (*Betula* spp.) are intermediately selected for, but constitute a central part of their diet (Mysterud et al. 2010). Red deer typically make extensive use of agricultural patches and forest edges when available, but also feed extensively within forests (Godvik et al. 2009). Despite their relatively wide diet range, I term red deer as 'browsers' throughout this thesis.

Figure 2. Red deer in an open part of the pine forest at Svanøy island, Western Norway. The pine forest understory is typically dominated by dwarf-shrubs, here heather (*Calluna vulgaris*), and in less open forest mainly by bilberry (*Bilberry myrtillus*). Photo by Johan Trygve Solheim.

5.2 Boreal forest

The boreal forest has a circumpolar distribution and is common in e.g. Alaska, northern and eastern Canada, Scandinavia, and northern Russia. In total, the boreal forest covers approximately 11 % of the terrestrial surface on Earth (Bonan and Shugart 1989). The dominating tree species are coniferous, often mixed with deciduous trees. The boreal forest has a specific structure: a distinct mature tree layer with the forest understory often dominated by dwarf-shrubs, and the bottom layer most often dominated by lichens in dryer sites, or weft-and carpet-forming bryophytes in more humid sites (Nilsson and Wardle 2005).

6 Methods

6.1 Study area

We performed an exclosure/exposure-experiment within old-growth bilberry-pine (*Vaccinium myrtillus - Pinus sylvestris*) forest at the 11 km^2 island Svanøy, Western Norway (61°30N, 5°05E, Fig. 3). Svanøy is situated approximately 2.5 km from the closest mainland, in the boreo-nemoral zone with an oceanic climate (mean annual precipitation about 2000 mm and an average temperature of about 8° C (http://www.eklima.met.no)). The terrain is small-scale rugged, with the highest elevation at 235 meter above sea level. The main vegetation cover is pine forest, with some smaller farmland areas, mires, and lakes (Skogen and Lunde 1997). The farmland is situated in the flatter parts of the island (Fig. 4). The human population on the island comprises approximately 70 people, and the main settlements are in the northeastern part of the island.

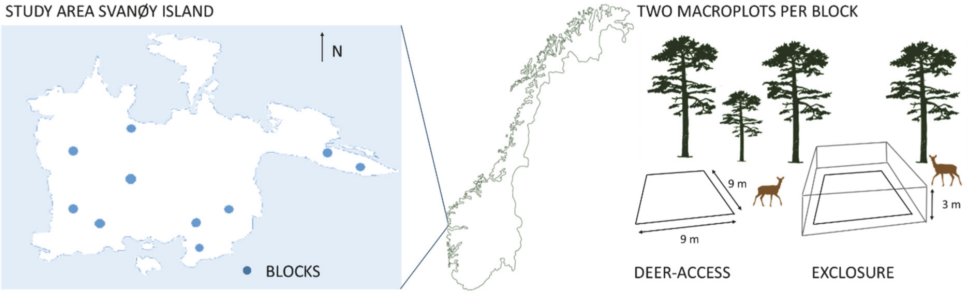

Figure 3. Illustration of the research design. We used Svanøy Island (61°30N, 5°05E) and its relatively closed and stable red deer population as the experimental area to investigate how red deer affect biodiversity in the boreal forest. The experimental framework consisted of twelve paired blocks, distributed across the island, in old-growth pine-bilberry forest. The blocks were established in 2000, and each block consisted of one exclosure and one deer-access macroplot of 9 × 9 m. Each macroplot contained seven permanent 1 × 1 m plots, where vegetation has been surveyed since 2001.

Figure 4. Arial photo of Svanøy (Source: Statens Kartverk, www.norgeskart.no). The island is mainly covered with pine (*Pinus sylvestris*) forest, but also contains some farmland, settlements, mires and lakes, as well as deciduous forests.

6.2 General study design

In December 2000, twelve blocks were established at different sites on the island, along a red deer density gradient. Each block contained two 9 × 9 m macroplots with each seven permanently marked 1 × 1 m plots. The plots were semi-randomly placed within the macroplot, and were established at a flat ground surface and at least 0.5 m from closest tree. In all blocks, one macroplot was kept as a control, which allowed deer access (hereafter 'deer-access plots'). We excluded red deer from the paired macroplots with a solid 3 m high fence (10 × 10 cm wire mesh), leaving 0.5 m around each of the macroplots to avoid edge effects. Birds, insects, and smaller mammals could move freely in and out of the exclosures. However, small mammal densities are extremely low at Svanøy. Boreal mammals as the mountain hare (*Lepus timidus*), common on the mainland, have not been observed on the island (J. T. Solheim pers. comm.), and during 350 trap nights in 2011, we did not succeed to trap small rodents, nor did we discover rodent feces during our field studies. Large predators do not occur in Svanøy.

The red deer population density at Svanøy is approximately 7.5 deer per km^2, which is considered high for Norway, but representative for most areas in Western Norway. The blocks were exposed to a varying degree of herbivory, with red deer browsing intensities ranging from low to extremely high. Ten blocks were established in pine-bilberry forest with wild red deer, and two blocks were established in pine-bilberry forest within a red deer farm to represent a population density above carrying capacity. The estimated deer density within the farm is approximately 30 animals per km^2. The farmed red deer were kept separate from the wild population with a > 4 m tall, solid fence. The wild red deer population is relatively stable, although animals may migrate to or from the mainland. The population is managed by hunting during the autumn. Some domestic sheep (*Ovis aries*) are free-ranging on the island, mainly during summer.

We estimated the red deer browsing intensity at each block to obtain a red deer density gradient in addition to the treatment vs. control design. We used browsing damage on the abundant and intermediately selected forage plant, the bilberry, as an indicator for red deer density (Mysterud et al. 2010). As bilberry is a relatively browsing-tolerant species, it has been shown to function as a good indicator for deer densities (Hegland et al. 2010, Mysterud et al. 2010). Species that are highly preferred would be browsed even if the herbivores are few, and are therefore not reliable for population density estimation (Mysterud et al. 2010). We measured the browsing level on bilberry ramets by estimating the number of annuals shoots browsed by red deer on a scale from 0 to 4, were 0 = no browsing, 1 = > 0–24.9 % of annual shoots browsed, 2 = 25–49.9% of annual shoots browsed, 3 = 50–74.9% of annual shoots browsed, and 4 = ≥ 75% of annual shoots browsed. In 2001 we did this on five ramets in all plots, in 2006 on three ramets in four out of seven plots in each macroplot, and from 2011 onwards, we did this on three ramets in all plots. We adjusted this measure by dividing it with ramet height, to better reflect the browsing severity. Parallel to the bilberry browsing surveys, we recorded the number of red deer fecal pellet groups in 100 randomly selected 1 m^2 plots within a 100 m radius from each deer-access macroplot. This measure correlated well with the browsing intensity estimates on bilberry ramets ($r = 0.94$, $N = 12$, $p < 0.001$).

When observations are either not independent in space and/or time, the responses must be analysed with statistical models that can account for such potential autocorrelation (Zuur et al. 2009, Crawley 2013). Due to the nested study design, with *plots* being nested in *macroplots* within paired *blocks*, I used statistical approaches that account for such dependencies (e.g. mixed-effect regression models) in all analyses.

6.3 Effects of red deer browsing on diversity and community ecology of the boreal forest understory vegetation (paper I and II)

We recorded plant species richness and the abundance of each species in the understory vegetation in all 1 m^2 plots (Fig. 5) in June 2001, 2006 and 2011. We subdivided each plot into 100 10 × 10 cm subplots. The abundance of each species was calculated as sum of occurrences in all subplots per plot. In addition, we measured richness and abundance of young understory trees on the macroplot scale, 9 × 9 m.

For our estimate of red deer browsing intensity, we used the mean estimate of all surveyed ramets per macroplot per year, for analyses of the spatial heterogeneity. For analyses on temporal heterogeneity, we used the mean of estimated browsing values across the periods 2001–2006 and 2006–2011.

Figure 5. Illustration of the research design for monitoring vegetation. In 2001, seven permanent 1 m^2 vegetation plots were established in each macroplot (n = 168), and species richness and abundances were estimated in June 2001, 2006, and 2011. The middle panel is an example of an exclosure plot, the right panel represents a deer-access plot. Photo: Lilleeng, M. S.

To describe the alpha (within-plot) diversity, we used species richness (number of species observed in observation unit, Paper I) and Shannon's diversity index (H´, Kindt and Coe 2005, Paper II). We used evenness (exp[H']/species richness, Kindt and Coe 2005) to describe whether the plant community and understory layers were dominated by a few species (low evenness), or if they were characterized by few dominating and many equally abundant species (high evenness, Magurran 2011, Paper II). We described the temporal species turnover, i.e. the percent dissimilarity between two surveys separated in time of the same plot, for the intervals 2001–2006 and 2006–2011 using the Bray-Curtis dissimilarity measure (percent dissimilarity/100, Legendre and Legendre 1998, Paper II). We estimated beta (between-plot) diversity, as the Bray-Curtis dissimilarity between each plot and all other plots surrounding the plot within each macroplot and year (Paper II). We analyzed all responses with linear mixed-effect regression models (Pinheiro and Bates 2013, Bates et al. 2014, Kuznetsova et al. 2015) in R version 2.15.0 (R Development Core Team 2013, Paper I) and 3.1.1 (R Core Team 2014, Paper II).

6.4 Effects of red deer browsing on diversity and community ecology of ground-dwelling beetles in boreal forest (paper III)

To identify the role of red deer browsing on the ground-dwelling beetle community, we collected ground-dwelling beetles with seven pitfall traps in each macroplot (Fig. 6). We started the trapping in mid May 2011, we collected the trap content every 4th week for three months. The pitfall traps were plastic cups with an inner diameter of 8.3 cm and a depth of 10 cm. We filled (2/3) the traps with a 1:1 mix of polypropylenglycol and water to conserve the beetles, and with a droplet of detergent to break the surface tension. We pooled the three collections from each trap into one composite sample. The beetles were stored on 70% ethanol and were later determined to the species level and functional group (based on diet: ‘predators’, ‘detritivores’, ‘omnivores’, ‘herbivores’, ‘fungivores’, ‘saproxylic’ and ‘others’) by Sindre Ligaard.

We related the diversity and distribution of the ground-dwelling beetle community to the red deer browsing intensity gradient, and used the mean of the browsing intensity measures across all ramets in each macroplot for each year as the ‘current herbivory intensity’. To account for potential legacy effects of browsing history prior to the establishment of the exclosures, we assigned to each macroplot the same browsing intensity value as we recorded for the corresponding deer-access macroplot, and termed this ‘historical herbivory intensity’.

To estimate the relative role of browsing compared to other environmental factors for shaping the beetle species assemblages, we included information on the environmental conditions at each pitfall trap, i.e. in the adjacent permanent vegetation plot in our analyses (Fig. 6). We used the vegetation characteristics investigated in paper I and paper II, and included the variables 'understory vegetation height' and 'abundance' of the following categories: bryophytes, ferns, grasses, herbs, dwarf shrubs, and tree saplings (≤ 50 cm). We also included information on soil moisture, nitrogen, and pH, as well as altitude in our analyses.

Figure 6. Illustration of pitfall traps in the macroplot (left). We collected ground-dwelling beetles with seven pitfall traps in each macroplot, placed adjacent to each permanent vegetation plot (middle). We protected each trap with a wooden roof, about 5–10 cm above the trap, to prevent litter to fall in, or rain to flood the trap (right). Photo: Lilleeng, M. S.

We investigated the role of both 'treatment' and 'current herbivory intensity' on the most common species (≥ 100 individuals in our samples). Due to zero-skewness in the abundances, we analyzed each species' response to browsing with negative binomial generalized mixed-effects models (glmmadmb, Skaug et al. 2016). Further, we related the two measures of browsing to the diversity measures species richness (alpha diversity) and evenness. Here, we applied linear mixed-effects models (Bates et al. 2015, Kuznetsova et al. 2016). We used Whittaker's index (Koleff et al. 2003) and compared these with 'permutest' procedures (Anderson et al. 2006) to estimate beetle assemblage similarity between the plots (beta diversity) in the two treatments. Next, we used ordination techniques (detrented correspondence analysis, DCA, and global non-metric multidimensional scaling, GNMDS, Hill and Gauch 1980, Minchin 1987) in combination with red deer browsing (treatment and current herbivory intensity) and other environmental factors to reveal the important gradients in the ground-dwelling beetle community in our study system. Finally, we used variation partitioning (Borcard et al. 1992, Økland 1999, 2003) to estimate the relative role of red deer browsing compared to the other environmental variables to explain structure and composition of the ground-dwelling beetle community. We based the variation partitioning on canonical correspondence analysis (CCA, ter Braak 1986) and Monte Carlo test (Oksanen et al. 2016).

6.5 Red deer browsing effects on other herbivores (paper IV)

To study the potential of red deer to induce a trophic cascade by modifying interactions between a key boreal plant species and an important insect group, we investigated red deer browsing and insect larvae herbivory in parallel and on their shared food plant, bilberry. We surveyed 3001 randomly selected bilberry ramets within the permanent vegetation plots (Fig. 3, Fig. 5) since 2001. In June 2001, five ramets in all vegetation plots were registered, while in 2006 three ramets in four out of the seven vegetation plots within each macroplot were registered. In June 2011, 2012, 2013 and 2016, we registered three ramets in each plot. On each ramet, we measured ramet height (cm), the number of annual shoots, and the number of flowers (Fig. 7). In 2001 and 2012, we additionally counted the number of leaves on each ramet, which allowed us to estimate the proportion of the available leaves that were defoliated (hereafter 'insect-chewed') by insect larvae. We counted number of insect-chewed leaves and number of deer-browsed shoots (Fig. 7) per ramet. We used the number of deer-browsed shoots to describe the gradient in deer-browsing intensity. As we for 2001, only had data on a five-level index, we transformed the number of deer-browsed shoots to this index in all analyses when the 2001-data was included. We binned the proportion of browsed shoots into the following categories: 'No' = 0%,'Light' = > 0–24.9 %, 'Moderate' = 25–49.9, 'High' = 50–74.9%, and 'Heavy' = ≥ 75% of annual shoots browsed, following Frelich and Lorimer (1985). With the ramet size measures, we estimated bilberry ramet biomass (drymass, gram) using a multiple regression model developed by (Hegland et al. 2010), which allows for non-destructive estimation of ramet size in the field. In early and late June 2012 and late June 2013, we also estimated abundance of Lepidoptera and Symphyta larvae in the understory vegetation by sweep netting each macroplot with a 25 cm diameter canvas net during day hours in dry weather. We counted and stored each larvae on 70 % ethanol. Thus, we obtained two estimates of herbivorous larvae abundances in the understory vegetation, at ramet (insect- chewing estimates) and macroplot (larvae abundance) scale, respectively.

We analyzed the effect of red deer browsing occurrence (exclosures vs. deer-access) and intensity on the following four responses: 1a) Number of insect larvae collected by sweep netting on the macroplot scale. This measure gave a snapshot of availability of larvae for, for example insectivorous birds; 1b) Number of insect-chewed leaves on the ramet scale. This measure provides information on the abundance of defoliating larvae from the whole season until the time of census; 2) Estimates of bilberry ramet biomass, which provides information on food availability for herbivorous larvae; and 3) larvae density.

We analyzed our responses with generalized linear mixed-effects models (lme4, Bates et al. 2015), negative binomial generalized linear mixed-effects models (glmmADMB, Skaug et al. 2016), and linear mixed-effects models (lmer, Kuznetsova et al. 2016) and accounted for spatial and temporal dependence between observation units with random effects. For this study we used R version 3.4.2 (R Core Team 2017).

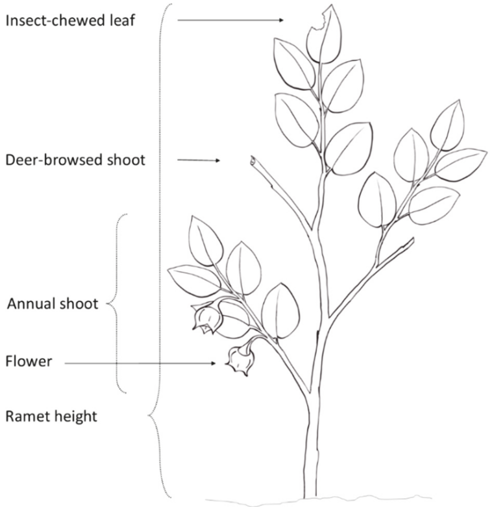

Figure 7. Illustration of a bilberry (*Vaccinium myrtillus*) ramet, and the measures we recorded in the field to estimate red deer browsing intensity, insect larvae herbivory, and to obtain a non-destructive measure of biomass. Illustration by R. Steen.

7 Results and discussion

7.1 Effects of red deer browsing on diversity and community ecology of the boreal forest understory vegetation (paper I and II)

We found that natural, but high, red deer browsing intensities can increase species richness of the forest understory (Paper I), towards a more homogeneous vegetation community (Paper II). Red deer browsing also favored short-lived species (Paper II). As expected, however, effects of browsing varied between plant species and functional groups, and some of the effects would not have been revealed in a short-termed study (Paper II).

Most of the plant species were robust towards variation in red deer browsing intensities, and 52 out of the 70 species in our study appeared both were deer had access and where they were excluded (Paper II). However, the ten species that only occurred in exclosures included the trees *Corylus avellana* and *Populus tremula* (Paper II). These are species that red deer selectively feed on (Mysterud et al. 2010). In general, all tree species were much less abundant were deer had access than in the exclosures (Hegland and Rydgren 2016). The youngest trees appeared to be protected against browsing by the surrounding field layer vegetation: Juvenile trees (height < 20 cm) performed better and became more species rich with increasing red deer browsing intensity (Paper I), likely because browsing opens up the understory vegetation and thereby increases the amount of light reaching the ground layers (Rydgren et al. 2004, Hegland and Rydgren 2016). However, few of these trees recruit to larger size classes, because of browsing (Hegland and Rydgren 2016). Kuijper et al. (2010) identified browsing as the single-most important factor that determines recruitment rates from tree seedlings to larger size classes. Although the study by Kuijper et al. (2010) was in a different forest type, the mechanisms are probably similar. Our findings suggest that certain tree species in the boreal forest may therefore depend on nurse plants (Garcia and Obeso 2003), or on fluctuations in deer densities to reach their reproductive stage.

Species unique to deer-access plots were the forbs *Viola riviniana*, *Maianthemum bifolium,* and *Veronica serpyllifolia* (Paper II), which are light-demanding species with small individuals that typically benefit from ungulate browsing (Evju et al. 2010, Boulanger et al. 2018a). Hegland and Rydgren (2016) showed that twice as many species benefitted from red deer browsing compared to those declining in numbers. We showed that overall, understory plant species richness increased with red deer browsing intensity, and that with an artificially high deer density, the richness slightly declined (Fig. 8, Paper I). Most of the functional groups responded positively towards red deer browsing intensity; species richness of tree-juveniles, forbs, ferns, graminoids, and mosses increased with increasing browsing intensity (Paper I).

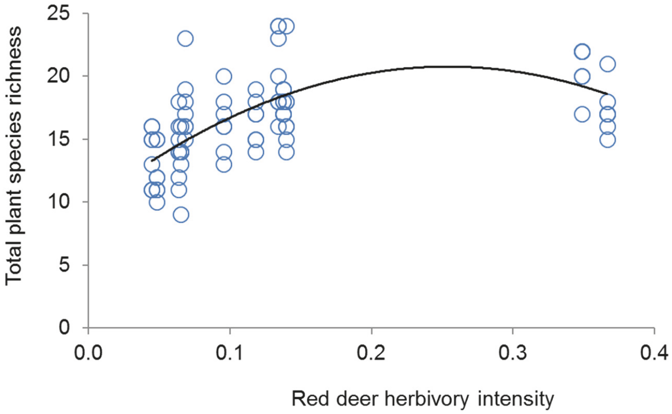

Figure 8. There was a unimodal relationship between red deer browsing intensity and total plant species richness in our study. The points to the right in this figure are observations from the red deer farm with extreme densities. Under typical densities for wild red deer in Norway, browsing increases the plant species diversity in the understory.

Red deer rarely consume weft- and carpet-forming mosses. Those species play key-roles in the boreal forests by buffering the temperature and flow of water and nutrients into the soil, which in turn may modulate seedling establishment of other species (Nilsson and Wardle 2005, Lett et al. 2017). The cover of these mosses is increasing in the northern hemisphere, likely because of climate change, as longer and milder autumns extend their growth period (Økland et al. 2004). However, reductions in the amplitudes of rodent population cycles may also partly explain the increase of some of these mosses (Rydgren et al. 2007). Our studies in Svanøy indicate that red deer can facilitate the growth and abundance of mosses by reducing vegetation in the field layer through browsing. Large herbivores can thus have potential to modify growth and abundance of mosses, an often overlooked functional group in ecology (Tanentzap et al. 2009).

Excluding red deer increased the temporal species turnover during the first five years of our experiment (Paper II), as expected when removing a disturbance (Beschta and Ripple 2009). After five years, temporal species turnover did not longer differ between exclosure and deer-access plots (Fig. 9, Paper II), which either reflects that intrinsic temporal turnover in a pine forest with and without red deer is similar, or that temporal turnover is lower in forests without deer. A longer time series of data (i.e. > 10 years) is required to fully understand this mechanism.

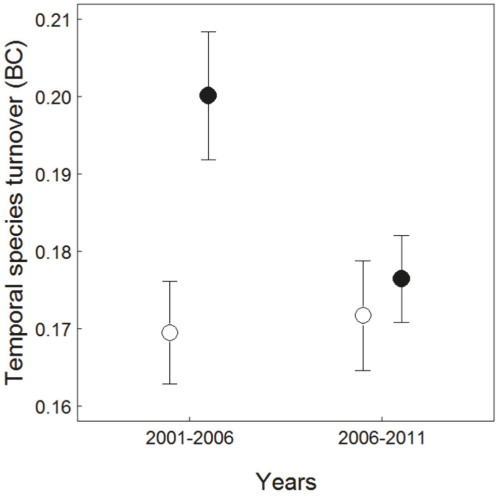

Figure 9. Mean (± SE) five-year temporal species turnover, measured by the Bray-Curtis dissimilarity index within exclosure (black circles) and deer-access (white circles) plots during 10 years of experiment.

Concurrent with increased temporal species turnover, red deer decreased the spatial species turnover (Fig. 10, Paper II), which homogenizes the forest floor. This effect was not significant five years after the experiment started, and it again highlights the importance of longer-termed studies. The mechanisms behind the browsing-induced biotic homogenization are likely a limitation of preferred species, and enhanced growth rates in browsing-tolerant and avoided plant species (Rooney 2009). Our studies indicate that future boreal forest landscapes with high densities of red deer will probably have similar, homogenized plant assemblages in areas used for browsing.

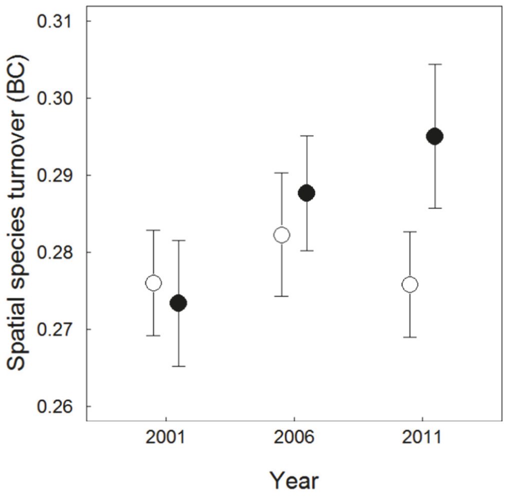

Figure 10. Mean (± SE) spatial species turnover, measured with Bray-Curtis dissimilarity index between plots (exclosures, black circles; deer access, open circles) within the same macroplots during the 10-year experiment.

In the ongoing biodiversity debate, it remains unclear if large herbivores are positive or negative for forest plant species diversity (e.g. Boulanger et al. 2018b, Fløjgaard et al. 2018). I suggest that providing general advice on how red deer affects biodiversity in the boreal forest is overambitious, as our studies pointed out that the browsing effects alone already depends on the focal plant species, density of deer, and the heterogeneity of co-occurring species. In addition, many other factors outside the scope of my study, such as, animal behavior, human perspectives and perceptions, hunting, large carnivores, productivity, and climate change also come into play (Proulx and Mazumder 1998, Ripple and Beschta 2004, Ciuti et al. 2012, Lone et al. 2015, Diekert et al. 2016).

7.2 Effects of red deer browsing on diversity and community ecology of ground-dwelling beetles in boreal forest (paper III)

While effects of red deer browsing on the understory vegetation can be relatively apparent, indirect effects on third parties, such as arthropod communities, are less obvious. We sampled 9733 beetles from 149 species on the forest floor in our blocks in Svanøy. We found strong evidence that red deer browsing was an important factor that structures the ground-dwelling beetle community (Paper III). Six out of seventeen beetle species that occurred with more than 100 individuals in the dataset showed a significant response towards red deer browsing, either by being more abundant ('winners', four species) or less abundant ('losers', 2 species) in deer-access plots compared to the exclosures (Fig. 11, Paper III).

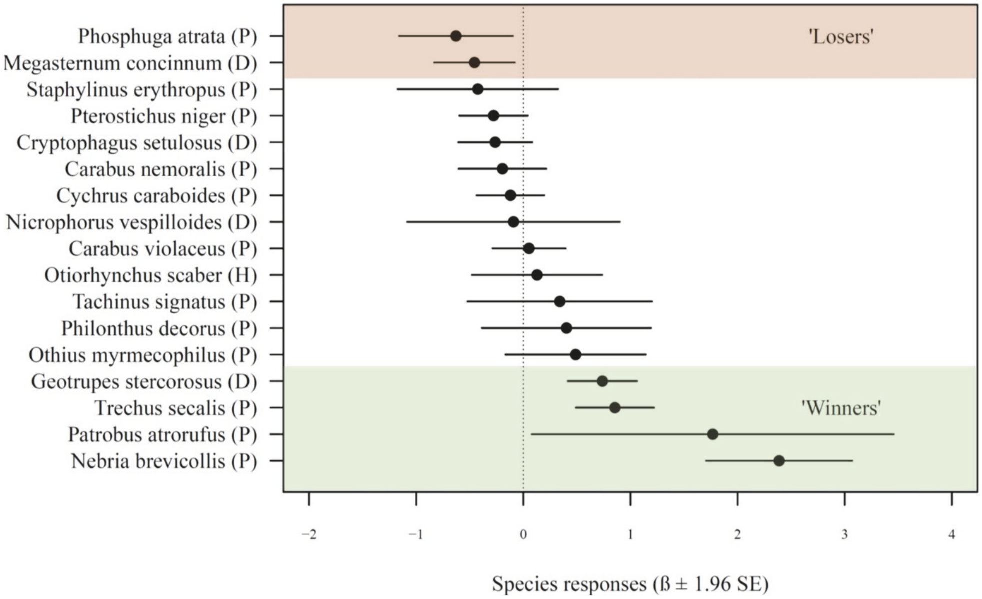

Figure 11. We tested numerical responses towards red deer browsing (exclosures vs. deer access) for seventeen ground-dwelling beetle species that occurred with > 100 individuals in the dataset. Six species showed a significant response, of which two were 'losers' (red) and four were 'winners' (green). The figure shows parameter estimates (± 1.96 SE) from mixed effects modelling of species abundance in deer-access plots vs exclosure plots. The functional role of each species is indicated after each species name (P = predator, D = detritivore, H = herbivore).

Our data did not reveal differences in species richness or evenness between deer-access and exclosure plots, or along the red deer browsing intensity gradient (Paper III), which concurs with Melis et al. (2006). However, other ungulates are often found to alter the richness of arthropods. Reindeer, for example, have been found to increase beetle species richness (Suominen et al. 2003), and moose have been reported to increase beetle abundances and decrease species richness (Melis et al. 2007). One possible explanation to why red deer may cause less change in beetle species richness compared to moose or reindeer can relate to selectivity of feeding. Red deer is an intermediate feeder, whereas moose and reindeer feed more selectively (Hofmann 1989, Adler et al. 2001), and thereby might have more profound effects on vegetation (Adler et al. 2001). However, the effect of browsing on vegetation is not necessarily a good predictor for the strength of the response of the arthropod communities (see review in van Klink et al. (2015)).

Another interesting divergence between the plant and ground-dwelling beetle communities was that while red deer browsing homogenized the distribution of plants (reduced beta diversity, Paper II), the beetle assemblages became more heterogeneous at the between-plot-scale (increased beta diversity, Paper III) (Fig. 12).

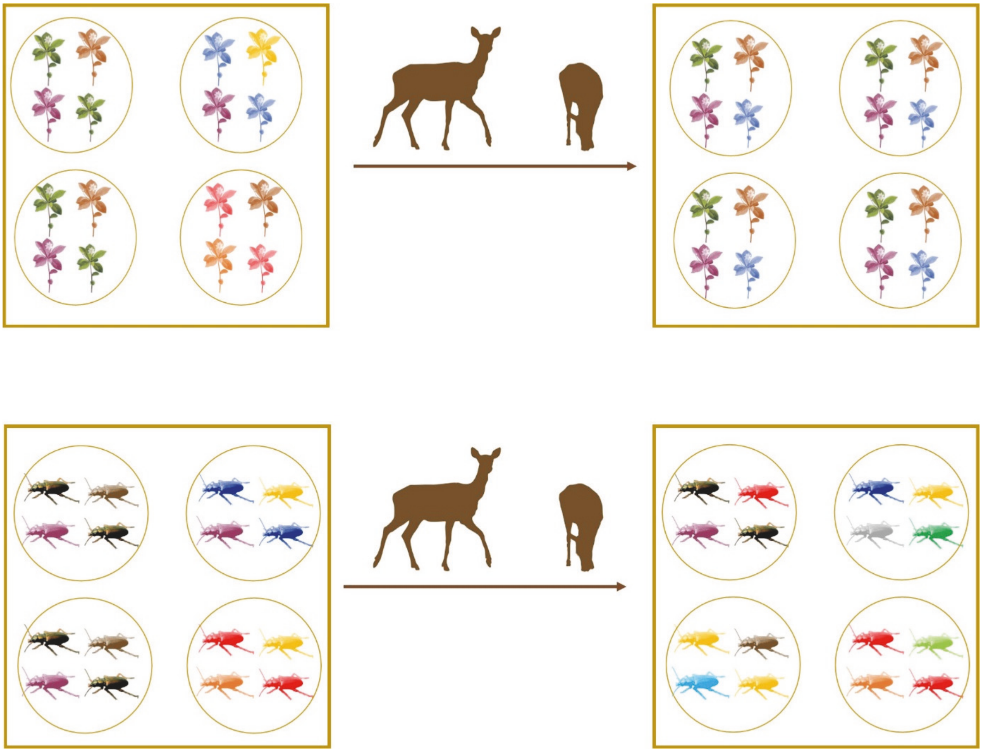

Figure 12. Illustration of how red deer browsing affects beta diversity differently in the plant and ground-dwelling beetle communities. Different species are illustrated with different colors. In this example, each circle with plants (upper panel) or beetles (lower panel) represents a plot where alpha diversity is 3 or 4. Beta diversity is the sum of the number of unique species between two plots. Here, I illustrate and compare an area without red deer (left panels) to a similar area, but with red deer (right panels). We found that red deer browsing homogenized the plant species assemblages, but made the beetle assemblages more heterogeneous (Paper II and III).

Measures such as species richness are easy to interpret, and may provide important information about ecosystems. However, using only a few univariate measures of diversity to investigate how specific factors affect an ecosystem or ecological community implies a risk of drawing incomplete conclusions. Here, our univariate measures of alpha diversity did not reveal strong red deer browsing effects on the beetle community. Using multivariate analyses (GNMDS), however, we revealed that red deer browsing was in fact an important determinant of the entire beetle species assemblage (Fig. 13, Paper III). We quantified the relative importance of red deer browsing and other environmental variables on the structure and composition of the ground-dwelling beetle community. Not surprisingly, variables related to soil characteristics (pH, nitrogen, moisture) and certain functional groups of vegetation (bryophytes, grass, herbs and dwarf-shrubs) were the most important factors for determining the distribution of beetle species (Paper III). This group of explanatory variables explained approximately 50 % of the total variation explained (FTVE), while red deer browsing intensity explained about 25 % of FTVE (Paper III).

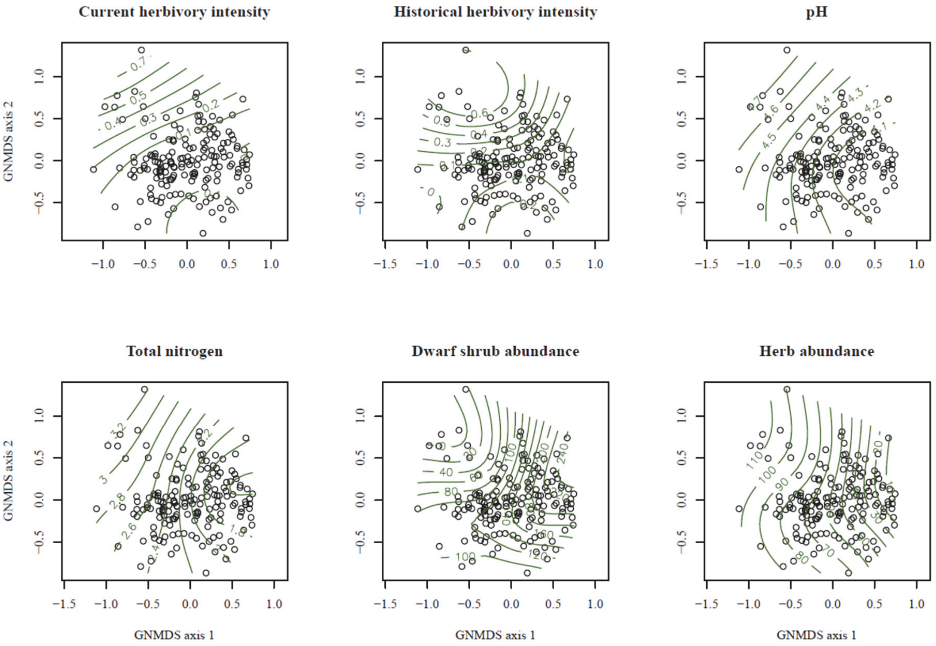

Figure 13. Isoline diagrams illustrate the relationship between the global non-metric multidimensional scaling (GNMDS) axis 1 and 2 and significant environmental variables ($p \leq$

0.05). Each circle represents one beetle trap. Raw explanatory variable values are indicated within the isolines.

7.3 Red deer browsing effects on other herbivores (paper IV)

Our study on indirect effects of red deer browsing on the herbivorous larvae feeding on bilberry suggests that red deer may limit the abundance of larvae. Using sweep netting as our sampling tool, we found 50% fewer larvae in deer-access plots compared to the exclosures (Fig. 14A, Paper IV). The number of insect-chewed leaves in deer-access plots were about one third of what we found in exclosures (Fig. 14B, Paper IV). This is consistent with the effects Baines et al. (1994) report from red deer browsing in Scottish pine forests, albeit that Baines et al. (1994) report an even stronger difference, probably because of higher deer densities in their study area. However, the larvae occur with multi-annual cycles in population densities (Berryman 1996, Selås et al. 2013), and direct comparisons between years and areas may not be relevant.

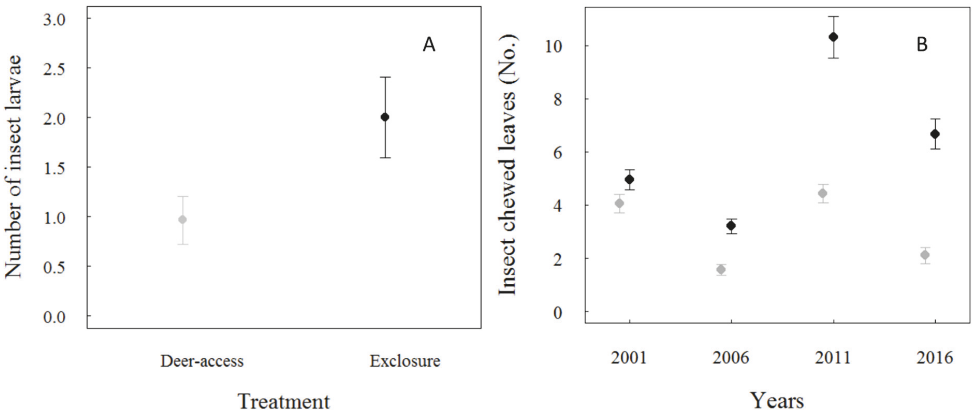

Figure 14. Mean (± SE) number of larvae per macroplot, caught by sweep-netting in 2012 and 2013 (A), and mean (± SE) number of insect-chewed leaves on bilberry ramets in 2001, 2006, 2011, and 2016 (B), in exclosures (grey) and deer-access (black) macroplots and plots, respectively.

The biomass of insect larvae is of critically importance for insectivorous bird species that depend on bilberry-feeding larvae for their survival and reproduction. For example, Lepidoptera larvae are, as the main food resource, essential for the survival of capercaillie (*Tetrao urogallus*) and black grouse (*Lyrurus tetrix*) chicks (Picozzi et al. 1999, Wegge et al. 2010).

We showed that the most relevant mechanism to explain the low number of larvae in deer-access plots compared to exclosures (Fig. 15A, Paper IV), was that bilberry ramet biomass was significantly lower in deer-access plots compared to the exclosures, most likely because of browsing. The average dry mass of bilberry ramets in deer-access plots were only one 9th of the ramet biomass within exclosures (Paper IV). Thus, other animal species that depend on bilberry as a food resource may experience strong competition by red deer browsing. Capercaillie chicks, for example, switch from a Lepidoptera dominated diet to a bilberry-dominated diet when they are about three weeks old (Picozzi et al. 1999, Wegge and Kastdalen 2008). This implies that red deer may limit food resources during various life stages of forest-dwelling grouse species like the capercaillie or the black grouse, in multiple ways. First, by reducing the abundance of bilberry-feeding insect larvae, the prime food of chicks, and later by reducing bilberry biomass, the prime food resource for juveniles and adults. How such indirect effects of red deer browsing influence the life history of third parties remains, however, unclear.

Finally, we showed that red deer browsing affected bilberry ramets beyond just biomass removal. Browsing-sensitive plants can respond to, and defend themselves against browsing, by inducing a chemical or physical defense (Gomez and Zamora 2002, Hester et al. 2006, Karban 2011). Insect herbivores are likely to be sensitive to chemical defenses (Nykänen and Koricheva 2004). Such defenses are difficult to detect in field experiments (Hegland et al. 2016). However, insect herbivory is typically considered as a proxy for ecologically effective chemical plant defenses (Hegland et al. 2016). We therefore assumed that the density of herbivorous larvae reflects the quality of the food plants. We found that larvae densities were higher on exclosure ramets compared to deer-access ramets (Fig. 15B, Paper IV), which indicates that either red-deer browsing reduced the food quality of bilberry ramets for other herbivores, or the higher biomass in exclosures had an additive effect to attract higher insect densities (Price 1991). However, we also found that the densities of larvae varied with red deer browsing intensity (Fig. 15B), with highest larvae densities detected at ramets that experienced a relatively high browsing intensity (Paper IV). Our findings indicate that red deer browsing may reduce chemical defense compounds in food plants, but that this quality increase is not sufficient if the bilberry biomass is below a certain level. Such a quality-quantity tradeoff is supported by the plant-stress hypothesis as proposed by White (1978).

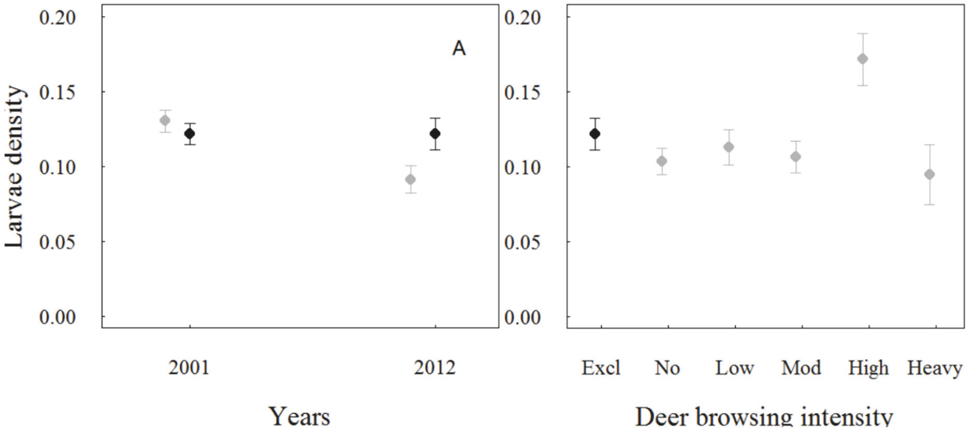

Figure 15. Mean (± SE) larvae density per ramet (number of larvae-chewed leaves/total number of leaves on ramet) of bilberry, in A) deer-access (grey) and exclosure plots (black) measured in 2001 and 2012 (the only years for which data on total number of leaves per ramet is available), and B) on ramets in deer-access plots exposed to different browsing intensities. In B) we include 'Exclosure' (the mean for 2012 to ensure that this point represents the treatment effect, while other categories are represented by the mean for 2001 and 2012), for comparison of unbrowsed ramets in deer-access plots and exclosure ramets.

Our results clearly show that red deer can induce numerical effects on third parties (Box 1), suggesting that red deer may induce trophic cascades that flow throughout food webs in the boreal forest ecosystem. Our results are not a surprising, as similar cervid induced mechanisms have been documented in several forest ecosystems (Allombert et al. 2005a, Allombert et al. 2005b). Maybe the most famous example comes from the Lamar Valley in Yellowstone, USA, where the reintroduction of the grey wolf (*Canis lupus*) induced a well documented trophic cascade (Beschta and Ripple 2009, Ripple et al. 2014). Prior to the reintroduction, elk (*Cervus canadensis*) were overabundant, limited the riparian vegetation, and extensively used open habitat types (Beschta and Ripple 2016). After the wolves were reintroduced, the elk population rapidly decreased, and the elk started to avoid open terrain (Mao et al. 2005). Following this, the riparian and open habitat vegetation restored, leading to increases in songbird abundances (Berger et al. 2001). Furthermore, the reduction in elk resulted in population growth in other herbivores as for example bison (Ripple and Beschta 2012). We expect that changes in population size and distribution of red deer have the potential to induce similar cascades in boreal ecosystems, although perhaps a bit less spectacular.

Box 1. Summary of main results

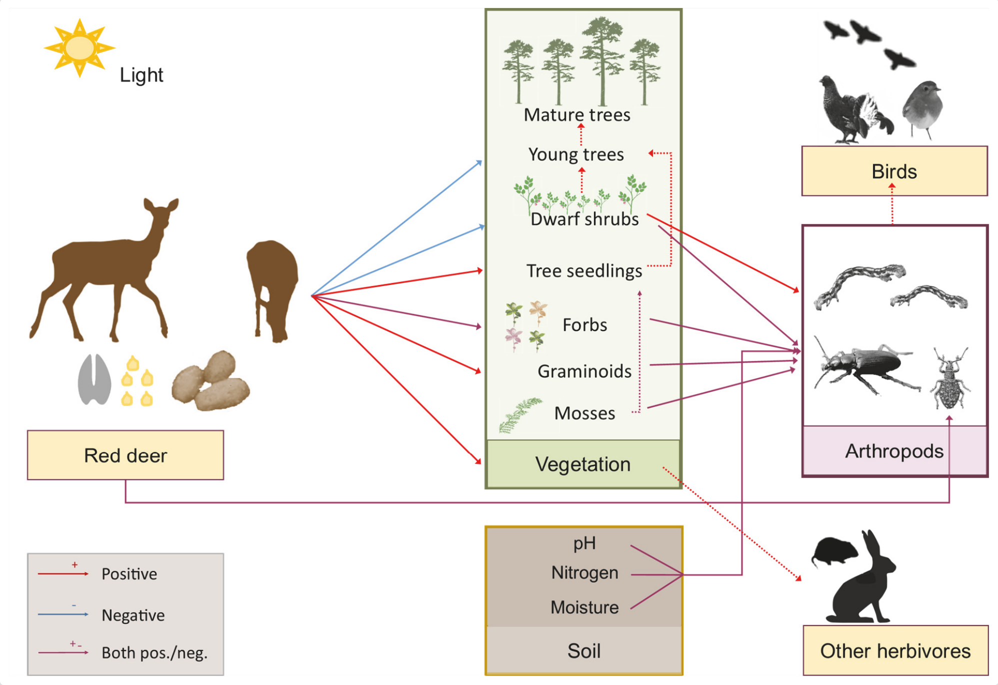

Illustration of the central findings. Significant relationships that we found in the studies included in my thesis, are shown with solid lines. Relationships that we discuss are indicated with dotted lines. Red = positive effects, blue = negative effects and purple = significant effects, both positive and negative. For vegetation we show only the most central growth forms.

8 Perspectives

I have studied the role of a very common ungulate, red deer, in one of the most widely distributed terrestrial biomes, the boreal forest. Virtually all the species I surveyed in this thesis are common, and one may question if this study is therefore a relevant one. In a paper published in Science, Kevin J. Gaston (2010), however, emphasized the ecological role of the commons: "the importance of naturally common species – those that are abundant and widespread – in shaping the world around us is so blatant that it is easily overlooked". In a thesis focusing on biodiversity, assessing the value of common species may seem somehow contradictive, but common species provide the fundament that many food webs and ecosystem services depend on. For example, the most common species often direct spatial patterns of species richness and turnover (Gaston et al. 2007), and habitat degradation and fragmentation mainly affect common species (Gaston 2010). A study on European birds shows a clear decline in total bird biomass and abundance, common species take the 'lion share' of that, and the abundance of rare species generally even increases (Inger et al. 2015). Population declines of common species may trigger disproportionally large ecological cascades, due to the numerous biotic interactions these common species are involved in (Gaston 2010). While it remains important for conservation and management to study rare and endangered species, I suggest that researchers also keep focus on the common ones, provided their immense ecological role.

Future ideas

When doing science, our aim is to answer specific questions. On the route to answer these questions, several new questions usually appear, and we often start realizing how little we actually know. Some of the questions that arose during my PhD project and that I would like to explore in the near future include:

- *The commons are important, but what happens with the rare?* In my thesis I have focused mainly on effects of red deer browsing on the community level for insects and plants, and we modelled 'winners' and 'losers' of species of the beetle community that had sufficient data. Studying rare species typically comes with several methodological challenges concerning zero-inflation. Relatively new statistical tools, such as zero-inflated mixed effects models (Zuur et al. 2012) or eHOF (Jansen and Oksanen 2013), are now available to overcome such challenges, and will most likely be useful in my future studies.

Knowledge about browsing-specific responses of rare beetles and plants will be valuable for nature conservation and management.

- *Quantifying all red deer-induced pathways?* Recently, Vandegehuchte et al. (2017) demonstrated mammalian herbivore induced trophic cascades, that link herbivory with several trophic levels of arthropods with elegant structural equation models. Structural equation models allow the simultaneous analyses of several mechanisms within complex networks of relationships, and can identify causality within such networks (Grace 2006). I would like to perform such structural equation modelling where I exploit all the data I have collected at Svanøy (abiotic factors, vegetation richness, composition and structure, and herbivore, detritivore, omnivore and predatory arthropods), to quantify how red deer affect each relationship between these components of the boreal forest understory.

- *Browsing induced chemical changes in bilberry leaves.* In paper IV we found that Lepidoptera and Symphyta larvae preferred the bilberry ramets that had been exposed to high browsing pressure from red deer above ramets that were exposed to both less and more red deer browsing. I suspect that the larvae's food choice reflects that these selected ramets contain the best nutritional quality. We plan to investigate this further in the lab, together with plant physiologists and with material from Svanøy.

- *Red deer on a larger scale.* Scandinavian red deer spend the most of their time within the boreal forest, which justified the design of my study. However, their foraging activity occurs mostly in open terrain and along habitat edges (Godvik et al. 2009). To fully understand how variation in red deer densities affect their environment, a broader research design, incorporating other habitat types (e.g. young forest, pastures, mires) would be desired. A broader approach would also allow to investigate the ecological interplay between habitat types, in which red deer functions as a connecting vector (e.g. nutrient redistributions, directed zoochory).

- *Life history, population dynamics, and evolution.* Within my project, I showed how red deer can affect species abundance and ecological communities, and can induce ecological cascades. However, they can also affect life-history parameters and population dynamics of certain species, and thus induce evolutionary change, as pointed out by Hegland et al. (2010) for bilberry. In the field, I observed how red deer browsing seem to affect life histories of *Luzula sylvatica*, as this species occurred with much fewer flowers outside the exclosures than inside (Fig. 16). It is also interesting to study whether red deer can have such effects on non-browsed species, such as bryophytes. One bryophyte well suited for such a study, is *Hylocomium splendens*, of which the population dynamics are already relatively well understood, with for example simulations of rodent grazing (Rydgren et al. 2001).

Figure 16. Illustration from the field: Red deer browsing potentially affects life history strategies of several of the organisms in the boreal forest. To the left on this picture is vegetation accessible to red deer. On the right side of the post, the vegetation is fenced in, and has not been exposed to red deer browsing since early 2001. *Luzula sylvatica* is abundant both inside and outside the exclosure, but the number of flowering individuals is strikingly less were red deer have access, indicating that red deer may affect the species' reproductive potential. Photo: Lilleeng, MS

Management implications

The findings in this thesis illustrate that red deer can induce change in various ecological communities of the boreal forest. They restructure the forest understory, which can influence several organisms and functional groups. Ungulates are inherent parts of the boreal forest, but many populations in the northern hemisphere do not show natural fluctuations, due to hunting and/or the lack of large carnivores. In many areas, it is a management goal to keep the productivity of the ungulate populations high and stable, to optimize venison harvest and sale of hunting licenses. There is an ongoing debate of the role of ungulates as drivers of forest dynamics, and at which level the populations should be maintained. I suggest such levels are context dependent varying with local red deer densities, ecosystem condition, and management concerns.

Several examples exist that illustrate how ungulates can limit the abundance of red listed species, such as the yew (*Taxus baccata*), limited by roe deer (*Capreolus capreolus*) in Norway (Mysterud and Østbye 2004), or *Trillium* spp., which became extinct in Minnesota, USA, because of by white-tailed deer (*Odocoileus virginianus*) (Augustine and Frelich 1998). The results from my thesis indicate that red deer can limit or facilitate individual species. Therefore, red deer density should be considered as an important factor in the management of browsing sensitive plant and insect species, or habitat types.

A new challenge for ungulates and their ecosystem

Ungulates in Scandinavia and Europe are currently facing a new challenge, with potentially dramatic consequences for many populations. In March 2016, the first detection of chronic wasting disease (CWD) was discovered outside North America, in wild reindeer in Nordfjella in Norway (Benestad et al. 2016). Later, CWD was found in two moose (2016) and one red deer (2017) individual, also within in Norway, but far away from the reindeer population. In 2018, CWD was also detected in a moose in Finland. After decisions from the Norwegian Government, the reindeer population of 2000 animals is now completely eradicated (Mysterud and Rolandsen 2018). The entrance of CWD and other diseases such as African swine fever (Mysterud and Rolandsen 2018) is a severe threat to ungulates in Europe and maybe we are now facing a tipping point in the management of large ungulates. From North America we have seen that CWD can threaten populations to go extinct (Edmunds et al. 2016). It is a scary, but not even completely unrealistic picture (e.g. Nordfjella) – ecosystems without their native large ungulates. Evidently, such ecosystems would experience rapid ecological change throughout most, if not all, ecological communities.

9 Acknowledgements

I would like to thank my three supervisors **Stein Joar, Knut** and **Stein** for the way you have guided me through this PhD, and I have always felt that you have prioritized my questions. Thank you **Stein Joar** for choosing me as your PhD student, even though you so precisely predicted, while we were sitting around the fire by Kvalstadvannet after one of the first field work days, that you expected me to have at least two maternity leaves during my PhD! You are such a generous, social, and positive person, and that is reflected in how you supervise, and how you write science. I am very grateful for how you have been supporting me during these years. Eagle eye **Knut**! Thank you for the low threshold policy you have for all my questions! You have shared your knowledge and invested so much time for me, I will always be grateful. You know this, but your ability to spot small details are very valuable for everyone working together with you. Thank you **Stein**, for always giving so quick feedback on my manuscripts. Your eye for the larger ecological lines have made our team complete.

I want to thank the extended EcoDynDeer-team. **Eelke**, thanks for teaching me IPM and welcoming us in Nijmegen and Radboud. I miss your biking lanes! I look forward to continue to work with you. Thanks also to **Rune** for discussions about methods, it was really nice to have you on the team for the beetle-paper. Thanks to field assistants **Torbjørn**, **Steinar**, **Fredrik**, **Tess,** and **especially Carolin** and **Agnes**, we have walked far for reindeer work before, and I am very happy that you could join on Svanøy too.

I am very grateful to **Johan Trygve** and **Norsk hjortesenter** at Svanøy for making this study possible, and providing me with office space and practical help whenever I needed you. Thanks for inviting me and my assistants to exclusive dinners at Hovedgården. I learned a lot about red deer from you, and from your deer themselves too.

Thanks to **Joachim** and **Mark** for nice stats discussions and for good teaching cooperation. I also want to thank **Vidar** for valuable comments to my mid seminar.

Inger, **Tarald**, **Liv Norunn**, **Anne**, **Denise**, it was nice to work with you in Sogndal. **Jacob** Yde og Stein Joar, the coffee meetings in the hallway was really nice, I miss you! Thanks to **Anne L**, **Inga**, **Anne T**, **Marian**, **Ingrid**, **Andre** and **Håvard** in Sogndal for the off-piste powder skiing fun, the hikes up small hills and high peaks, discussions and dinners – I wish we did more of all that!

I want to thank, **Sjur**, **Ågot** and MINA, NMBU for providing me work space and facilities here in Ås. **Leif Egil**, getting the opportunity to teach your courses was a really nice challenge for me, I wonder if I will ever again have such interested students! Thanks to **Tone** for hay and good conversations, **Ronny**– thanks for the nice illustration. Thanks to **Jan** and **Susi** for sharing office with me and letting me disturb you.. **Jonathan** you are a unique person. I do not think you know how important you are for so many people.

Thanks to **Andrés**, **Richard**, **Pierre**, **Cyril**, **Mahdieh**, **Eshan**, **Joe**, **Hailu** and **Jon** for pulling me out of the office for the fun lunchbreaks. **Kate**, thanks for language advice!

Thanks to all the students that I was so lucky to lecture for – all the discussions and interesting questions you challenged me with was fun and I learned a lot from you.

Simen, Anneli, Matt, Annelene, **Ane, Hanne, Therese, Håvard.** Some of you I studied with, some I just climb with, and some I have always known.. Even if we don't always meet so often, you are always there with me, and we always have fun when we play together.

I send a big thanks to **Chris**, **Eric**, **Mamma** and **Pappa** – you have also contributed to this PhD! You have been babysitting while I traveled for courses, on field work and in very busy periods. Thanks for always answering with a yes when we needed you!

To my beloved ones. I am so proud of our family. **Matilda** and **Vilja** – my two stars! Without you I think I would have drifted away in stress this last stretch of the PhD-period. You have reminded me of the relevance of my office challenges, and brought so much positive energy and laughter into every day. **Sam**, you have been my supporting rock through this PhD, you always believed in me and my skills – even when *I* did not. You are such a talented researcher with a vivid creativity, precision, eye for good design and research questions, and writing skills – and therefore you are my idol. You made our family's everyday life go around this last period. Thank you for all the cooking! Now there will be a lot of fishing!

Marte, Ås Juli 2018

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Paper I

Forest Ecology and Management 310 (2013) 267–274

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Old-growth forest floor richness increases with red deer herbivory intensity

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ARTICLE INFO

Article history:
Received 5 July 2013
Received in revised form 15 August 2013
Accepted 16 August 2013
Available online 13 September 2013

Keywords:
Browsing
Cervus
Disturbance
Diversity
Functional group
Grazing

ABSTRACT

Herbivory is one of the most important biotic disturbance types globally and is important for community structure and composition through species filtering. In northern forest ecosystems the population densities of wild-ranging ungulates, which are managed through hunting, have reached historically high numbers. Conservation concerns frequently arise, both in media and scientific literature. One key question is whether increased deer densities negatively affect biodiversity and whether management should implement reduction in deer densities. Few studies have addressed wild herbivores-plant richness relationships using a full length gradient of herbivory. Such gradient approach where herbivory is studied from very low to very high intensity, may enable us to develop operational management guidelines for deer densities We recorded the ungulate herbivory intensities on the island Svanøy in west Norway across 10 years and related this to the present plant richness of an old-growth pine-forest system, recording all plant species groups of the forest understory. The herbivory intensity-plant richness relationship followed a unimodally peaked curved, but plant richness was lower only at forest sites with artificially high red deer herbivory. Overall, the herbivory-richness relationships of functional groups fitted expectations in that the richness of low-growing functional groups as forbs, graminoids and mosses all increased within natural levels of herbivory intensities, whereas the richness of the taller growing woody species of the forest understory, dwarf-shrubs and young trees, decreased along the intensity gradient. We validated the gradient approach by experimental exclosure data. Management for relatively high deer densities may benefit the overall understory plant richness of such forest ecosystems at the expense of richness of woody plants. We suggest that the herbivory-induced reduction of the understory woody layer is the key to understand the overall increase in plant species richness.

1. Introduction

Globally, herbivory by large grazers is one of the most important biotic disturbance types that influence community composition and structure (Diaz et al., 2007) and in many cases it is a disturbance type that is influenced by management decisions. In northern forest systems wild free-ranging ungulates are often a major determinant of plant community structure, composition and dynamics (Pastor et al., 1988; Suzuki et al., 2013) and populations can be partly controlled by hunting based management. The populations of large, wild ungulates such as red deer (*Cervus elaphus*) and moose (*Alces alces*) have expanded and grown rapidly for several decades in Scandinavia, Europe and Northern America, often to concern of conservationists (Côte et al., 2004). The increasing population densities may create a disturbance regime for northern forest ecosystems to which they are not evolutionary adapted (sensu Milchunas and Lauenroth, 1993). On the other hand, historical population levels are largely unknown, but the increasing cervid densities have mainly been a response to lower livestock numbers in forested areas, increasing forest cover and improved hunting management during the last millennia (e.g. Putman et al., 2011). Whether the present population densities are normal or not there is a current need for operational knowledge on how wild, free-ranging ungulates affect northern forest community composition.

Studying ecological interactions along gradients of environmental stress represent a powerful way to develop knowledge under realistic ecological conditions as well as operational guidelines in nature management (e.g. Brooker et al., 2006; Stewart et al., 2006, 2009). One approach to this has been by applying the intermediate disturbance hypothesis to a given disturbance-richness relationship (IDH; e.g. Grime, 1973; Connell, 1978). The hypothesis

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http://dx.doi.org/10.1016/j.foreco.2013.08.031

predicts that the richness of species should be greatest when the intensity, frequency or size of a disturbance is at intermediate level (Svensson et al., 2012; Fox, 2013). Too much disturbance means that long-lived species will not survive and too little disturbance results in competitive exclusion of pioneer species (e.g. Shea et al., 2004). The hypothesis has been criticised for low precision in explaining diversity patterns and because of its relative character (Mackey and Currie, 2001), i.e. what is intermediate? Nevertheless, the hypothesis can act as a theoretical background to a gradient approach in ecology dealing with herbivory, both as it introduces herbivory as a disturbance as well as predicting that species richness will follow a unimodally peaked relationship with, for example, herbivory intensity. A recent review showed that the intermediate disturbance hypothesis was indeed successful in predicting disturbance-diversity relationships when, according to the original hypothesis, testing is done with richness and not abundance based diversity indices as response variable (Svensson et al., 2012).

Many other disturbances that influence plant communities, such as storms and fires, are non-selective (Laliberté et al., 2013) and outside the direct influence of humans. On the contrary, herbivory by domestic and wild herbivores are both selective (Augustine and McNaughton, 1998) and among those ecological factors that can partly be controlled by managers. Therefore, herbivory disturbance by large herbivores may have complex influence on community composition and can interact with different parts of the species pool in contrasting ways. Which plant traits are advantageous in a given plant community is most often an interplay between tolerance and avoidance (Augustine and McNaughton, 1998), which may also change competitive interactions among plants (Hester et al., 2006). Most studies show that both the richness and abundance of woody vegetation may decline when herbivory from ungulates becomes more intense (reviewed by Gill, 2006). Also, plants with a short growth form have an advantage in grazed landscapes (Diaz et al., 2007; Evju et al., 2006), and this may be even more prominent in forest ecosystems as large herbivores may selectively utilise taller understory plants, especially during wintertime (Danell et al., 2003). Herbivory may thus increase the total species richness of the lower growing non-woody species if herbivores selectively decrease woody abundance and richness (c.f. Paine, 1966).

Surprisingly few studies have addressed the effect of herbivory on plant diversity by large free-ranging herbivores in natural systems within long gradients of herbivory disturbance (but see Stewart et al., 2006, 2009). For example, in reviews of the intermediate disturbance hypothesis (Mackey and Currie, 2001; Shea et al., 2004; Svensson et al., 2012) the few studies on large animal herbivory deals with livestock in grasslands. Experimental simulation of full length gradients of herbivory intensity may be challenging, because it is difficult to obtain reliable data on intensity gradients of wild animal herbivory. In this study we used 10 years of monitored herbivory intensity by the most numerous wild ungulate, red deer, in the most common forest type in Norway, as model system to examine present spatial patterns in plant species richness. We validated the herbivory gradient approach using experimental exclosure data. The effect on community composition is likely to be an effect of herbivory intensity which may filter species according to their adaptations to herbivory and competition (Augustine and McNaughton, 1998; Suzuki et al., 2013). Specifically, we asked whether variation in red deer herbivory intensity could explain the variation in plant species richness, both in total and for functional groups of this forest ecosystem (e.g. trees, dwarf-shrubs, various field plant groups and bryophytes). The results have the potential to guide ecosystem management of such large free-ranging grazers. We expected that (1) overall species richness will show a unimodally peaked-relationship with disturbance intensity, and (2) richness within low-growing functional groups will have a positive response to herbivory in contrast to the richness within the taller-growing woody groups.

2. Materials and methods

2.1. Study area and study design

The study was carried out in 2001 to 2011 on the 11 km^2 island Svanøy at the western coast of Norway (61°30N, 5°05E). Svanøy is situated in the boreonemoral zone and old-growth forest vegetation dominated by pine (*Pinus sylvestris*) and an understory dominated by Ericacea dwarf-shrubs covers most of the island. Twelve study sites were located within old-growth pine-bilberry forest, according to a vegetation map (Skogen and Lunde, 1997), and spread across the island on elevations from 20 to 140 m during wintertime 2000–2001 (see also Hegland et al., 2005 for more details). The study sites can be viewed as communities and all sites as a meta-community. A macroplot of 9 × 9 m was located at each site adjacent to a deer exclosure (see also model validation). We randomly placed seven permanent plots of 1 × 1 m on flat ground at least 0.5 m from the closest tree within the macroplot. Tree height and canopy openness showed relatively little variation between sites (pers. obs.). The sites experienced herbivory intensities varying from very low to extremely high (Fig. 1; see also Data collection). Ten of the sites were situated in forest with wild free-ranging red deer and data suggest they cover a natural variation from very low to naturally high herbivory intensities (see 2.2). Two sites were located within the forest areas of a deer farm representing deer densities at artificially high levels that would represent a population level beyond carrying capacity because these animals receive supplementary feeding. Thus, our data represents a gradient in herbivory intensity.

Red deer, *C. elaphus*, is a forest-dwelling mixed-feeder ungulate species. It has been speculated that the period from ca. 1995 until today has experienced the greatest post-glacial densities of red deer in Norway. In this period 20,000–40,000 deer has been harvested nationally per year (e.g. Statistics Norway, 2009) corresponding to >1 deer harvested per km^2 forest area in the study county Sogn og Fjordane (Solberg et al., 2012). The dense population of red deer at Svanøy is likely to be representative for most areas in western Norway (Hegland et al., 2010). Assuming that about 20% of the population is culled each year implies that deer numbers are on average 5–6 animals per km^2 productive forest area in the county. Absolute densities of forest-dwelling cervids are difficult to accurately establish and population estimates used for management of wild-ranging forest ungulates in Norway are generally index-based (e.g., Mysterud et al., 2007).

2.2. Data collection

We recorded plant species richness in each of the seven permanent plots per macroplot in 2011, except for understory trees (20–300 cm) which were recorded on the 9 × 9 m macroplot-level. All plant species in the understory layer were sampled: (1) understory trees (ca. 20–300 cm); (2) tree juveniles (trees < 20 cm); (3) dwarf-shrubs (here Ericacea); (4) forbs; (5) graminoids (Poaceae, Juncaceae and Cyperaceae); (6) ferns; (7) mosses and (8) liverworts.

We recorded red deer browsing on the dominant winter forage plant bilberry, *Vaccinium myrtillus*, and used this as basis for estimating herbivory intensity of red deer. Bilberry is highly abundant in boreal forests, it is intermediately preferred by red deer (Mysterud et al., 2010), but both individual plants and populations survive rather well even at high intensities of browsing and accordingly

Fig. 1. Photographs showing from left to right: an intensive herbivory farm-forest site with the exclosed macroplot as background, a typical forest site with moderate herbivory intensity including a permanent 1 × 1 m plot for species recordings, and a low-intensity herbivory forest site.

bilberry is a good indicator plant for herbivory intensity (Hegland et al., 2010; Mysterud et al., 2010). Although the level of bilberry browsing largely estimate autumn-to-spring herbivory, red deer in Norway has been found to use the winter ranges on average 8 months of the year (Bischof et al., 2012), and browsing on bilberry correlate strongly with other indices of population densities such as winter-spring pellet counts or autumn harvest data (Mysterud et al., 2010). We therefore believe that level of bilberry browsing is a suitable proxy for the herbivory intensity at individual sites.

As changes in plant species assemblages occur at relatively slow pace in these northern forest systems, we need to monitor herbivory intensity on a sufficient time scale. We performed sampling in June of 2001, 2006, and 2011 within the permanent plots to acquire a measure of red deer herbivory intensity that included a timeframe that could result in present-time plant community composition. The browsing level was measured on a scale from 0 to 4; 0: no browsing, 1: >0–24.9% of annual shoots clipped, 2: 25–49.9% of annual shoots clipped, 3: 50–74.9% of annual shoots clipped, and 4: >75% of annual shoots clipped. In 2001 five randomly selected bilberry ramets in each of the seven permanent plots per macroplot was measured, but because of time constraints we only sampled three ramets in a random selection of four of the seven permanent plots per macroplot in 2006 and three ramets in each of the seven permanent plots per macroplot in 2011. The varying sampling effort did not influence the variance strongly (SD: 0.16 in 2001, 0.18 in 2006 and 0.25 in 2011). We also obtained biometric measures (see Hegland et al., 2005 for details) of the sample ramets. The herbivory intensity was calculated as the browsing level divided on the plant height. To further confirm that this index reflected red deer herbivory intensity, we correlated the variable with the frequency of faeces groups sampled in 2001, 2006 and 2011 in 100 1-m^2 square plots randomly distributed within a radius of 100 m around each site. There was a strong association ($r = 0.94$, $N = 12$, $p < 0.001$) between these independent measures. Although these variables were obtained on different scales the correlation strengthens the assumption that the herbivory intensity could be described using the browsing level on bilberry ramets divided by plant height. The measure has the advantage that it was obtained at the same scale as plant species richness and is more robust than the density indicator represented by faeces as it is not confounded by, for example, weather dependent decaying rates (e.g. Putman, 1994). Fig. 1 shows examples of the visual difference among sites with high, intermediate and low herbivory intensities.

2.3. Data analysis and model validation

To investigate the relationships between plant species richness and herbivory intensity we used linear mixed effects models. Plots were nested within sites and accounted for in the random effects using R 2.15.0 (R Development Core Team, 2013), library nlme (Pinheiro and Bates, 2013) and lme4 (Bates et al., 2011). To test whether relationships between herbivory intensity and plant richness showed a unimodal peak or were linear within the studied herbivory gradient we first included a quadratic component of the mean herbivory intensity index (at site level) before we tested a linear relationship and compared models using AIC-values. We used total plant species richness and richness within functional groups (at plot level) as response variables. In the total plant richness model understory trees (<20 cm) were not included as they were sampled on site level. The understory tree model was hence not nested. As the red deer farm sites represent artificially intensive herbivory we also ran models without these sites when quadratic models were selected to test whether quadratic relationships were merely caused by these extreme disturbance conditions.

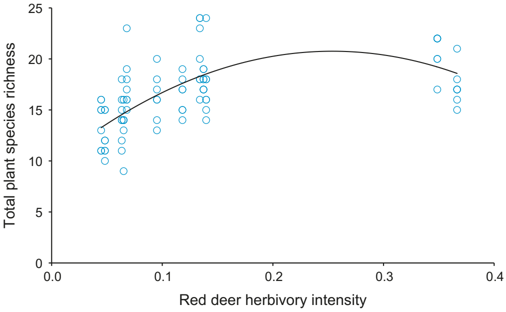

Fig. 2. The relationship between red deer herbivory intensity index and total species richness of the forest understory at Svanøy, western Norway. Line is shown for significant relationships of the selected model (quadratic), but do not take the random effects from the mixed effects modelling into account.

Table 1
Linear mixed effects models that explained plant species richness as a function of red deer herbivory intensity and herbivore exclosures (experimental validation models).

Richness variable	Gradient in herbivory intensity					Experimental validation model: herbivore exclosure				
	Predictor	Coef	SE	DF	P	Variable	Coef	SE	DF	P
Total richness	Intercept	9.71	1.75	72	<0.001	Intercept (herbivore 01)	15.61	0.67	332	<0.001
	Herbivory intensity	86.99	24.46	9	0.006	Herbivore 06 vs 01	0.27	0.27	332	0.318
	Herbivory intensity2	−171.36	57.39	9	**0.015**	Herbivore 11 vs 01	0.88	0.27	332	**0.001**
						Main effect 01	0.23	0.4	155	0.569
						Exclosure 06 vs 01	−1.02	0.39	332	**0.008**
						Exclosure 11 vs 01	−1.19	0.39	332	**0.002**
Trees (20–300 cm)	Intercept	3.3698	0.45		<0.001	Intercept (Herbivore 01)	1.58	0.36	55	<0.001
	Herbivory intensity	−9.479	2.63		**0.005**	Herbivore 06 vs 01	0.50	0.47	55	0.287
						Herbivore 11 vs 01	0.50	0.48	55	0.287
						Main effect 01	0.58	0.49	55	0.215
						Exclosure 06 vs 01	1.17	0.66	55	0.081
						Exclosure 11 vs 01	1.42	0.66	55	**0.036**
Tree juveniles (poisson)	Intercept	−0.02	0.17		0.923	Intercept (Herbivore 01)	0.06	0.13		0.622
	Herbivory intensity	1.78	0.86		**0.038**	Herbivore 06 vs 01	−0.06	0.15		0.709
						Herbivore 11 vs 01	0.16	0.14		0.259
						Main effect 01	−0.08	0.15		0.599
						Exclosure 06 vs 01	−0.06	0.22		0.797
						Exclosure 11 vs 01	0.02	0.2		0.914
Dwarf-shrubs (poisson)	Intercept	1.16	0.12		<0.001	Intercept (Herbivore 01)[a]	2.94	0.25	332	<0.001
	Herbivory intensity	−1.69	0.79		**0.033**	Herbivore 06 vs 01	−0.19	0.07	332	**0.007**
						Herbivore 11 vs 01	−0.35	0.08	332	**<0.001**
						Main effect 01	0.24	0.1	155	**0.027**
						Exclosure 06 vs 01	0.04	0.1	332	0.721
						Exclosure 11 vs 01	0.14	0.1	332	0.154
Forbs	Intercept	0.80	1.31	72	0.544	Intercept (Herbivore 01)	3.70	0.38	332	<0.001
	Herbivory intensity	44.60	18.09	9	0.036	Herbivore 06 vs 01	0.17	0.12	332	0.185
	Herbivory intensity2	−105.17	42.16	9	**0.034**	Herbivore 11 vs 01	0.06	0.13	332	0.636
						Main effect 01	0.05	0.18	155	0.796
						Exclosure 06 vs 01	−0.21	0.18	332	0.228
						Exclosure 11 vs 01	−0.51	0.18	332	**0.004**
Graminoids (poisson)	Intercept	0.53	0.12	4.40	<0.001	Intercept (Herbivore 01)	0.70	0.11		<0.001
	Herbivory intensity	2.09	0.59	3.51	**<0.001**	Herbivore 06 vs 01	0.12	0.10		0.234
						Herbivore 11 vs 01	0.11	0.10		0.299
						Main effect 01	0.10	0.10		0.348
						Exclosure 06 vs 01	−0.18	0.15		0.227
						Exclosure 11 vs 01	−0.30	0.15		**0.048**
Ferns (binomial)	Intercept	−3.32	1.06		0.002	Intercept (Herbivore 01)	−4.35	0.94		<0.001
	Herbivory intensity	39.83	13.97		0.004	Herbivore 06 vs 01	1.34	0.57		**0.02**
	Herbivory intensity2	−98.93	32.78		**0.003**	Herbivore 11 vs 01	1.91	0.58		**<0.001**
						Main effect 01	0.30	0.87		0.735
						Exclosure 06 vs 01	0.41	0.85		0.629
						Exclosure 11 vs 01	−1.72	0.84		**0.04**
Mosses	Intercept	4.25	0.58	72	<0.001	Intercept (Herbivore 01)	5.46	0.44	332	<0.001
	Herbivory intensity	11.92	3.36	10	**0.005**	Herbivore 06 vs 01	−0.02	0.17	332	0.89
						Herbivore 11 vs 01	0.42	0.17	332	**0.016**
						Main effect 01	−0.15	0.23	155	0.5
						Exclosure 06 vs 01	−0.54	0.24	332	**0.028**
						Exclosure 11 vs 01	−0.24	0.24	332	0.327
Liverworts (binomial)	Intercept	−1.15	2.03		0.570	Intercept (Herbivore 01)	−6.40	1.25		<0.001
	Herbivory intensity	−11.69	16.10		0.468	Herbivore 06 vs 01	0.30	0.73		0.685
						Herbivore 11 vs 01	2.75	0.75		**<0.001**
						Main effect 01	−3.60	1.70		**0.035**
						Exclosure 06 vs 01	3.54	1.74		**0.042**
						Exclosure 11 vs 01	3.62	1.77		**0.041**

Example of model validation: if values in exclosure models are increasing forherbivore vs exclosure plots this is consistent with findings of both positive linear models and quadratic peaked spatial models. All gradient models were validated by exclosure models except for tree juveniles and liverworts (see Appendix A for details on model validation).

[a] Distribution of selected models was consistent between gradient and exclosure models for functional groups except for dwarf-shrubs where exclosure model could be analysed with a normal distribution model.

In studies that utilise natural gradients as ours we must minimise and control for potential confounding effects deriving merely from herbivore preferences rather than herbivory effects of red deer. First, the potential preference effects were minimised through study design; study sites were placed in a geographically restricted area (one island), within one main vegetation type (pine-bilberry forest), and within a limited elevation gradient (20–140 m). Investigating relationships across multiple scales can result in erroneous correlations (Crawley, 2007), and we believe preference effects could have acted stronger if our study had sampled on coarser scales, i.e. in larger areas, across vegetation types and, for example, between sites at low and high altitude. Second, we validated the herbivory intensity models with analyses from an exclosure based temporal data-set on species richness from the same study area. In every site a 10 × 10 m exclosure was established during winter 2001 together with the herbivory macroplots

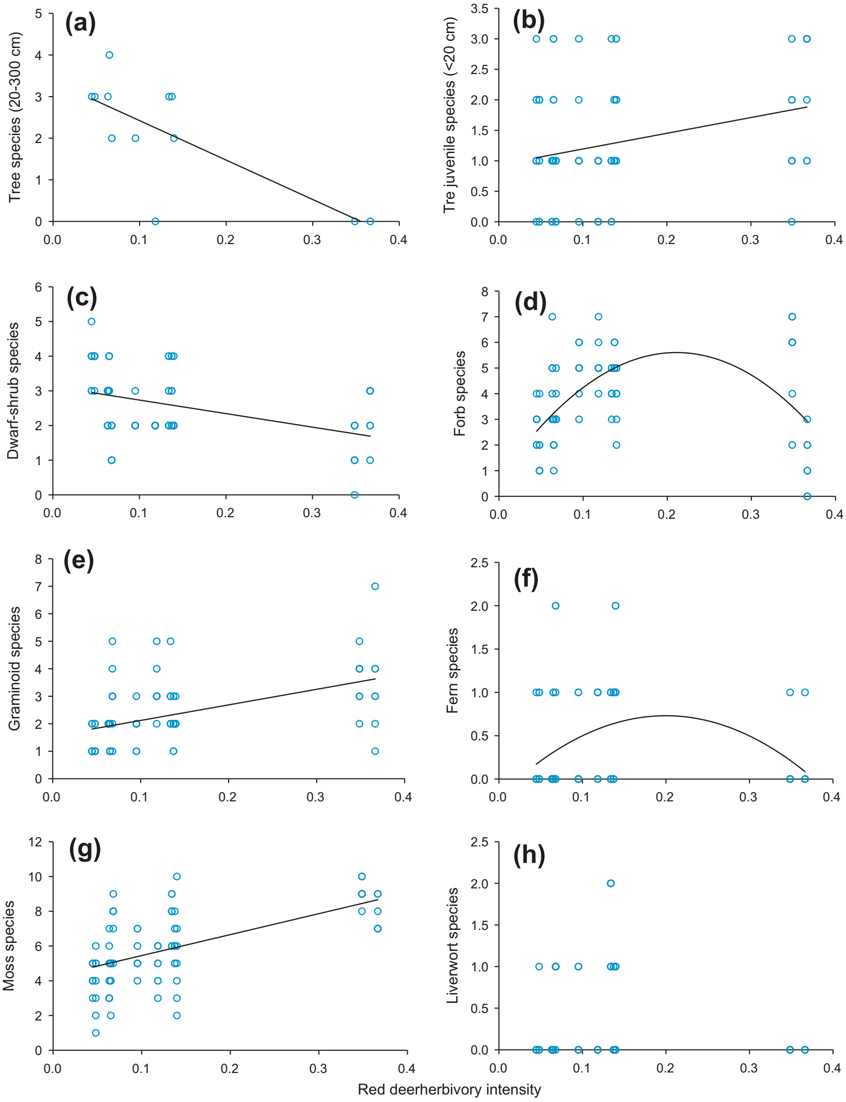

Fig. 3. The relationship between red deer herbivory intensity index and the species richness of the functional groups (a-h) of the forest understory at Svanøy, western Norway. Lines are shown for significant relationships of the selected models (linear vs quadratic), but do not take the random effects from the mixed effects modelling into account.

that are the main study subjects in this study. We established a 9 × 9 m macroplot and permanent plots corresponding to herbivory areas within the exclosures. We sampled plant species richness accordingly in June 2001, 2006 and 2011. The change in species richness during time between herbivory plots and exclosure plots was addressed by means of linear mixed effects models where the nested design (site, macroplot and plot) was addressed in the random effects. Standard models were performed with the herbivory plots in 2001 as reference. The interaction between time and treatment tell us whether the change under ceased herbivory was different than in the herbivory controls. If the temporal change was consistent with the findings along the spatial gradient of herbivory intensity, we concluded that the spatial model was validated. For example, to validate a statistical positive or a unimodally peaked herbivory – richness relationship, the temporal change should be statistically positive in herbivory plots relative to exclosure plots.

3. Results

3.1. Herbivory intensity-plant richness relationships

The total species richness increased significantly with increasing herbivory intensity within natural levels until it declines slightly under the artificially high densities of red deer (Fig. 2 and Table 1). If we visually inspect Fig. 2 we can see that the decline in richness under high red deer herbivory intensities are quite small compared to the increase under natural levels of herbivory. Models without farm data showed positive linear relationship between herbivory intensity and plant species richness (Coef = 50.5; SE = 14.2, DF = 60, 8; $P = 0.007$).

When we analysed the functional groups separately only the richness of forbs and ferns resulted in significant peaked quadratic models (Fig. 3d and f and Table 1). This was merely because of the decline under experimentally very high herbivory intensities, which is underlined by the positive linear relationships found between herbivory intensity and forb richness (Coef = 21.9; SE = 8.4, DF = 60, 8; $P = 0.03$) and fern richness (Coef = 22.3; SE = 8.5, DF = 60, 8; $P = 0.008$) when excluding farm sites. Richness of trees and dwarf-shrubs showed negative linear responses along the full herbivory intensity gradient (Fig. 3a and c and Table 1), whereas richness of tree-juveniles, graminoids and mosses showed positive linear responses (Fig. 3b, e and g and Table 1) to the herbivory intensity. Liverworts showed no significant richness response to red deer herbivory intensity (Fig. 3h and Table 1).

3.2. Model validation

In general our herbivory intensity-plant richness models were validated by the temporal exclosure-based models (Table 1 and Fig. A1), i.e. the temporal change in plant richness in herbivore vs exclosure plots was largely consistent with the findings along the spatial gradient of herbivory intensity. For example, in the temporal models the overall richness declined slightly when red deer herbivory ceased whereas it increased slightly under continuous herbivory. Most other models (i.e. for different functional groups) were also validated, either by showing a temporal similar response under ceased herbivory or under continuously red deer herbivory (Table 1 and Fig. A1 for details). The only functional groups where the findings of spatial gradient models and temporal exclosure models did not directly link to each other was for richness of tree juveniles (spatial: positive linear relationship; temporal: no significant changes) and liverworts (spatial: no significant relationship; temporal: positive effects of ceased herbivory). Both of these functional groups showed only a statistical weak or no relationship, respectively, between herbivory intensity and functional species richness.

4. Discussion

The herbivory intensity-plant richness relationship followed a unimodally peaked curved, but plant richness was lower only at forest sites with artificially high red deer populations (i.e. the local deer farm). As such, the result presented here shows mainly a positive overall effect of red deer herbivory on the understory species richness of the old-growth pine-bilberry forest. The combined design attributes (i.e. restricted geographic and ecological range of the study and the relative long term monitoring) along with the model validation (i.e. using temporal models to confirm the spatial models) strengthen our conclusions and minimize the potential confounding effects of herbivore preference. We believe the strength of our study is that we have used a full-length gradient of herbivory, spanning from very low to very high herbivory intensity, to explain the effects of large animal herbivory on species richness in terrestrial non-cultivated ecosystem. Such gradient approaches has earlier been used to show that community biomass production may peak along herbivory intensity gradients (Stewart et al., 2006), which again may influence the plant diversity patterns (Stewart et al., 2009).

The unimodally peaked signal in the herbivory-richness relationships was, however, not very strong and dependent on artificial high disturbance levels in our study. In general, the disturbance from free-ranging large herbivores is seldom severe enough to kill significant parts of adult plants. When disturbance becomes substantial, such as in the deer farm in our study, colonising plants are predated at early stage before they are able to tolerate biomass loss. Thus space and safe sites required for plant colonisation (e.g. Hegland et al., 2001) are not present simultaneously in these forest communities. One may speculate that the lack of these requirements is one reason why so few studies have published verifications of the intermediate disturbance hypothesis in forests with disturbance from free-ranging ungulates (e.g. Mackey and Currie, 2001; Svensson et al., 2012). Also, in forest communities with greater diversity of tree species than our study system the plant diversity response may be more pronounced because large herbivore disturbance has the clearest impact on this structural layer (Connell, 1978; Molino and Sabatier, 2001). For example, the maximum number of tree species at any site at any time in the study sites during 2001–2011 was only seven. In our study system we have sampled all understory plant species, but most ungulate-plant interaction studies do not include the bryophytes (i.e. mosses and liverworts) in the species recordings but as a cover estimate (e.g. Singer and Schoenecker, 2003; Tanentzap et al., 2009). A simple exercise of investigating artefacts of sampling effort or researcher choices is to examine how removing bryophytes from the dataset affects the overall herbivory-richness relationship. Mixed effect modelling then resulted in a negative linear disturbance-richness relationship (Coef = −11.3; SE = 4.5; DF = 72, 10; $P = 0.032$). Thus, if the ecological important group of bryophytes had not been recorded in this study, the ecological, and hence management interpretation of our analysis could have been the opposite in that red deer herbivory reduce plant richness in the forest understory.

There were distinct differences in functional group responses. Five of eight functional groups showed linear relationships between species richness and herbivory intensity (three positive and two negative) and one functional group showed no relationship. Only two functional groups showed a quadratic relationship when analysed separately, but these unimodal relationships were caused strictly by the artificially high herbivory intensities at farm sites and showed positive linear relationships when analysed within the natural gradient only (see 3.1). Overall, the herbivory-richness responses of the different species groups fitted our expectations based on findings from meta-studies and literature reviews (Hester et al., 2006; Diaz et al., 2007; Skarpe and Hester, 2008). Low-growing groups such as forbs, grasses and mosses increased in richness in contrast to woody dwarf shrubs and trees. This is in line with Evju et al. (2006) who showed that low stature species profited from ungulate grazing in a mountain area in Scandinavia. In other studies of red deer impact on plant diversity (Woodward et al., 1994; Schreiner et al., 1996), specific responses of plant groups or growth forms have tended to vary and be less predictable and few have studied functional group responses along gradients of disturbance. The detailed sampling of all understory plant species over a considerable time period (sensu Mackey and Currie, 2001) may also be a key to why our results fitted expectations better than many other similar studies. The difference in response to herbivory intensity found between understory and juvenile trees (Fig. 3a and b; i.e. complete opposite relationships) may indicate that deer herbivory have opposite effects on recruitment and survival of trees. These results also point towards the driving mechanism behind the red deer herbivory effects on plant richness. Periodic heavy grazing and browsing may increase the recruitment of trees through increased germination caused by reduced competition for light and space between the herbaceous layer and trees (e.g. Riginos, 2009). Studies from Białowieża forest in Poland underpin that fluctuations in ungulate density may drive tree recruitment patterns (Kuijper et al., 2010) and it is also known from agricultural systems that rotational stock management, varying the intensity of large herbivore disturbance, may increase overall biodiversity (Sjödin et al., 2008; Farruggia et al., 2012). When dominant plants are preferred by ungulates, plant diversity is expected to increase, whereas diversity may decrease if herbivory-tolerant or resistant species become dominant as a result of herbivory (Côte et al., 2004; Hester et al., 2006). The key mechanism to the overall increase in plant species richness along the red deer herbivory intensity gradient in our study is thus likely the reduction of dominant woody vegetation that increases resource and substrate availability at the benefit of a richer low-growing species assemblage.

A starting point to operationalize the knowledge from gradient approaches such as ours into management guidelines is to examine when key variables start to decline. As the studied gradient has a gap between the highest natural and artificial levels of herbivory intensity we cannot be conclusive in this study. However, the highest herbivory intensity found in unfenced forest concurs with 56% of the current shoots of bilberry browsed and a bilberry plant height of 11.7 cm in 2011 (vs 9% and 14 cm, respectively, in the site with the lowest herbivory intensity). At this level of red deer herbivory, species richness in our study system was not reduced and we may therefore speculate that the herbivory intensity must be greater to cause richness reduction in these northern forest ecosystems. Holechek et al. (1999) found that heavy livestock grazing was equivalent to 57% biomass removal. Although these measures are not directly comparable, i.e. biomass vs frequency of shoots browsed in our study, the comparison may point towards a resilient study system that can tolerate quite high herbivory intensities. According to the analysis of Mysterud et al. (2010) a browsing frequency on bilberry of ca. 50% is equal to densities in areas were 2–3 red deer/km^2 are harvested, whereas the average harvest at the whole island in our study was ca. 1.8 deer/km^2 (J.T. Solheim, pers comm.). In conclusion, the herbivory intensities that occur in areas were about 50% of bilberry shoots are browsed or 2–3 red deer/km^2 are harvested appear largely to be positive for understory plant species richness. Red deer densities are rarely at such high levels in Norway when assessed at the same spatial scale as our study island (i.e., 10 km^2; Statistics Norway, 2013).

4.1. Conclusions and implications for management

The relative long-term (10-years) nature of the study presented here suggests that the increasing densities of free-ranging red deer in northern forest ecosystems may not necessarily adversely affect the plant richness aspect of biodiversity. The old-growth forest understory species richness at Svanøy, western Norway, increased along with greater deer densities except at artificial high levels. Considering the extreme high herbivory intensity in the deer farm sites, the main message from our study is that within the densities and timeframes studied here moderate to relatively high red deer densities lead to greater understory species richness than low deer densities. Based on this particular study, and comparing herbivory intensity and harvest data with literature and statistics from other areas, we may conclude that the red deer densities currently found in Norway rarely reach levels that reduce plant species richness.

Richness of several individual functional groups showed a positive response to increased herbivory intensities. If management goals imply targeting specific groups of species this study suggest that intense herbivory is favourable mainly for richness of forbs, grasses and mosses whereas low herbivory intensities are required, spatially or temporally, for preserving the richness of woody species. An important lesson from the functional group approach is that the herbivory-richness relationship may strongly be influenced by which functional groups are sampled. Our results therefore call for additional long-term studies including other sessile groups such as fungi and adult trees, as well as multitrophic aspects.

Acknowledgements

We thank K.-K. Berget, P. Greve, I. G. Hårstad, M.C. Knagenhjelm, T.R. Paulsen, T. Seldal, F. Solheim, T. Stokke, S. Vatne, V. Veiberg, T. Wiberg, K.F. Øi and H. Øyrehagen for invaluable assistance in collecting data, and the Norwegian Research Council through the Miljø 2015-programme (Project number 204403/E40) for funding.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2013.08.031.

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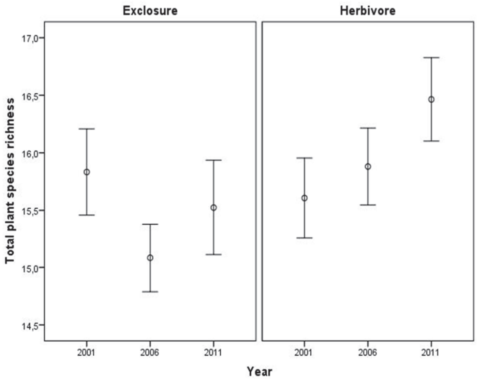
Appendix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15,0
14,5
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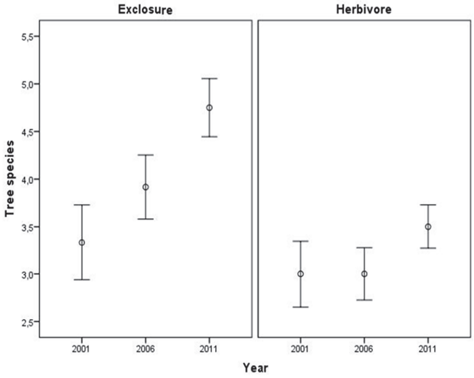
2011
2001
2006
2011
Year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Herbivore
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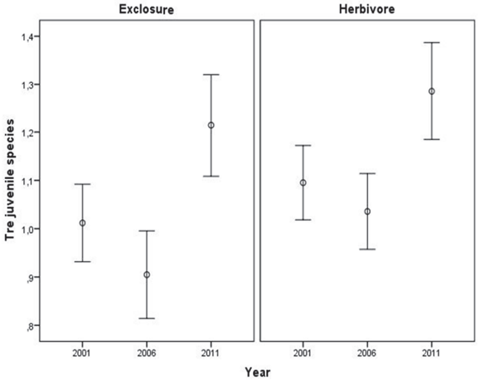
2001
2006
2011
2001
2006
2011
Year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Herbivore
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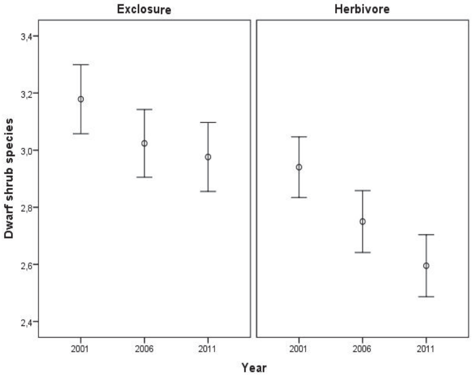
1,1
1,0
,9
,8
2001
2006
2011
2001
2006
2011
Year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2,4
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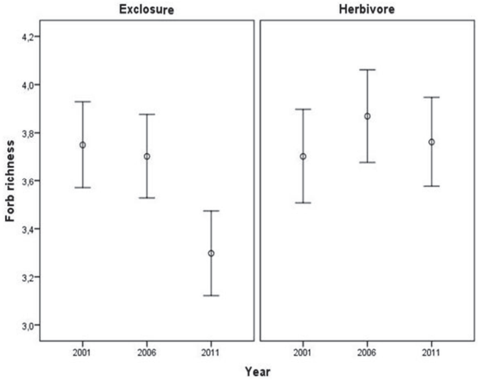
Year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Herbivore
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2001
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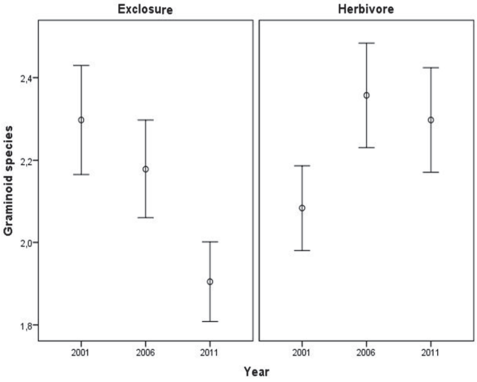
Year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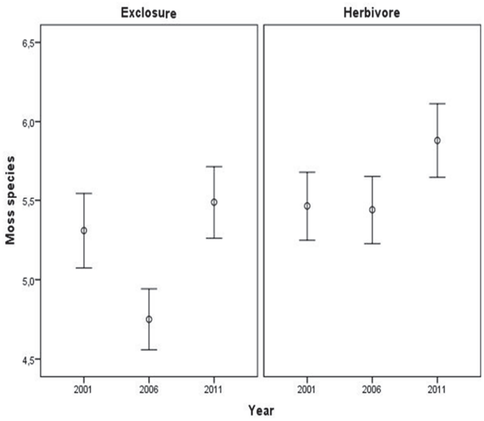
2001
2006
2011
2001
2006
2011
Year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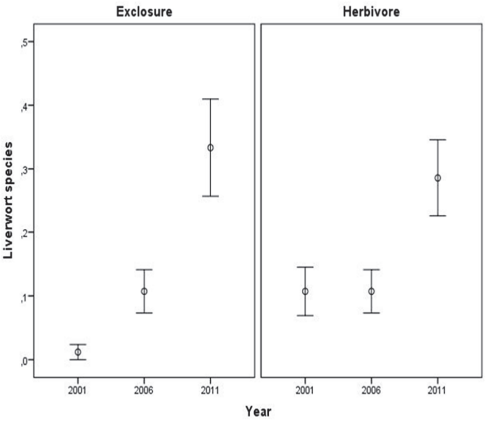
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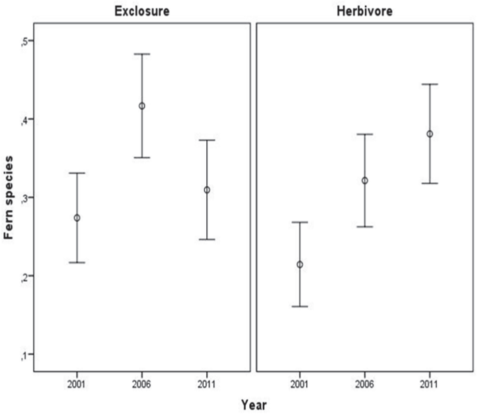
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Paper II

Ecol Res
DOI 10.1007/s11284-016-1391-6

ORIGINAL ARTICLE

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Red deer mediate spatial and temporal plant heterogeneity in boreal forests

Received: 11 March 2016 / Accepted: 7 August 2016

Abstract Selective herbivory can influence both spatial and temporal vegetation heterogeneity. For example, many northern European populations of free-ranging ungulates have reached unprecedented levels, which can influence plant species turnover, long-term maintenance of biodiversity and the subsequent stability of boreal ecosystems. However, the mechanisms by which large herbivores affect spatial and temporal vegetation heterogeneity remain poorly understood. Here, we combined a 10-year exclusion experiment with a herbivore intensity gradient to investigate how red deer (*Cervus elaphus*) acts as a driver of temporal and spatial heterogeneity in the understory of a boreal forest. We measured the two dimensions of heterogeneity as temporal and spatial species turnover. We found that temporal heterogeneity was positively related to herbivory intensity, and we found a similar trend for spatial heterogeneity. Removing red deer (exclosure) from our study system caused a distinct shift in species composition, both spatially (slow response) and temporally (quick response). Vegetation from which red deer had been excluded for 10 years showed the highest spatial heterogeneity, suggesting that the most stable forest understory will occur where there are no large herbivores. However, excluding red deer resulted in lower species diversity and greater dominance by a low number of plant species. If both stable but species rich ecosystems are the management goal, these findings suggest that naturally fluctuating, but moderate red deer densities should be sustained.

Keywords Biodiversity · Cervids · Ecosystem stability · Herbivory intensity · Plant communities

Introduction

Vegetation heterogeneity has two broad functional roles in ecosystem stability: temporal heterogeneity (i.e., temporal species turnover) destabilizes, whereas spatial heterogeneity (i.e., spatial species turnover) stabilizes ecosystems (May 1974). However, factors such as the presence or absence of disturbance can determine the nature of these roles. For example, severe disturbance often leads to high temporal species turnover, dominated by pioneer species, but when long-lived and slower growing species dominate, temporal species turnover is low (Rydgren et al. 2004). Spatial species turnover is the difference in species composition across both local and regional assemblages, with high values reflecting a patchy distribution of plant species at various spatial scales (Koleff et al. 2003). High spatial heterogeneity can make an ecosystem more robust to disturbances. It also facilitates important ecosystem functions such as dispersal and recolonization, and by increasing resources and refugia (Hovick et al. 2015). Therefore, spatial heterogeneity is also important for ecosystem resilience (the ability to reorganize and renew itself following disturbance; Elmqvist et al. 2003).

Large herbivores can act as ecosystem engineers by trampling and feeding selectively (Jones et al. 1994), thereby modifying plant species composition and dynamics. The influence of herbivory on vegetation heterogeneity depends on ecosystem productivity (Proulx and Mazumder 1998), herbivore selectivity (Adler et al. 2001) and intensity (Mackey and Currie 2001), as well as the species of herbivore, as use of habitat and feeding patterns are species specific (Côté et al. 2004; DeGabriel et al. 2011). Some general patterns

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Electronic supplementary material The online version of this article (doi:10.1007/s11284-016-1391-6) contains supplementary material, which is available to authorized users.

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are apparent: strongly preferred or herbivory-sensitive plant species become less abundant in the presence of herbivores, whereas herbivory-tolerant and non-preferred species increase (Augustine and McNaughton 1998). Herbivores can also increase vegetation heterogeneity when preferred plant species are unevenly distributed in the landscape (Hester et al. 2000), or if they forage more patchily than the vegetation pattern (Adler et al. 2001), for example, when external factors such as disturbance or stress influence a herbivore's spatial use of habitat.

Few studies simultaneously address the effects of herbivores on spatial and temporal vegetation heterogeneity (Adler et al. 2001), with most focussing on simple measures of diversity such as species richness or alpha diversity (within-plot diversity). However, also other aspects of diversity are important in understanding how herbivory impacts vegetation. For example, landscapes with several sites of low alpha diversity can still be heterogeneous if the variation in diversity between sites is high. Large herbivores can contribute to this spatial heterogeneity by feeding patchily (Adler et al. 2001; Koleff et al. 2003), and herbivory that affects temporal heterogeneity can alter colonization opportunities for new plant species (Bakker et al. 2003). Few studies have examined herbivory-induced changes in the vegetation by conducting long-term monitoring across herbivory-intensity gradients (although see Heckel et al. (2010)), but such studies are crucial for understanding how the intensity of herbivory disturbs ecosystems (Hester et al. 2000; Nuttle et al. 2014).

Densities of red deer (*Cervus elaphus*) have reached unprecedented levels in Northern Europe (Fuller and Gill 2001), causing management concerns for ecosystem stability and biodiversity (Côté et al. 2004). In Fennoscandia, herbivore assemblages have changed from livestock dominance to cervid dominance during the past 60 years, alongside a reduction in total herbivory (Austrheim et al. 2011). However, cervid herbivory has increased most in relatively resource-poor inland forest areas. Differences in both use-of-area and year-round presence compared with past livestock herbivory can be expected (Austrheim et al. 2011). The present intensity of herbivory by red deer may represent a disturbance regime to which the plant species in the Fennoscandian boreal forests are not evolutionarily adapted.

In this paper we investigate how red deer herbivory mediates spatial and temporal vegetation heterogeneity in the understory of a boreal forest ecosystem by combining a 10-year red-deer exclosure experiment with a substantial natural gradient in herbivory intensity. We monitored plant-species richness and abundance at 12 sites, each with one exclosure macroplot paired with one macroplot open to red deer herbivory. The open macroplots covered a range of intensities of herbivory, allowing us to examine the importance of herbivory along gradients of intensity. Removing herbivory can reveal vegetation resilience in relation to long-term disturbance (Elmqvist et al. 2003; Beschta and Ripple 2009). We previously investigated the effect of herbivory intensity on species richness, and found that overall species richness showed a unimodal peaked response to increasing herbivory, in accordance with the intermediate disturbance hypothesis (Hegland et al. 2013). However, the functional groups differed in their responses. The richness of forbs, graminoids and mosses increased, while dwarf-shrubs and young trees decreased with increasing herbivory intensity (Hegland et al. 2013). There was actually twice as many species benefitting from red deer herbivory. However, how this translates into spatial and temporal heterogeneity remains unclear.

We predicted that excluding red deer would lead to higher temporal species turnover shortly after exclusion, but reduced turnover in the long term (Prediction 1a). As intense herbivory can enhance light availability and opportunities for recruitment of new species (Rydgren et al. 2004), we expected a positive relationship between the intensity of herbivory and temporal species turnover (Prediction 1b). We also hypothesized that red deer reduce species turnover spatially, because selective herbivory may depress highly digestible plant species, enhance browse-tolerant and avoided ones (Augustine and McNaughton 1998), and aid seed dispersal through zoochory (Steyaert et al. 2009). Therefore, we predicted that excluding red deer would increase spatial species turnover (Prediction 2a), and expected a negative relationship between the intensity of herbivory and spatial species turnover (Prediction 2b; Rooney 2009).

Methods

Study area

We conducted our study at Svanøy Island (61°30′N, 5°05′E), western Norway. The island is situated in the boreo-nemoral zone and covered mainly by old-growth boreal forest dominated by Scots pine (*Pinus sylvestris*, Skogen and Lunde 1997). Mean annual precipitation and temperature are 2000 mm and 8 °C, respectively (Florø airport, http://www.eklima.met.no). The deer density is approximately 7.5 deer km^{-2}, which is considered high in Norway (Hegland et al. 2013). The island includes a red-deer farm with more than 30 deer km^{-2}, but wild and farmed deer are separated by a game fence. Some domestic sheep (*Ovis aries*) are free-ranging, mainly during summer.

Study design and sampling

In 2001, we established 12 sites in pine-bilberry (*Vaccinium myrtillus*) forest. Each site contained one exclosure macroplot and one open macroplot, both 9 × 9 m with seven permanent 1 × 1 m plots inside (Fig. 1). All plots were in flat areas, randomly placed but rejected and re-placed if adult trees were within 0.5 m. The

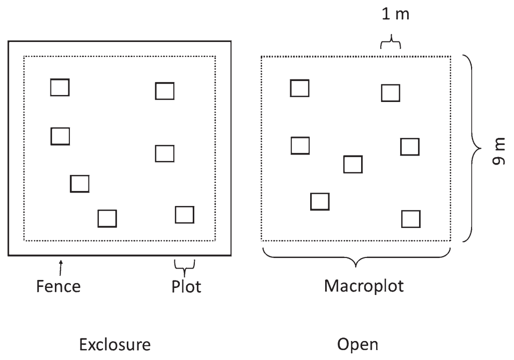

Fig. 1 Our study included 12 sites. The design shows the placement of seven plots in one open and one exclosure macroplot at each site. Due to topography, the distance between exclosure and open macroplots varied between 10 and 50 m

exclosures were surrounded by 3 m tall fences with 10 × 10 cm wire mesh. To avoid edge effects, we left a 0.5 m zone between the fence and the macroplot. Small herbivores could move freely into the exclosures, although few or none were present. Common boreal herbivores such as the mountain hare (*Lepus timidus*) have not been observed on the island, and we caught no rodents in 350 rodent trap-nights during 2011. Henceforth, 'treatment' refers to exclosures and open plots. Two sites were situated within the red deer farm, and these contained only six and three open plots, respectively, because some plot positions were lost. We surveyed the vegetation in June 2001, 2006 and 2011. Each 1 × 1 m plot was divided into 100 subplots. We recorded the vascular and bryophyte species in each plot and measured their abundance as frequency in these 100 subplots. In addition, the abundance and richness of young trees (50–400 cm in 2011) was recorded at the macroplot scale.

The intensity of red deer herbivory varied among the 12 open macroplots. To quantify this we estimated the intensity of herbivory on randomly selected bilberry ramets at each site (see also; Hegland et al. 2013). Bilberry is widely distributed, abundant, intermediately preferred by red deer, and therefore a good indicator species for monitoring the intensity of red deer herbivory (Mysterud et al. 2010). In June 2001 and 2011, we measured five and three randomly selected ramets, respectively, in all seven plots in each macroplot, and three ramets in four randomly selected plots per macroplot in 2006. We calculated the intensity of herbivory on each ramet as the percentage of annual shoots browsed, in five categories: 0, 1 (1–24 %), 2 (25–49 %), 3 (50–74 %), 4 (75–100 %), (sensu Frelich and Lorimer 1985), divided by ramet height. Hereafter we term this as 'herbivory intensity'. We used the mean herbivory intensity of all ramets per macroplot per year as our measure of intensity when analysing spatial heterogeneity statistically. To analyse temporal heterogeneity we compare these mean values across the periods 2001–2006 and 2006–2011. Our herbivory-intensity measure was strongly related to an independent fecal count survey (r = 0.94, N = 12, P < 0.001, Hegland et al. 2013).

Heterogeneity measures

To calculate alpha diversity we used the Shannon diversity index (H′) and evenness (exp[H′]/S, where S is the number of species; (Kindt and Coe 2005)) for all species pooled and repeated this for the bottom layer (bryophytes), field layer (all vascular plants, including trees < 50 cm), and the understory tree layer (trees 50–400 cm). For temporal species turnover (Predictions 1a and 1b), we calculated Bray-Curtis dissimilarity (per cent dissimilarity/100, BC; Legendre and Legendre 1998) within each plot for the first five years (2001–2006) and the last five years (2006–2011). For spatial species turnover (Predictions 2a and 2b), we calculated BC between each plot and all other plots within each macroplot and year and used the mean of these six values as the BC value for each plot. Prior to all BC calculations we changed the range of the abundance scale for each species from 100 to 16 with a power function (van der Maarel 1979), and thereby achieved a recommended intermediate weighting of species (Økland 1990; Rydgren 1993).

Statistical analyses

We analysed all responses with linear mixed effects models (packages lme4 (Bates et al. 2014) and lmerTest (Kuznetsova et al. 2015) in R version 3.1.1 (R Core Team 2014). We started with full models, applied backward elimination of fixed effects, and validated the final models as proposed by Crawley (2007, Table S1). Although species turnover is a proportion, we specified all our models for Gaussian distribution, as the residuals showed normal distributions, resulting in more conservative p-values. As the two sites in the red deer farm had much higher red deer densities than the other sites, we ran all models with and without 'farm' as a factor.

Results

Across the three sampling years, we recorded 70 plant species, 52 of which occurred in both treatments. Overall, the mean number of species per plot was 16 (±0.2 SE). *Vaccinium myrtillus*, *Avenella flexuosa* and *Hylocomium splendens* were common, and occurred in almost all plots all years (Table 1). *Viola riviniana*, *Maianthemum bifolium* and *Veronica serpyllifolia* were among the eight species only occurring in open plots. *Corylus avellana* and *Populus tremula* were among the 10 species unique to the exclosure plots. Occurences of species unique to one treatment were rare, however.

Table 1 Frequency, F (percent of all plots where the species occurred; $n = 84$ for each treatment), and mean subplot frequency, MSF (arithmetic mean of the subplot frequencies for a species, calculated from the plots where the species occurred), for species occurring in ≥ 25 % of the plots in one year and treatment

Species	Grazed						Ungrazed					
	2001		2006		2011		2001		2006		2011	
	F	MSF	F	MSF	F	MSF	F	MSF	F	MSF	F	MSF
Calluna vulgaris	33	16	25	25	21	24	42	24	45	55	39	62
Empetrum nigrum	54	38	46	54	43	56	58	34	48	47	48	32
Pinus sylvestris	0	0	6	1	44	3	0	0	5	1	30	2
Sorbus aucuparia	74	6	70	6	64	7	69	4	58	6	64	6
Vaccinium myrtillus	100	74	100	82	99	81	100	68	99	80	99	80
Vaccinium vitis-idaea	98	47	93	35	88	27	96	47	93	43	94	36
Agrostis capillaris	5	32	24	35	25	41	5	29	14	18	11	15
Anemone nemorosa	29	10	31	10	26	8	17	8	12	9	12	12
Avenella flexuosa	100	85	100	95	100	92	100	85	100	96	100	96
Linnaea borealis	77	31	80	33	76	19	74	29	85	28	73	17
Luzula sylvatica	60	35	57	35	61	43	58	40	56	44	58	48
Melampyrum pratense	32	9	33	8	44	6	57	8	62	12	51	7
Oxalis acetosella	56	20	58	28	54	31	51	26	52	23	60	21
Potentilla erecta	58	22	63	25	60	29	57	19	54	22	54	25
Pteridium aquilinum	10	6	19	15	21	14	12	4	26	8	18	14
Trientalis europaea	68	12	75	11	65	10	70	9	63	10	49	7
Dicranum spp.	69	22	68	25	70	26	65	20	64	14	63	19
Hylocomium splendens	100	73	100	79	100	88	100	70	99	63	100	82
Plagiothecium undulatum	21	11	18	9	31	8	25	16	14	7	27	11
Pleurozium schreberi	52	9	38	7	31	3	46	9	27	4	36	5
Polytrichum spp.	33	17	31	23	40	16	30	20	27	19	32	14
Pseudoscleropodium purum	58	19	69	20	71	17	60	18	73	20	81	18
Ptilium crista-castrensis	71	22	68	26	77	26	63	16	58	18	67	26
Rhytidiadelphus loreus	85	29	83	20	83	29	82	27	71	17	76	15
Sphagnum spp.	26	22	32	22	32	28	29	26	29	26	31	27

Ten years of excluding red deer significantly decreased alpha diversity (Shannon index 2011 ± SE: open plots, 2.21 ± 0.02; exclosure plots, 2.14 ± 0.03, $T = -2.046$, $df = 332$, $P = 0.042$, Table S2). However, herbivory intensity and alpha diversity were uncorrelated ($P = 0.918$, Table S2). Evenness did not differ between open and exclosure plots (evenness 2011 ± SE: open plots, 0.57 ± 0.01; exclosure plots, 0.57 ± 0.01, $P = 0.568$), but there was a negative effect of herbivory intensity on evenness within the open plots ($\beta = -0.132 \pm 0.043$, $T = -3.052$, $df = 25.7$, $P = 0.005$, Table S2). Excluding red deer did not affect the alpha diversity within the bottom, field or understory tree layer (all, $P > 0.05$, Table S3), but herbivory intensity reduced the field layer alpha diversity ($\beta = -0.747 \pm 0.239$, $T = -3.121$, $P = 0.002$, Table S3). Evenness was negatively related to herbivory intensity in the field ($\beta = -0.201 \pm 0.060$, $T = -3.331$, $P = 0.002$) and understory tree layers ($\beta = -0.464 \pm 0.1655$, $T = -2.807$, $P = 0.010$, Table S3).

Effect of red deer herbivory on temporal heterogeneity

Temporal species turnover (Bray-Curtis dissimilarity, BC, within plot, between years) was significantly higher in exclosure plots than in open ones for the first five-year period ($P = 0.005$). In the last five-year period, however, temporal species turnover in the exclosures was reduced ($P = 0.023$), reaching the same level as in the open plots (Fig. 2; Table 2). Temporal species turnover increased significantly with increasing intensity of herbivory ($P < 0.001$, Fig. 3; Table 2), but became non-significant, although still positive, when the plots in the red deer farm were omitted ($P = 0.136$, Table S4, Fig. S1).

Effect of red deer herbivory on spatial heterogeneity

Spatial species turnover (BC between plots in same macroplot) was higher in exclosures than in open plots 10 years after the experiment started ($P < 0.001$), whereas five years of exclusion was not enough to reveal the effect of red deer ($P = 0.270$). On the open plots, BC remained stable throughout (Fig. 4; Table 2). Similar results were obtained when plots in the red deer farm were omitted (Table S4). Spatial species turnover tended to be positively correlated with the intensity of herbivory overall ($P = 0.089$, Table 2), but the effect disappeared when the plots in the red deer farm were omitted from the model ($P = 0.488$, Table S4).

Discussion

The two dimensions of vegetation heterogeneity have contrasting characteristics. Temporal heterogeneity can

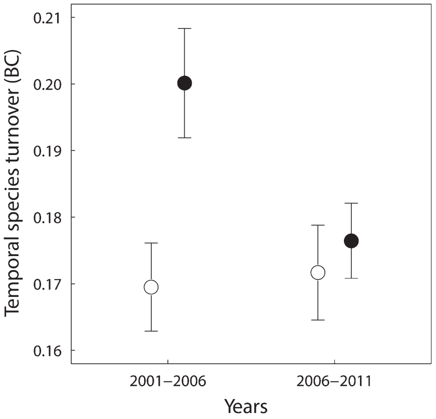

Fig. 2 Mean (± SE) five-year temporal species turnover, measured by the Bray-Curtis dissimilarity index within plot: exclosure (*black circles*) and open (*white circles*) plots during 10 years of experiment

destabilize the ecosystem, whereas spatial heterogeneity can stabilize the ecosystem (May 1974). A temporally heterogeneous forest will favour early succession species and will be more susceptible to invading species, stochastic events such as small-scale fires or wind throws, and state shifts. A spatially heterogeneous forest, on the other hand, will have higher resilience, and will thus be more robust to stochastic events.

In this study, we investigated the role of the red deer in forming the heterogeneity of the boreal forest understory vegetation over 10 years, and found two key effects. Firstly, excluding red deer caused a distinct shift in species composition, reflected in both spatial and temporal species turnover (Predictions 1a and 2a). Secondly, we found that the intensity of herbivory had a strong positive impact on temporal species turnover (Prediction 1b), and a weak positive impact on spatial species turnover (Prediction 2b).

Higher temporal species turnover in sites with high intensities of herbivory (Prediction 1b) implies that the species composition in such sites was less stable than in sites with lower herbivory intensity. High levels of herbivory benefit pioneer and unpalatable species, and inhibit the growth and reproduction of slow growing species such as trees or shrubs (Hegland and Rydgren 2016), and this pattern is reflected in the reduction in evenness among the plant species (Table S2). By contrast, unpalatable species declined under high densities of white-tailed deer (*Odocoileus virginianus*) in Pennsylvania, USA, perhaps because trampling by the deer caused soil compression, limiting the growth potential of all plants (Heckel et al. 2010). In an old-growth, temperate forest in Poland, Kuijper et al. (2010) found that herbivory limited trees from growing larger than 50 cm. Likewise, we have previously shown that in our study area young deciduous trees germinated better in sites experiencing high levels of herbivory, but when seedlings became taller than the field layer vegetation, tree species richness decreased (Hegland et al. 2013). Red deer also strongly limit the abundance (number of individuals) in this size class (Hegland and Rydgren 2016). Thus, increased herbivory intensity reduces the number of trees reaching reproductive age, and therefore is a crucial factor in forest regeneration (Tremblay et al. 2006).

Temporal species turnover increased significantly in the exclosures during the first 5 years of the study. This implies that removing red deer herbivory from the system created a distinct and rapid shift in the species

Table 2 Effect of (a) exclosure treatment, and (b) herbivory intensity on temporal and spatial species turnover (BC); parameter estimates for the most parsimonious model of the effects of year, treatment or herbivory intensity, and interactions

(a) Exclosure vs open plots						(b) Herbivory intensity					
Fixed effects	Estimate	SE	df	*t*	*P*	Fixed effects	Estimate	SE	df	*t*	*P*
Temporal species turnover											
(1a)						(1b)					
Intercept	0.173	0.011	17.5	15.652	< 0.001	Intercept	0.136	0.008	8.2	17.690	< 0.001
Exclosure (vs open)	0.027	0.009	25.1	3.069	**0.005**	Herbivory intensity	0.287	0.044	13.0	6.507	**< 0.001**
Year 2006–2011 (vs 2001–2006)	0.002	0.008	161.0	0.271	0.787						
Exclosure × year 2006–2011	−0.026	0.011	161.0	−2.298	**0.023**						
Spatial species turnover											
(2a)						(2b)					
Intercept	0.281	0.019	18.3	15.157	< 0.001	Intercept	0.276	0.017	12.3	16.374	< 0.001
Exclosure (vs open)	−0.007	0.019	11.6	−0.369	0.719	Herbivory intensity	0.055	0.032	168.3	1.712	0.089
Year 2006	0.007	0.005	314.2	1.591	0.113						
Year 2011	0.001	0.005	314.2	0.162	0.872						
Exclosure × year 2006	0.007	0.006	312.0	1.106	0.270						
Exclosure × year 2011	0.021	0.006	312.0	3.268	**0.001**						

The models are linear mixed models fit with REML Satterthwaite approximations to calculate degrees of freedom, with spatial random factor plot in macroplot by site for model 1a and 2a, and plot by site for model 1b, and plot by site plus temporal random factor year for 2b. Reference factors are Open 2001–2006 and Open 2001 for 1a and 2a, respectively, and represented by the intercept. A significant interaction term means that the turnover is different in exclosure than in open plots the last five years (1a) and after 10 years (2a)

Bold values indicate significant *p*-values ($p \leq 0.05$)

SE standard error, *df* degrees of freedom

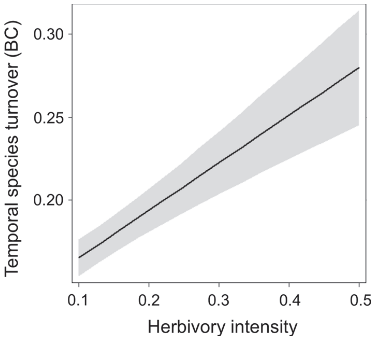

Fig. 3 Fitted relationship (*black line*, $P < 0.001$) and 95 % CI ($\beta \pm 1.96 * SE$, *grey shade*) between temporal species turnover, measured with Bray-Curtis dissimilarity index within plot between years, in relation to the gradient of herbivory intensity

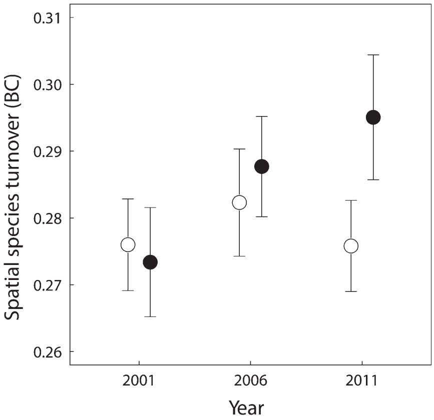

Fig. 4 Mean (±SE) spatial species turnover, measured with Bray-Curtis dissimilarity index between plots within the same macroplots: exclosure (*black circles*) and open (*white circles*) plots during the 10-year experiment

composition. Changes in vegetation inside exclosures after removing a cause of disturbance can reveal the plants' recovery abilities (Beschta and Ripple 2009). The marked increase in temporal species turnover demonstrated in our exclusion plots is an important finding because it shows the high capacity of boreal forest plant species to recover, even after experiencing high levels of herbivory. Nevertheless, the effect of herbivory will likely persist for some decades after the reduction or removal of red deer (Nuttle et al. 2014), probably depending on the original density of herbivores (Schütz et al. 2003).

Temporal species turnover did not differ significantly between exclosures and open plots (Prediction 1a) during the last 5 years of the study, which suggests rapid stabilization of species composition in our study system. When we omitted data from the red deer farm (those sites with extremely high red deer densities) from our analyses, however, temporal species turnover remained higher in the exclosure plots than in the open plots 10 years after excluding red deer (Table S4). This indicates that rapid changes in temporal species turnover can be expected after dramatic changes in an ecosystem (e.g., removing large herbivores). The continued difference in temporal species turnover between the exclosures and open plots outside the farm shows that red deer can increase temporal species turnover, also at low to medium densities, but that the effect is stronger at high densities.

Spatial species turnover did not decrease as red deer density increased (Prediction 2b); instead it increased weakly. However, in line with Prediction 2a, we found that excluding red deer from forest patches stimulated spatial species turnover. This suggests that red deer herbivory can have a homogenizing effect on the forest understory although in our study, this effect took 10 years to become apparent. The potential for herbivores to alter vegetation heterogeneity depends on the intrinsic spatial pattern of the vegetation and its interaction with that of herbivory (Adler et al. 2001). Our study examined the effects of herbivory in a boreal forest, with relatively homogenous vegetation. Although red deer use a range of different habitat types, productive boreal forest is the habitat where Scandinavian red deer spend most of their time during daylight, as it is more important for foraging than earlier believed (Godvik et al. 2009). Red deer feeding in the forest understory is not spatially homogeneous, based purely on the availability of forage plants, but depends also on factors such as the distance to human infrastructure or predators, and the availability of resting spots and high quality forage (e.g. pastures and meadows, Adrados et al. 2008; Godvik et al. 2009).

Exclusion of red deer resulted in 7 % reduction of the plant species diversity [transforming Shannon index to effective numbers, exp(H′), Jost (2006)]. If all species were evenly common (which they are not), this diversity would translate to a species loss of 1.2 species. Such loss may not seem substantial, but if there are no other functionally similar species, it may affect long-term ecosystem functioning (e.g. Mori et al. 2013; Sitters et al. 2016).

Our study was conducted over a relatively small area, within an island of 11 km^2. By locating our sites along a gradient of herbivory intensity within this island, and focusing on the fine-grained plant-species responses within these sites and all within the pine-bilberry forest ecotype, we eliminated as many sources of variation as possible. We are thus able to isolate the effect of herbivory intensity on plant species heterogeneity. A study across a larger spatial extent and with several vegetation types, could potentially reveal greater effects of excluding red deer, but may not detect the fine scaled effect of herbivory intensity seen here.

Selectivity and aggregation are two important processes governing the effects of herbivory on vegetation heterogeneity and diversity (Augustine and McNaughton 1998). Patch-grazing herbivores are more likely to increase spatial heterogeneity than species that feed homogenously or highly selectively (Adler et al. 2001). Studies on other large herbivores have shown that herbivory can either reduce (white-tailed deer, Rooney 2009) or increase (sheep, (DeGabriel et al. 2011); black-tailed deer, *Odocoileus hemionus,*(Gaston et al. 2006)) spatial heterogeneity. For example, in a study on the previously ungulate-free islands in British Columbia, Canada, Gaston et al. (2006) found that uninvaded islands were more similar in plant species composition than islands with introduced black-tailed deer. Islands without deer were smaller than those with deer, and therefore theoretically should be more homogeneous (MacArthur and Wilson 1963), suggesting that deer drove biotic differentiation rather than homogenization. Red deer, being intermediate feeders, may have less of an effect on spatial heterogeneity. They feed on a broader range of species than black-tailed deer (Hofmann 1989) and aggregate in smaller groups (Adler et al. 2001). Our results indicate that red deer herbivory spatially homogenize even relatively uniform vegetation, whereas the opposite would be expected (Adler et al. 2001).

Preferred species in heavily browsed areas may depend on ephemeral recruitment opportunities; that is, periods when herbivore populations are low (Fornara and du Toit 2007). Fluctuations in the density of large herbivore populations, spatially and in time, is therefore likely to be important for plant recruitment (Kuijper et al. 2010). Such ephemeral windows are not always sufficient for vegetation regeneration, especially if the ecosystem is not adapted to herbivory by the particular species. For example, in New Zealand, introduced red deer populations were reduced by about 92 % and were kept at low densities for four decades (Tanentzap et al. 2009). Despite this, tree recruitment remained low; showing that recovery in heavily herbivore-disturbed systems, particularly those that have evolved in absence of large herbivores, can take decades (Tanentzap et al. 2009). To permit natural regeneration, managers in areas with high red-deer densities need to provide for periodic ephemeral windows for recruitment, either in time or spatially, in their management plans (Sage et al. 2003).

Conclusions

Understanding both the spatial and the temporal components of vegetation heterogeneity is crucial to advancing our knowledge of ecosystem functioning and the associated role of large herbivores (Soininen 2010). Our results show that a combined focus on the effects of exclusion and the intensity of herbivory provides new insights into the ecological role of red deer in boreal forests. Interestingly, temporal heterogeneity of the forest understory increased with increasing red deer herbivory intensity, as well as when red deer were excluded. Increased temporal heterogeneity after excluding red deer either suggests that low densities of deer stabilize the species turnover, or that the recovery after long-term herbivory takes more than a decade. Further monitoring of the vegetation will illuminate this uncertainty. However, the spatial heterogeneity was indeed highest where red deer were excluded. Thus, our results suggest that removing red deer would effectively result in the most stable ecosystem over a prolonged period of time. However, the lowest species diversity of plants appeared where red deer were excluded. If both stable but also species rich ecosystems are the management goal, managers should sustain naturally fluctuating, but moderate red deer densities.

Acknowledgments This study was supported by the Norwegian Research Council under the Miljø 2015 programme (project number 204403/E40) and the Norwegian Environment Agency. Thanks to Norwegian Red Deer Centre and K.-K. Berget, P. Greve, I. G. Harstad, M. Knagenhjelm, T. R. Paulsen, T. Seldal, F. Solheim, T. Stokke, S. Vatne, V. Veiberg, T. Wiberg, K. F. Øi and H. Øyrehagen for their valuable help in the field. Sam Steyaert commented on drafts of the manuscript, and Peter Frost did copy editing. Thanks also to Mark Gillespie language help. We would like to thank the two anonymous reviewers for comments that helped improving the manuscript.

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Appendix

Table S1 Factors included in full models before backward elimination (Crawley 2007).

Prediction	Fixed factor	Random factor
1a	Treatment (open or exclosure) × Time period (2001–2006 or 2006–2011)	Plot in macroplot by site
1b	Herbivory intensity + Herbivory intensity^2	Plot by site
2a	Treatment (open or exclosure) × Year (2001, 2006 or 2011)	Plot in macroplot by site
2b	Herbivory intensity + Herbivory intensity^2	Plot by site and year

Table S2 Effect of (a) exclosure treatment, and (b) herbivory intensity on alpha diversity measured with Shannon diversity index and evenness. SE = standard error, d.f. = degrees of freedom.

(a) Exclosure vs open plots						(b) Herbivory intensity					
Fixed effects	Estimate	SE	d.f.	*t*	*P*	Fixed effects	Estimate	SE	d.f.	*t*	*P*
SHANNON DIVERSITY INDEX											
Intercept	2.237	0.046	21.1	48.541	< 0.001	Intercept	2.221	0.052	13.5	43.002	< 0.001
Exclosure (vs Open)	−0.020	0.050	13.7	−0.389	0.703	Herbivory intensity	0.013	0.125	109.0	0.103	0.918
Year 2006	−0.017	0.020	332.0	−0.846	0.398						
Year 2011	−0.024	0.020	332.0	−1.219	0.224						
Exclosure × Year 2006	−0.039	0.028	332.0	−1.388	0.166						
Exclosure × Year 2011	−0.058	0.028	332.0	−2.046	**0.042**						
EVENNESS											
Intercept	0.609	0.011	14.5	57.481	< 0.001	Intercept	0.613	0.016	4.0	39.145	< 0.001
Year 2006	−0.015	0.007	334.0	−2.232	**0.026**	Herbivory intensity	−0.132	0.043	25.7	−3.052	**0.005**
Year 2011	−0.040	0.007	334.0	−6.041	**< 0.001**						

Note: Evenness is calculated as exp(Shannon diversity index)/species richness. The models are linear mixed models fit with fit by REML Satterthwaite approximations to calculate degrees of freedom. We fitted models with fixed factors year (2001, 2006, and 2011), treatment, and interaction, with random factor plot in macroplot in site (Exclosure vs open plots) and fixed factors herbivory intensity and herbivory intensity^2 with random factors plot in site and year (Herbivory intensity). Evenness did not differ between open and exclosure plots. Preliminary model with the treatment effect, gave P = 0.568.

Table S3 Effect of (a) exclosure treatment, and (b) herbivory intensity on alpha diversity measured with Shannon diversity index and evenness in three understory layers: bottom, field and understory trees.SE = standard error, d.f. = degrees of freedom.

a) Exclosure vs open plots						b) Herbivory intensity					
Fixed effects	Estimate	SE	d.f.	*t*	*P*	Fixed effects	Estimate	SE	d.f.	*t*	*P*
SHANNON DIVERSITY INDEX											
Bottom layer											
Intercept	1.135	0.084	329	13.573	< 0.001	Intercept	1.102	0.103	14.0	10.673	< 0.001
Year 2006	−0.101	0.025	329	−3.985	**<0.001**	Herbivory intensity	0.288	0.262	146.8	1.097	0.275
Year 2011	−0.014	0.025	329	−0.566	0.572						
Field layer											
Intercept	1.759	0.035	329	49.408	< 0.001	Intercept	1.820	0.052	17.4	34.649	< 0.001
Year 2006	0.007	0.015	329	0.496	0.627	Herbivory intensity	−0.747	0.239	141.7	−3.121	**0.002**
Year 2011	−0.082	0.015	329	−5.483	< 0.001	Herbivory intensity ^{2}	0.718	0.350	166.5	2.051	**0.042**
Understory tree layer											
Intercept	0.300	0.101	57	2.962	0.004	Intercept	0.655	0.158	9.6	4.141	0.002
Exclosure (vs Open)	0.145	0.079	57	1.851	0.069	Herbivory intensity	−1.073	0.577	10.0	−1.858	0.093
Year 2006	0.283	0.096	57	2.939	**0.005**						
Year 2011	0.258	0.096	57	2.679	**0.010**						
EVENNESS											
Bottom layer											
Intercept	0.641	0.015	329	41.791	< 0.001	Intercept	0.618	0.027	6.8	22.678	< 0.001
Year 2006	−0.034	0.013	329	−2.677	**0.008**	Herbivory gradient	−0.061	0.094	29.5	−0.648	0.522
Year 2011	−0.061	0.013	329	−4.830	**< 0.001**						
Field layer											
Intercept	0.670	0.016	327	42.112	< 0.001	Intercept	0.677	0.018	8.5	38.130	< 0.001
Exclosure (vs Open)	−0.038	0.016	11	−2.430	**0.033**	Herbivory gradient	−0.201	0.060	42.2	−3.331	**0.002**
Year 2006	−0.019	0.012	327	−1.572	0.117						
Year 2011	−0.045	0.012	327	−3.741	**< 0.001**						
Exclosure x Year 2006	0.034	0.017	327	2.057	**0.041**						
Exclosure x Year 2011	0.053	0.017	327	3.205	**0.002**						
Understory tree layer											
Intercept	0.906	0.046	46	19.689	< 0.001	Intercept	0.924	0.050	2.8	18.450	< 0.001
Exclosure (vs Open)	−0.083	0.058	46	−1.415	0.164	Herbivory gradient	−0.464	0.165	24.2	−2.807	**0.010**
Year 2006	−0.001	0.060	46	−0.013	0.990						
Year 2011	−0.126	0.061	46	−2.054	**0.046**						
Exclosure x Year 2006	−0.233	0.080	46	−2.903	**0.006**						
Exclosure x Year 2011	−0.144	0.082	46	−1.768	0.084						

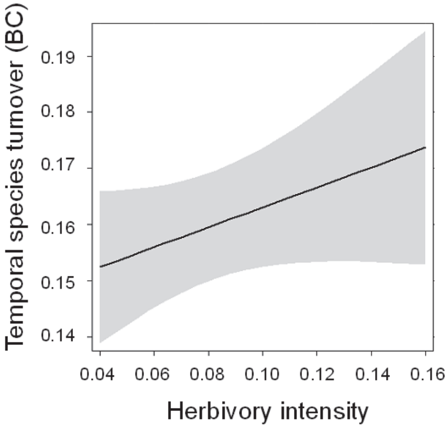
Note: Evenness is calculated as exp(Shannon diversity index)/species richness. The models are linear mixed models fit by REML Satterthwaite approximations to calculate degrees of freedom. We fitted models with fixed factors year (2001, 2006, and 2011), treatment, and interaction, with random factor plot in macroplot by site (Exclosure vs open plots) and fixed factors herbivory intensity and herbivory intensity^2 with random factors plot in site and year (Herbivory intensity). For Shannon bottom and understory tree layer, and evenness bottom layer the null model was the best model.

Table S4 Effect of a) exclosure treatment, and b) herbivory intensity on temporal and spatial species turnover. Parameter estimates for the most parsimonious model of the effects of year, treatment or herbivory intensity, and interactions, when plots situated in red deer farm is omitted from the analyses.

(a) Exclosure vs open plots without red deer farm plots						(b) Herbivory intensity without red deer farm plots					
Fixed effects	Estimate	SE	d.f	*t*	*P*	Fixed effects	Estimate	SE	d.f.	*t*	*P*
TEMPORAL SPECIES TURNOVER											
(1a)						(1b)					
Intercept	0.162	0.007	43.0	24.195	< 0.001	Intercept	0.145	0.011	115.8	13.543	< 0.001
Exclosure (vs Open)	0.017	0.009	245.3	2.030	**0.043**	Herbivory intensity	0.177	0.118	127.4	1.502	0.136
Year 2006–2011 (vs 2001–2006)	−0.005	0.007	138.0	−0.633	0.528						
Exclosure x Year 2006–2011	−0.001	0.010	138.0	−0.111	0.912						
SPATIAL SPECIES TURNOVER											
(2a)						(2b)					
Intercept	0.264	0.015	10.6	17.501	< 0.001	Intercept	0.263	0.016	10.3	16.882	< 0.001
Exclosure (vs Open)	−0.001	0.008	225.8	−0.160	0.873	Herbivory intensity	0.032	0.046	69.1	0.697	0.488
Year 2006	0.005	0.005	276.0	0.995	0.321						
Year 2011	0.000	0.005	276.0	−0.009	0.992						
Exclosure × Year 2006	0.010	0.007	276.0	1.452	0.148						
Exclosure × Year 2011	0.024	0.007	276.0	3.559	< **0.001**						

Note: The models are linear mixed models fit with fit by REML Satterthwaite approximations to calculate degrees of freedom, with spatial random factor plot in macroplot by site for model 1a & 2a, plot by site for model 1b, and site pluss temporal random factor year for 2b. Reference factors are Open 2001–2006 and Open 2001 for 1a and 2a, respectively, and represented by the intercept.

Figure S1 Fitted relationship (black line, P = 0.136) and 95 % CI (grey shade) between temporal species turnover, measured with Bray-Curtis dissimilarity index within plot between years, in relation to the gradient of herbivory intensity, when plot situated in red deer farm is not included.



Paper III

Biodivers Conserv (2018) 27:2507–2525
https://doi.org/10.1007/s10531-018-1550-x

ORIGINAL PAPER

Red deer structure the ground-dwelling beetle community in boreal forest

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Received: 23 November 2017 / Revised: 23 March 2018 / Accepted: 12 April 2018 /

Abstract Changes in large herbivore distribution and abundance can have effects that potentially cascade throughout the trophic structure of an ecosystem. Little is known about these indirect trophic effects of ungulate herbivory, so the aim of this study was to investigate the role of red deer (*Cervus elaphus*) in determining the distribution and diversity of ground-dwelling beetles. We collected > 9000 beetles belonging to 149 species in a Western Norway boreal forest by pitfall trapping inside and outside red-deer exclosures placed along a gradient in herbivory intensity. Our study showed that red deer herbivory had a significant effect on structuring ground beetle communities in this boreal ecosystem. Key findings were that: (1) out of 17 beetle species represented by more than 100 specimens, four species benefited from red deer herbivory and associated impacts, while two were detrimentally affected; 2) red deer herbivory did not affect beetle abundance or alpha diversity, but increased local variation in beetle community structure (higher beta diversity); and 3) red deer browsing is important for the composition of the ground-beetle fauna. Herbivory improved the explanation of variation in beetle species composition on the forest floor by 40%. Given that herbivory is an indirect but central predictor of ground-dwelling

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Communicated by Peter Bridgewater.

This article belongs to the Topical Collection: Forest and plantation biodiversity.

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s10531-018-1550-x) contains supplementary material, which is available to authorized users.

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beetle communities, it should be included in future studies or monitoring programs of red listed or keystone ground-dwelling beetles.

Keywords Browsing · *Cervus elaphus* · Coleoptera · Grazing · Insect diversity · Species richness · Ungulates

Introduction

In recent decades, large herbivores have extended their range and increased in local abundance throughout the northern hemisphere (Côté et al. 2004). Explanations proposed for this expansion include shifts to a milder climate, regulated hunting, and local extirpation of large predators (Mysterud et al. 2010; Ripple et al. 2014). Because selective herbivory modifies plant communities, large herbivores can modify ecosystem structure and function (Augustine and McNaughton 1998), for example by limiting forest regeneration and promoting field and bottom layer vegetation (Hegland and Rydgren 2016). This can occur even at low population densities if herbivores selectively feed on tree seedlings and saplings (Côté et al. 2004; Mysterud et al. 2010; Beschta and Ripple 2016; Lilleeng et al. 2016). Studies of how large herbivores induce effects on ecosystems typically focus on plant communities. Herbivory by large mammals can, however, also have far-reaching effects on other trophic levels. Affected organisms include birds, other mammals and invertebrates such as arthropods (deCalesta 1994; Pedersen et al. 2011; Foster et al. 2014; Chollet et al. 2016).

Arthropods comprise a diverse and species-rich group, and are important providers of ecosystem services by occupying crucial positions in all terrestrial food webs (Gullan and Cranston 2005; Prather et al. 2013). Large herbivores can affect arthropod communities directly and indirectly, generating cascading effects throughout the arthropod interaction web (van Klink et al. 2015). Direct impacts include accidental consumption and disturbance (Ben-Ari and Inbar 2013; Gish et al. 2017), whereas indirect effects on arthropod communities can occur through modifications to the soil and changes to vegetation structure, diversity and biomass (van Klink et al. 2015). Such modifications can facilitate or inhibit the population dynamics of arthropod species. Arthropod diversity tends to increase when large herbivores increase plant species diversity and structural heterogeneity, but there are also examples were large herbivores increase plant species diversity but reduce arthropod diversity (van Klink et al. 2015). Effects of large herbivores are typically most pronounced on vegetation-dwelling arthropods (Suominen and Danell 2006; Brousseau et al. 2013).

Most studies of how herbivory affects arthropod communities have been done in grasslands, although studies from forests are also emerging (e.g. Baines et al. 1994; Allombert et al. 2005b; Melis et al. 2006, 2007; Martin et al. 2010; Brousseau et al. 2013; Bachand et al. 2014; Iida et al. 2016). Still, the mechanisms by which large herbivores affect these communities in other ecosystems remains poorly understood (van Klink et al. 2015). Moreover, most studies of how herbivores affect arthropods focus on single-species responses. A comprehensive approach, one that addresses changes in species richness, species composition and relationships to important environmental factors, would greatly improve our understanding of the complex ecological effects herbivores have on ecosystems (Dornelas et al. 2011; Foster et al. 2014).

Boreal forests are widespread on the northern hemisphere and cover 11% of the Earth's terrestrial surface (Bonan and Shugart 1989). Whereas boreal forests can be strongly affected by large herbivores (Côté et al. 2004), no consistent patterns have been found so far for the effects of large herbivores on arthropod communities in this system (Suominen and Danell 2006). Variation in species assemblages of ground-dwelling beetles (henceforth 'beetles') in boreal forests is driven primarily by soil moisture and plant species composition (Birkemoe 1993; Toivanen et al. 2014), whereas plant species richness per se does not determine beetle richness (Similä et al. 2006). A clear relationship between beetle abundance and site productivity has been shown (Birkemoe 1993; Simila et al. 2002). Moreover, beetles demonstrably respond to many sorts of disturbance at a local scale (Koivula 2011; Kotze et al. 2011). Thus open patches, brought about by disturbances such as wildfire, wind throw and clear-cutting, often show higher beetle species richness than undisturbed sites (Koivula et al. 2002; Toivanen et al. 2014).

In Norway, red deer (*Cervus elaphus*) have reached unprecedented levels, best reflected by the harvest numbers, which for example increased by 70% from 1999 to 2009 (Austrheim et al. 2011). There is little or no natural predation on red deer in Norway, and populations are regulated by climate (winter severity) and, mainly, hunting. Selective herbivory by red deer affects plant species composition and structure, and consequently light and moisture conditions near the forest floor (e.g. Baines et al. 1994; Fuller and Gill 2001; Tremblay et al. 2006; Hegland et al. 2013; Hegland and Rydgren 2016). Red deer can have a range of community- and ecosystem-level impacts beyond that of herbivory itself (Côté et al. 2004). Consumption of plant parts can affect plant survival, structure and productivity, but also change plant chemistry, litter, and nutrient and water cycles, and defecation and trampling can alter soil chemistry, moisture, and soil physical properties (Augustine and McNaughton 1998, and references therein). We use the term 'herbivory' to encompass this range of influences because they all stem from that basic process. Although red deer have been found previously to spatially homogenize the understory plant community (Lilleeng et al. 2016), our knowledge of red deer effects on other trophic levels is still fragmentary (Similä et al. 2006). This is unfortunate because assessments of the state and functioning of ecosystems requires knowledge of the status for several functional groups (Koivula 2011).

The few studies that have addressed relationships between beetles and red deer in boreal forests do not show clear and consistent patterns. Most have focused only on carabids, ignoring other ground-dwelling species. Whereas one study indicates that herbivory by red deer do not affect carabid diversity even though the total number of beetles increased (Melis et al. 2006), studies on moose and reindeer find a unimodal response of beetle species richness to herbivory intensity (Suominen et al. 2003; Melis et al. 2007). Environmental conditions like soil moisture and vegetation are important determinants of carabid species compositional variation (Niemelä et al. 2007; Toivanen et al. 2014), but as far as we know, no studies have yet disentangled the relative contribution of large herbivores compared to key environmental variables in structuring the composition of ground-beetle communities.

Identifying how large herbivores affect biodiversity can provide important insights into the effects of the currently unprecedented high ungulate levels on long-term ecosystem stability of boreal forests. The aim of our study was to quantify the potential impacts of red deer herbivory on the ground-dwelling beetle community. We used an experimental research design with pitfall traps inside and outside red deer exclosures in a boreal forest with varying levels of red deer herbivory. Specifically, we asked: (Q1) Which ground-dwelling beetle species benefit from, or are detrimentally affected by red deer herbivory?

(Q2) How does red deer herbivory influence the alpha and beta diversity and the evenness of ground-dwelling beetles? (Q3) What proportion of the variation in the ground-dwelling beetle species assemblage can be explained by red deer herbivory intensity, relative to other environmental variables?

Methods

Study area

We conducted our study on Svanøy Island (11 km^2, 61°30′N, 5°05′E), situated 2.3 km off the mainland, Sogn og Fjordane county, western Norway. The climate is oceanic with mean annual precipitation and temperature of ca. 2000 mm and 8 °C, respectively (Skogen and Lunde 1997, Florø www.met.no). Svanøy is located in the boreo-nemoral zone (Moen 1999) and the dominant vegetation type is bilberry-pine (*Vaccinium myrtillus–Pinus sylvestris*) forest. Red deer density at Svanøy is estimated at ca. 7.5 deer km^{-2}, relatively high for western Norway (Hegland et al. 2013). The island also includes a fenced red deer farm with > 30 deer km^{-2} (Fig. 1). Although such high densities are not found in wild populations in Norway, some Islands in British Columbia, Canada do reach such high levels (Allombert et al. 2005a). Red deer browsing limits the dwarf shrubs and young trees, but is beneficial for tree seedlings, ferns, forbs and bryophytes in our study area (Hegland and Rydgren 2016). High levels of red deer over longer time periods is likely to limit the number of trees that reach the reproductive stages (Lilleeng et al. 2016), which may in turn cause a major shift in abiotic conditions for arthropods communities.

Study design and beetle sampling

In 2001, we established twelve blocks within old-growth pine forest at altitudes between 20 and 140 m, each block containing one exclosure and one open (control) macroplot, both 9 × 9 m (Fig. 1). We excluded deer from the exclosures by fencing a 10 × 10 m area with the macroplot in the center, using 3-m high fences of 10 × 10 cm wire mesh, and leaving a buffer zone of 0.5 m around the exclosure macroplot. In each macroplot, we randomly placed seven 1 × 1 m permanent vegetation plots, restricting them to flat terrain > 0.5 m from trees > 2 m high (Fig. 1). Accordingly, we had 7 × 2 × 12 = 168 plots overall. Plant

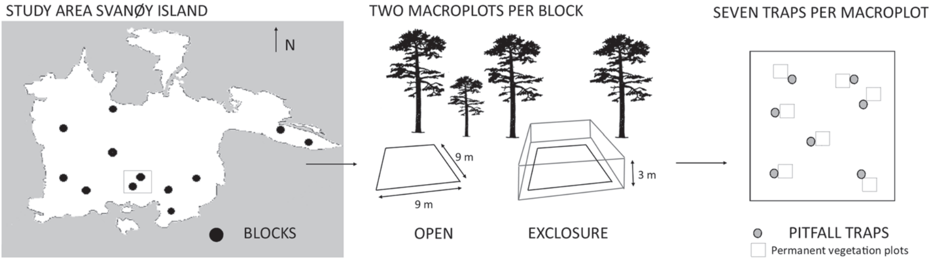

Fig. 1 Illustration of our research design for sampling ground-dwelling beetles inside and outside red deer (*Cervus elaphus*) exclosures, along a natural gradient of red deer herbivory intensity. Positions of the twelve study blocks are indicated by black dots, and red-deer farm blocks indicated with a square on the map. See text for details

species composition was recorded in each plot in June 2001, 2006 and 2011 and we recorded the abundance of all plants in each plot as frequency out of 100 equally sized subplots (Hegland et al. 2013; Hegland and Rydgren 2016; Lilleeng et al. 2016). In 2011, we captured ground-dwelling beetles in one pitfall trap adjacent to each permanent plot (total number of traps = 168). We used the vegetation characteristics and other environmental variables sampled in each permanent plot as explanatory variables for each trap. We henceforth used 'plot' as a collective term for pitfall trap together with its adjacent permanent vegetation plot. For pitfall traps we used plastic cups with an inner diameter of 8.3 cm and depth 10.0 cm, dug into the ground with the top of the cup level with the soil surface. To preserve the beetles and prevent evaporation we filled the cups 2/3 with a 1:1 mixture of polypropylenglycol and water to which we added a droplet of detergent to break the surface tension. We placed a 15 × 15 cm wooden plate 5–10 cm above each trap to prevent flooding and litter infall. We started trapping in May 2011 and collected the contents of each trap at monthly intervals until August 2011. We pooled the three samples from each plot into a composite sample. We used the number of individuals as a measure of each species' abundance (the maximum collected in any one plot was 53). All invertebrates were stored in 70% ethanol.

Pitfall traps, which are commonly used for trapping ground-dwelling beetles, are assumed to capture more active species at a faster rate than sedentary species (Andersen 1995). We assume that this potential bias did not differ between the open and exclosure plots, and therefore did not affect comparisons between these treatments. All beetle specimens were identified to species and classified to functional group according to their diet: 'predators', 'detritivores', 'omnivores', 'herbivores', 'fungivores', 'saproxylic' and 'others'.

Herbivory intensity

In 2011, we quantified local herbivore density in the twelve open macroplots indirectly, by estimating the extent of browsing on bilberry (*Vaccinium myrtillus)* ramets. Red deer have an intermediate preference for bilberry, which is thus a good indicator species for assessing herbivore density in an area (Mysterud et al. 2010). In June 2011, we selected three bilberry ramets at random in each of the 168 plots. For each ramet, we recorded the percentage of annual shoots browsed using a five-grade ordinal scale: 0 (0–0.9%), 1 (1–24%), 2 (25–49%), 3 (50–74%), 4 (75–100%). Our measure of herbivory intensity is adjusted for plant size by dividing the herbivory scale value by ramet height (Lilleeng et al. 2016). The mean of adjusted values for the 7 × 3 ramets in each macroplot (which was 0 in exclosure plots) was termed 'current herbivory intensity' (HI_C) and used as an explanatory variable in our analyses. This index correlates well with fecal pellet counts (Hegland et al. 2013), which are also often used to estimate herbivore density. We have recorded browsing on bilberry since 2001, and the distribution of the blocks along the herbivory intensity gradient has remained similar over the years. To quantify any legacy of former browsing or grazing on the beetle assemblage, we also included a variable, termed 'historical herbivory intensity' (HI_H), by assigning to each exclosure macroplot the same herbivory intensity value as recorded for the corresponding open macroplot in 2011.

Environmental variables

We characterized the vegetation in each plot by measuring the height of the understory vegetation (average of three measures of the tallest plant in each plot, in cm) and by recording the abundance of six plant growth forms: bryophytes, ferns, grasses, herbs, dwarf shrubs and trees (saplings $\leq$ 50 cm) as the sum of abundances for the species belonging to the particular growth form.

Soil samples were obtained by mixing three samples taken adjacent to each plot. Soil organic matter% (SOM) was measured as loss on ignition (100 – ash%). The total nitrogen in the soil sample, obtained as weight% by the Dumas method (Bremmer and Mulvaney 1982), was recalculated as weight% of organic matter by dividing by 0.01*SOM. The resulting variable, termed 'total nitrogen', was used in the analyses. pH was recorded in a water solution with a WTW720 pH-meter and a WTW SenTix81 pH-electrode. Soil moisture was measured once in the four corners of all plots following at least two days without rain. All 168 plots were measured within 48 h, using an AT Delta-T moisture meter, type HH2 SM300 v 4.0, by Delta-T Devices Ltd. We used the mean of the four measurements per plot in the analyses. There was insufficient variation in light levels between plots to include this as a meaningful explanatory variable in the analyses, because all blocks had dense canopy cover (spherical densitometer measurement of canopy cover: mean = 97%, range 83–100%). We estimated altitude at each block with a handheld GPS.

Data analysis

We performed all statistical analyses in R, version 3.4.2 (R Core Team 2017), except for 'glmmadmb' models (see under), which we ran on R, version 3.1.3 (R Core Team 2015). For *Questions 1 & 2*, we used raw variable values in our analyses. Before using multivariate analyses to address *Question 3* we transformed all environmental variables, except HI_C, HI_H, and herb and fern abundances, to zero skewness (Økland et al. 2001; Økland 2003) and ranged them on a 0–1 scale (Table 1). HI_C, herb and fern abundances included too many zero values to allow transformation to zero skewness, so these variables were ranged without being transformed. HI_H was also only ranged, to facilitate comparison with HI_C. Results of multivariate analyses using just the raw values for all environmental variables

Table 1 List of explanatory variables used in multivariate analysis

Explanatory variables	Mean (SE)	Min–max	Transformation	Group
Altitude (m)	85 (3.55)	21–143	e^{cx}	E
Soil moisture (%)	42 (1.13)	20–94	$\ln(c+x)$	E
Total nitrogen	2.1 (0.05)	1.31–5.19	$\ln(c+\ln(c+x))$	E
pH	4.2 (0.02)	3.83–5.24	$\ln(c+x)$	E
Vegetation height (cm)	19 (0.67)	2–46	$\ln(c+x)$	E
Dwarf-shrub abundance	145 (8.50)	0–345	$\ln(c+x)$	E
Herb abundance	57 (5.05)	0–268	–	E
Grass abundance	133 (5.26)	14–273	$\ln(c+x)$	E
Fern abundance	5 (1.18)	0–77	–	E
Bryophyte abundance	176 (8.37)	20–406	$\ln(c+x)$	E
Young tree abundance	6 (0.98)	0–93	$\ln(c+x)$	E
Current herbivory intensity, HI_C	0.08 (0.01)	0–0.63	–	H
Historical herbivory intensity, H_{IH}	0.16 (0.01)	0.01–0.63	–	H

Group = affiliation to explanatory variables group: environmental (E) and herbivory intensity (H) variables. All variables were continuous did not differ significantly from those reported here, indicating that our conclusions were not influenced by the choice of data transformation. We validated our final models by assessing normality of residuals with quantile–quantile-plots and plots of residuals vs fitted values, as well as comparing the models with the null model, as suggested by e.g. Zuur et al. (2012).

Species responses (Q1)

To examine the beetle species' responses to red deer herbivory, we estimated the effects of treatment (all plots) and current herbivory intensity (HI_C, open plots) for species that were represented by at least 100 individuals in our collections. We used negative binomial generalized linear mixed effects models with AD model builder (glmmadmb Skaug et al. 2016), including random factors *macroplot* nested in *block* for exclosure models, and *block* for herbivory intensity models. To evaluate if the number of species responding to herbivory differed from that expected from a random distribution, we used the 'exact binomial test' with $p = 0.05$, and alternative = 'greater'.

Diversity measures (Q2)

To address how red-deer herbivory influence different aspects of beetle diversity, we used the R package 'BiodiversityR' version 2.5-3 (Kindt and Coe 2005) to calculate beetle species richness (α diversity, the number of species) and evenness (exp(H′)/species richness, where H′ is Shannon's diversity index). H′, which combines measures of richness and abundance, gave no additional information and was not used, other than to calculate evenness. We estimated the effects of treatment (open vs exclosure, all plots) and current herbivory intensity (HI_C, open plots) on these diversity measures by using linear mixed effects models [lme4 (Bates et al. 2015) and lmerTest (Kuznetsova et al. 2016)], with *macroplot* nested in *block*, and *block*, respectively, as random factors. To evaluate whether species richness differed between the open and exclosure plots when differences in the number of sampled individuals were taken into account, we calculated individual-based rarefaction curves using the function 'accumcomp' (1000 permutations) in the BiodiversityR package (Kindt and Coe 2005) with treatment as the factor.

We used the functions 'betadisper' and 'betadiver' from the vegan package version 2.3-3 (Oksanen et al. 2016), to calculate Whittaker's index (Koleff et al. 2003) as a measure of beta diversity between treatments. Open and exclosure plots were compared by the permutation test for homogeneity of multivariate dispersions (function 'permutest' with 999 permutations, Anderson et al. 2006).

Composition of beetle assemblages (Q3)

Multivariate analysis was used to assess the relative importance of red-deer herbivory and environmental variables in determining the composition of beetle assemblages. We first summarized the patterns of variation in beetle species assemblages in the 168 plots by parallel use of both global non-metric multidimensional scaling (GNMDS, Minchin 1987) and detrended correspondence analysis (DCA, Hill and Gauch 1980), as implemented in the vegan package (Oksanen et al. 2016). Parallel ordination (Økland 1996; van Son and Halvorsen 2014) was motivated by the argument that since all ordination methods may occasionally produce inappropriate results (artefactual axes), similar results obtained by two conceptually different ordination methods makes a strong case that the axes represent real compositional gradients. Similarity of axes from different ordinations was assessed using Kendall rank correlation coefficients (cf. Liu et al. 2008). GNMDS ordination diagrams showed no evidence of methodological artefacts, while the DCA diagrams showed a clear tongue-shaped structure which often indicates inappropriate handling of data by the detrending procedure (Økland 1990). We therefore chose GNMDS results for further interpretation. We investigated the relationship between the two GNMDS ordination axes and the ranged and zero-skewness transformed explanatory variables: treatment, herbivory intensity, and environmental variables, evaluated at three nesting levels, *block* (df = 12), *macroplot* nested in *block* (df = 24), and *plot* nested in *macroplot* (df = 168), using split-plot GLM (generalized linear models McCullagh and Nelder 1989; Auestad et al. 2008).

See Online Resource 1 for supplementary details for the ordination analyses.

We used variation partitioning (Borcard et al. 1992; Økland 1999, 2003) with canonical correspondence analysis (CCA; ter Braak 1986) and a Monte Carlo test with 999 permutations (Oksanen et al. 2016) to assess the relative importance of herbivory and the environmental variables in explaining the variation in beetle species composition. Prior to variation partitioning, we evaluated all explanatory variables individually. Only those with $\alpha \leq 0.05$ in the Monte Carlo permutation test were eligible for inclusion in the analysis. We selected variables for inclusion in the two groups, environmental influences and herbivory intensity, by performing separate forward selections of variables. Only those that explained significant ($p < 0.01$) additional variation (i.e. variation not explained by the previously selected variables) were incorporated in the subsequent analyses (Økland 2003). The final group of environmental variables, denoted E, consisted of altitude, soil moisture, pH, total nitrogen and vegetation height, whereas the herbivory intensity group, H, consisted of HI_C and HI_H (Table 1). We performed a sequence of (partial) CCA analyses to quantify the variation explained by H not shared with E ($H| E$), E not shared with H ($E| H$), and the variation shared by the two groups ($H \cap E$). All variation components are expressed as fractions of the total variation explained (Økland 1999). Supplementary details in Online Resource 1.

Results

We collected 9733 individuals of beetles representing 149 species. Of these, 129 species and 4913 individuals were collected in the herbivore open plots and 113 species and 4820 individuals in the exclosure plots. The mean (± SE) number of species and individuals in each plot was 16 species (± 0.6) and 59 individuals (± 3.4) in open plots, and 15 species (± 0.5) and 57 individuals (± 3.0) in exclosure plots(n = 84 for both groups). Of the 23 families recorded, three were dominant: Carabidae (n = 4570 individuals), Staphylinidae (n = 2728), and Hydrophilidae (n = 1149). The three most abundant species were *Pterostichus niger* (Fam. Carabidae, n = 1968), *Megasternum concinnum* (Fam. Hydrophilidae, n = 1134), and *Philonthus decorus* (Fam. Staphylinidae, n = 1024). Many species were rare, but all plots had five or more species. Out of the species with five or more individuals, *Drusilla canaliculata, Loricera pilicornis*, *Notiophilus biguttatus* and *Proteinus atomarius* were only recorded from open plots while *Megarthrus nitidulus* and *Rhizophagus ferrugineus* were found in exclosure plots only.

The largest functional groups in our material were predatory beetles (77% of the total number of beetles) and detritivores (16%). Omnivores comprised 6% of the total, fungivores and saproxylics 0.3% each, herbivores 0.2% and unclassified 0.1%. We found no significant effects of treatment on the overall abundance of the respective groups, except for saproxylic beetles which were more abundant (27 out of 34 individuals) in open plots. A complete species list with abundance and feeding guilds in open and exclosure plots can be found in Online Resource 2.

Total nitrogen, pH, herb and bryophyte abundances were positively correlated, and vegetation height and dwarf-shrub abundance were negatively correlated with current herbivory intensity (HI_C, Online Resource 3). Historical herbivory intensity (HI_H) was related to these variables in largely the same way, and was also positively correlated with soil moisture, grass abundance, bryophyte abundance and the abundance of tree saplings (Online Resource 3).

Species responses (Q1)

Four out of the 17 most abundant species (those with > 100 individuals) were categorized as 'winners' and two as 'losers', with increasing or declining abundances in relation to red deer herbivory (Fig. 2 and Online Resource 4). The proportion of species responding to herbivory was significantly higher than expected (observed proportion = 0.35 vs. expected = 0.05, $p < 0.001$). The declining species were *Phosphuga atrata* (estimates are exclosure vs open; $\beta = 0.63$, $SE = 0.27$, $z = 2.30$, $p = 0.022$) and *Megasternum concinnum* ($\beta = 0.46$, $SE = 0.19$, $z = 2.36$, $p = 0.018$), and the increasing species were *Geotrupes stercorosus* ($\beta = -0.68$, $SE = 0.31$, $z = -2.23$, $p = 0.026$), *Trechus secalis* ($\beta = -0.86$, $SE = 0.23$, $z = -3.70$, $p < 0.001$), *Patrobus atrorufus* ($\beta = -1.77$, $SE = 0.86$, $z = -2.05$, $p = 0.040$), and *Nebria brevicollis* ($\beta = -2.40$, $SE = 0.43$, $z = -5.54$, $p < 0.001$, Fig. 2). The abundances of *P. atrorufus* ($\beta = 10.79$, $SE = 4.28$, $z = 2.52$, $p = 0.012$) and *N. brevicollis* ($\beta = 17.09$, $SE = 5.46$, $z = 3.13$, $p = 0.002$) were positively related to current herbivory intensity, whereas *Cryptophagus setulosus* ($\beta = -5.85$, $SE = 1.91$, $z = -3.06$, $p = 0.002$), *P. atrata* ($\beta = -6.09$, $SE = 2.09$, $z = -2.91$, $p = 0.004$), and *Nicrophorus vespilloides* ($\beta = -7.28$,

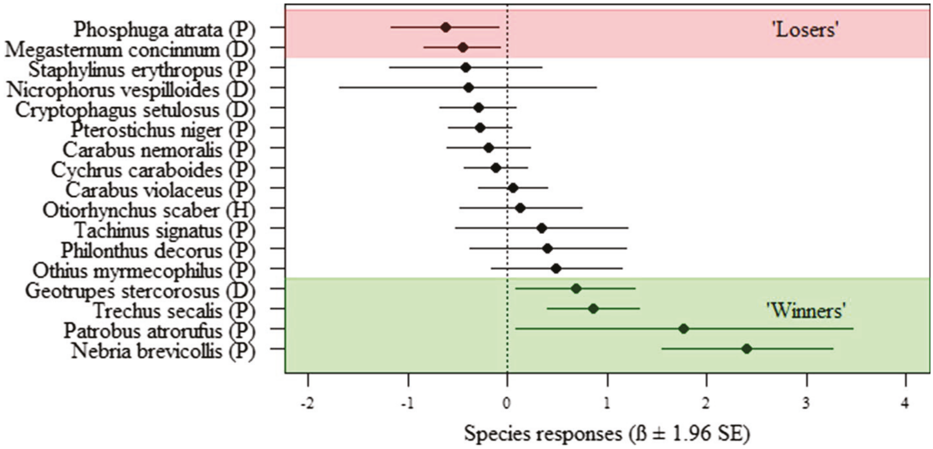

Fig. 2 Responses of the 17 most abundant beetle species (> 100 individuals in total) to exclusion of red deer, categorized as 'winners' or 'losers'. Parameter estimates (± 1.96 SE) from mixed models comparing abundance in open and exclosure plots are given on the horizontal axis. Affiliation of beetle species to functional group is given in brackets, *P* predator, *H* herbivore, *D* detritivore

SE = 3.60, z = − 2.02, p = 0.043) abundance was negatively related to current herbivory intensity (Online Resource 4). The abundance of all beetles pooled was not related either to treatment (open/exclosure) or to herbivory intensity (p values > 0.05, Table 2).

Beetle diversity responses to red deer herbivory (Q2)

Neither species richness nor evenness were significantly related to treatment (open vs exclosure, p-values > 0.05) but for herbivory intensity there was a trend towards increasing richness and reduced evenness with increasing herbivory intensity (p values = 0.090, Table 2). The cumulative number of species, however, was smaller in the exclosures (Online Resource 3). Red deer herbivory increased the heterogeneity of the beetle assemblages, judging from the beta diversity value, which was higher in open than in exclosure plots (permutation test; 999 permutations; F = 6.56, p = 0.009).

Composition of beetle assemblages related to herbivory and environment (Q3)

The first GNMDS axis, the main beetle compositional gradient, explained most of the variation in species composition at the block level (fraction of total sum-of-squares explained, FVE = 0.78), followed by plot in macroplot (FVE = 0.17), and macroplot within block (FVE = 0.06) levels (Table 3). It was negatively related to current herbivory intensity (HI_C), soil chemistry (pH and total nitrogen), and grass and bryophyte abundance, but positively related to herb and dwarf-shrub abundance (Table 3, Online Resource 6). More than half of the variation along the second GNMDS axis was explained at the block level (FVE = 0.62), while plot in macroplot was again important (FVE = 0.26) and macroplot in block explained the rest (FVE = 0.12). The second GNMDS axis was associated with both current and historical herbivory intensity (HI_H) and separated blocks situated inside the red deer farm from other blocks (Online

Table 2 Parameter estimates from linear mixed effects models with *macroplot* nested in *block* as random factors for exclosure models and random factor *block* for current herbivory-intensity models

	Estimate	SE	t	P		Estimate	SE	t	p
Richness									
Intercept	16.012	0.983	16.291	< 0.001	Intercept	14.371	1.291	11.131	< 0.001
Exclosure vs open	− 1.024	0.916	− 1.118	0.287	Herbivory intensity	10.041	5.252	1.912	0.085
Evenness									
Intercept	0.615	0.024	25.357	< 0.001	Intercept	0.652	0.029	22.226	< 0.001
Exclosure vs open	− 0.012	0.028	− 0.445	0.665	Herbivory intensity	−0.224	0.119	− 1.878	0.090
Abundance									
Intercept	58.488	6.575	8.896	< 0.001	Intercept	54.280	10.450	5.193	< 0.001
Exclosure vs open	− 1.107	5.812	− 0.190	0.852	Herbivory intensity	25.760	42.520	0.606	0.558

We validated each final model by visually investigating normality in model residuals with a quantile–quantile-plot and plots of residuals versus fitted values, in addition to comparing it with the null model. We report model estimates with explanatory variable treatment or herbivory intensity also for models were there were no significant effect of these variables, i.e. when the null model were the most parsimonious, to provide information for the reader

Table 3 Relationship between the two GNMDS ordination axes (response variables, scaled in half-change units), representing gradients in beetle species assemblages, and the ranged and zero-skewness transformed explanatory variables: treatment, herbivory intensity, and environmental variables, evaluated at three nesting levels, *block* (df = 12), *macroplot* nested in *block* (df = 24), and *plot* nested in *macroplot* (df = 168) by split-plot GLM

Explanatory variable	GNMDS 1											
	Block				Macroplot within block				Plot within macroplot			
	$SS_{block} = 22.24$				$SS_{macroplot} = 1.64$				$SS_{plot} = 4.74$			
	FVE = 0.78				FVE = 0.06				FVE = 0.17			
	SS_{expl}/SS_{block}	F	p	coef	$SS_{expl}/SS_{macroplot}$	F	p	coef	SS_{expl}/SS_{plot}	F	p	coef
Treatment					0.21							
HI_C	0.09				0.37	6.42	0.028	–				
HI_H	0.09											
Total nitrogen	0.63	17.04	0.002	–	0.36	6.19	0.030	–	0.01			
pH	0.52	10.83	0.008	–	0.31	5.06	0.046	–	0.02			
Soil moisture	0.13				0.05				0.01			
Altitude	0.06											
Vegetation height	0.11				0.19				0.00			
Bryophyte	0.14				0.31	4.87	0.049	–	0.00			
Herb	0.69	22.48	0.001	+	0.06				0.00			
Grass	0.50	10.40	0.010	–	0.06				0.01			
Fern	0.03				0.00				0.00			
Dwarf shrub	0.71	20.10	0.001	+	0.08				0.02			
Young tree	0.15				0.02				0.01			

Table 3 (continued)

Explanatory variable	GNMDS 1											
	Block				Macroplot within block				Plot within macroplot			
	$SS_{block} = 13.13$				$SS_{macroplot} = 2.55$				$SS_{plot} = 5.59$			
	FVE = 0.62				FVE = 0.12				FVE = 0.26			
	SS_{expl}/SS_{block}	F	p	coef	$SS_{expl}/$ $SS_{macroplot}$	F	p	coef	SS_{expl}/SS_{plot}	F	p	coef
Treatment					0.00							
HI_C	0.45	8.08	0.018	+	0.14							
HI_H	0.45	8.09	0.017	+								
Total nitrogen	0.00				0.07				0.00			
pH	0.15				0.06				0.00			
Soil moisture	0.01				0.02				0.02			
Altitude	0.00											
Vegetation height	0.13				0.02				0.00			
Bryophyte	0.02				0.01				0.00			
Herb	0.04				0.43	8.34	0.015	–	0.01			
Grass	0.06				0.08				0.00			
Fern	0.23				0.01				0.00			
Dwarf shrub	0.04				0.10				0.04	5.52	0.010	+
Young tree	0.03				0.18				0.01			

For each of the two response variables and at all three nesting levels both the total sum-of-squares (SS) and fraction of total sum-of-squares explained (FVE) are tabulated. The variation explained (SS_{expl}/SS_{level}) by each variable is given for all nesting levels and both GNMDS axes. Significant ($p \leq 0.05$) relationships are presented with F-value for an F-ratio test of difference from a random variable and p-level for this test. We indicate sign of model coefficients (coef) with + and – for positive and negative model coefficients, respectively

Resource 6, Fig. 3). Herb abundance was negatively related to the second GNMDS axis (Table 3).

Although open and exclosure plots were not significantly separated along GNMDS axis 1 (split-plot glm, $p > 0.05$, Table 3), species composition varied in response to whether herbivory had ceased for the past 10 years of the study. In all but two blocks, plots in exclosures tended to be placed further towards the high-score end of this axis, being more like open plots with lower current herbivory intensity ($F = 3.037$, $p = 0.109$, Fig. 3).

The two groups of explanatory variables, herbivory intensity and environmental attributes, explained 16.2% of the total variation in beetle composition. Of this, herbivory intensity alone explained 28% of the total variation explained (FTVE), the environmental variables alone explained 56% of the variation, and 16% of the FTVE was shared by herbivory intensity and the environmental variables (Online Resource 7).

Discussion

Species responses (Q1)

Red deer herbivory resulted in both benefiting and detrimentally affected species among the ground-dwelling beetles. Because herbivores consume arthropods only unintentionally

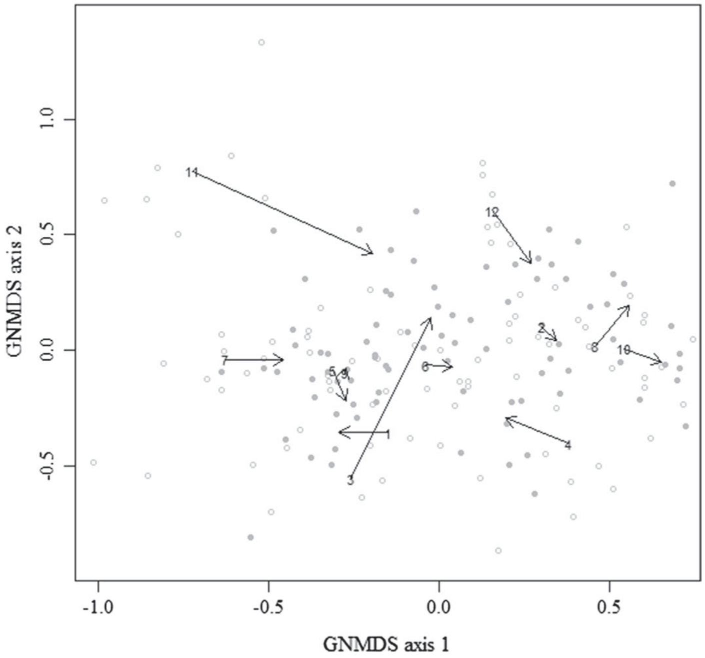

Fig. 3 Global non-metric multidimensional scaling ordination of beetles, sampling plot scatter. Plots with similar species assemblages occur close to each other in the ordination diagram. GNMDS axes 1 and 2 are scaled in half-change units. Arrows connect the centroids of the twelve open plots with the centroids of the corresponding exclosure plots. We used numbers to identify blocks. For block 9, the centroids of open and exclosure plots did not differ much related to the GNMDS axes, and therefore this arrow is short and not clearly visible in the figure. Blocks 11 and 12 are located in the red deer farm. Open and filled circles represent open and exclosure plots, respectively

(Gish et al. 2017), these changes in beetle abundance are most likely an indirect effect of ground disturbance by red deer. The predatory beetle *Nebria brevicollis* is common in forests, but is also found in disturbed areas (Elek et al. 2017). This may explain why *N. brevicollis* showed the strongest positive response to red deer herbivory observed in our study (see also Stewart (2001). *Patrobus atrorufus*, another predator, was also more abundant in red deer plots. Melis et al. (2007) report *P. atrorufus* only from areas with no or low moose browsing but, in contrast to our results where the species was abundant, they only recorded four specimens in their study. *Trechus secalis* has previously been characterized as a generalist predator, not responding to forest age or vegetation cover (Koivula et al. 2002), but we found it positively associated with red deer herbivory. Conversely, Melis et al. (2007) found most *T. secalis* individuals in moist areas experiencing low-intensity browsing. Niemelä et al. (2007) classify both *P. atrorufus* and *T. secalis* as well adapted to both open and closed forests. Therefore, one possible explanation for the positive response of these generalist predators to red deer herbivory may be reduced competition from other predatory species that is not adapted to the disturbance from red deer. Finally, the coprophagus species *Geotrupes stercorosus* lays eggs in tunnels dug under the feces of large herbivores, which may explain its positive response to the presence of red deer.

The two loser species in our study were *Phosphuga atrata,* a flightless predator specializing on gastropods (Ikeda et al. 2007), and *Megasternum concinnum*, which lives among and feeds on dead plants. Red deer herbivory opens-up the vegetation and removes biomass from the forest floor (Hegland and Rydgren 2016). Although we did not find a significant negative correlation between current herbivory intensity and soil moisture, herbivory likely reduces aboveground humidity by opening-up the vegetation, making the environment less suitable for gastropods. Thus, the loser species are possibly indirectly affected by red deer herbivory via their feeding habits. Although none of the winners or losers are rare or red listed (Henriksen and Hilmo 2015), our results show that red deer herbivory significantly affected the abundance of some major ground-dwelling beetle species. This effect is likely to cascade through their trophic relationships.

Both Melis et al. (2006) and Gonzalez-Megias et al. (2004) found higher total ground beetle abundance in grazed than ungrazed areas and explained this as being due to differences in shrub cover. Although dwarf-shrub cover in our study area was also negatively affected by red deer herbivory (Hegland and Rydgren 2016), we found no effect of herbivory on beetle abundances. Therefore, dwarf-shrub cover does not seem to be a suitable indicator of total beetle abundance.

Red deer influence on diversity measures (Q2)

We found no effects of red deer herbivory on beetle species richness or evenness. This accords with the results of the study of red deer–carabid relationships by Melis et al. (2006). In contrast, moose and reindeer herbivory appears to affect beetle alpha diversity (Suominen et al. 2003; Melis et al. 2007), possibly a response to these ungulates' more selective diet compared with red deer (Hofmann 1989; Adler et al. 2001). However, although often expected to be positive, there is currently no consensus about existence of a general, causal relationship between vegetation diversity and beetle diversity (van Klink et al. 2015). In some studies, no significant effect of grazing on plant species richness has been found even though grazing negatively impacts arthropod species richness by reducing the availability of food for herbivorous or detritivorous arthropods (van Klink et al. 2015).

Gonzalez-Megias et al. (2004) observed variable responses in beetle-species abundance, biomass and diversity in relation to herbivory, depending on the measure being compared, habitat and time. In our study, although plant species richness was lower in exclosures than in open plots, and showed a unimodal relationship to a gradient of herbivory intensity (Hegland et al. 2013), this did not translate into effects on beetle-species richness. The number of beetle species and total abundances thus seem stable at low and high deer population densities.

Although the number of beetle species is not affected by red deer herbivory, beetle species composition was less similar among the open plots (i.e. beta diversity was higher). We have previously shown an opposite effect of red deer herbivory on the plant community, with the number of plant species increasing while beta diversity decreased (Lilleeng et al. 2016). In contrast, moose herbivory has been found to reduce beta diversity in both vegetation and ground-dwelling beetles (Melis et al. 2007), although this could be due to site- or region-specific differences in the importance of vegetation structure complexity to beetles rather than to differences in the effects of different herbivores.

Composition of beetle assemblages related to herbivory and environment (Q3)

As expected, environmental variables are more important than herbivory in determining beetle-community composition, with soil chemical factors and relative abundance of different plant growth forms as the most important variables. Suominen et al. (2003) likewise found that the main source of variation in beetle-species assemblages is among-site environmental differences. Furthermore, physical barriers between the blocks that limit the distribution of species will also contribute to variation between blocks. Despite this, we found a significant independent effect of red deer herbivory on forest beetle assemblages that alone contributed 28% of the explained variation in the dataset.

Soil moisture did not have as pronounced effect on the local distribution of beetles as suggested by Toivanen et al. (2014). Soil moisture was a significant variable in our variance-partitioning analyses, but was not significant in explaining variation along the two GNMDS axes. The likely explanation for this is that our blocks are pine-dominated with a short soil-moisture gradient, restricted to the relatively dry side of the soil-moisture gradient investigated by Toivanen et al. (2014). Soil pH and nitrogen content were both important in explaining beetle composition, perhaps because of the beetles own preference for pH (Paje and Mossakowski 1984), or due to their prey species' sensitivity to pH and nitrogen. Defecation by large herbivore can enrich both nitrogen and pH levels in the soil (Moe and Wegge 2008; Abbas et al. 2012). We found stronger correlation between both pH and nitrogen and 'historical herbivory intensity', than with 'current herbivory intensity' (Online Resource 2), suggesting that the most important source of variation in pH and nitrogen among plots is natural between-block-variation. If soil nitrogen was causally related to red deer abundance, then total nitrogen should be more strongly correlated with current herbivory intensity, than with historical herbivory intensity.

In our study area, dwarf shrubs are functionally important for ground-dwelling beetles. The cover and assemblage of mature trees is probably the most important factor for beetle species assemblages within the boreal forest (Niemelä et al. 2007). However, red deer herbivory does not affect the short term density of mature trees in the studied pine forests (Lilleeng et al. 2016). Our results show that beetle assemblages strongly relates to the abundance of dwarf shrubs (Online resource 4). On the forest floor, dwarf shrubs like *Calluna vulgaris* and *Vaccinium myrtillus* play an important ecological role. Shrubs provide shade and influence soil moisture conditions and vertical vegetation structure and cover

(Stewart 2001), thus affecting both herbivorous insects and their predators. Increases in red deer density may thus eventually impact the functioning of forest ecosystems also when they do not affect the mature trees, if the deer dramatically reduce dwarf-shrub populations (Hegland and Rydgren 2016). Keystone herbivores may alter the structure and composition of ecological communities, and unprecedented herbivore densities can result in trophic cascades (Polis 1999; Terborgh et al. 2001; Rooney and Waller 2003; Côté et al. 2004; Lilleeng et al. 2016). We have shown that red deer induce changes in beetle species groups with which they do not directly interact, suggesting that the arthropod food web is being altered by red deer herbivory, underlining the potential of large herbivores to function as ecosystem engineers (Jones et al. 1994). Only a fraction of the red deer's potential to moderate boreal forest ecology has been explored here. In areas with threatened or near-threatened beetle species, red deer should be considered as a potential powerful moderator of species' assemblages, favoring beetle species associated with high grass- and bryophyte-cover, and suppressing beetles depending on herb- and dwarf shrub-cover.

Acknowledgements Sindre Ligaard did the taxonomic determination of the beetles and scored the species to ecological niches. Annie Aasen and Irene Dahl, MINA, NMBU, did the soil analyses. Katrine Eldegard gave early comments on the study design, and Sam Steyaert commented on earlier versions of this manuscript. Peter Frost did copy editing. Two anonymous referees provided constructive comments to earlier drafts. The study was supported by the Norwegian Research Council under the Miljø 2015 programme (project number 204403/E40) and the Norwegian Environment Agency. We thank the Norwegian Red Deer Centre for support during field work.

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Appendix

Online Resource 1 Supplementary details for section Methods - Data Analysis

Composition of beetle assemblages (Q3)

Ordination analyses

Prior to ordination analyses, we weighted each matrix element using the power function with an exponent w = 0.698 (y = x0.698 where y is the weight and x the original beetle individual counts: (Økland 1986)). This scaled the abundance values on a 0–16 scale to achieve a recommended intermediate weighting of species (Økland 1990; Rydgren 1993). GNMDS was run with the functions monoMDS and postMDS, with the following specifications: Bray-Curtis (B-C) dissimilarity index; unreliable dissimilarities (B-C values > 0.8) replaced by geodesic distances (Mahecha et al. 2007); number of dimensions = 2; number of random starting configurations = 400; maximum number of iterations = 600; convergence criteria smin and sgfrmin = 1e–7. We ranked the GNMDS solutions by stress and accepted the lowest-stress solution if it was not dissimilar to the solution ranked second (by a Procrustes test). We compared pairs of GNMDS and DCA axes by calculating Kendall rank correlation coefficients, and found both pairs to be negatively correlated, although the second axes are only weakly correlated ($\tau_{GNMDS1\&DCA1} = -0.42$, $\tau_{GNMDS2\&DCA2} = -0.21$, $p < 0.001$). The opposite axes of both methods were tested in the same way (correlations $\tau_{GNMDS1\&DCA2} = -0.29$, $p < 0.001$, $\tau_{GNMDS2\&DCA1} = 0.15$, $p = 0.004$). GNMDS ordination diagrams showed no evidence of methodological artefacts, but the DCA diagrams showed a clear tongue structure (Økland 1990). We therefore interpreted the GNMDS results further. The accepted GNMDS solution was subjected to varimax rotation using Principal Component Analysis and the resulting axes rescaled in half-change units. We interpreted the ordination axes environmentally by modelling each of the two vectors of GNMDS axes-scores as a response to one environmental variable at the time (including herbivory intensity), using split-plot GLM models (generalized linear models McCullagh and Nelder 1989; Auestad et al. 2008).

To account for the nested hierarchical sampling design (except for HI_H and altitude, for which only *block* was used as a random variable) we specified the error structure with *macroplot* in *block* as random variables. For each GNMDS axis, we calculated the overall fraction of total variance explained (FVE) at both macroplot and block level as the sum of squares at the level in question (SS_{block} or $SS_{macroplot}$) divided by total sum of squares (SS_{total}). The variation explained by each variable at each level was calculated as the sum of squares explained by the variable at this level (SS_{var}) divided by sum of squares at this level (SS_{level}). For all significant models we indicated the sign of the relationship given by the regression coefficients *c* with + for positive and – for negative relationships. To test if treatment was related to the first GNMDS axis at the plot level, we performed a split-plot GLM with *macroplot* in *block* as random variable. We used isoline diagrams, obtained by using the function 'ordisurf' in the vegan package (Oksanen et al. 2016), to visualize the relationship between GNMDS axes 1 and 2 and the most important explanatory variables. This function fits a generalized additive model with a Gaussian error structure to each explanatory variable in turn.

Variation partitioning

Prior to variation partitioning, we evaluated all explanatory variables individually. Only variables with $\alpha \leq 0.05$ in the Monte Carlo permutation test were eligible for inclusion in the analysis. We selected variables for inclusion in the two groups by performing separate forward selections of variables: only those variables that explain significant ($p < 0.01$) additional variation (i.e. that not explained by the previously selected variables) were used to represent the group in the subsequent analyses (Økland 2003).

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Online Resource 2 Total number of individuals in each species trapped in open vs exclosure plots.

Species	Family	Feeding guild	Open plots	Exclosure plots
Leistus terminatus	Carabidae	Predator	8	8
Nebria brevicollis	Carabidae	Predator	98	9
Notiophilus biguttatus	Carabidae	Predator	10	0
Carabus coriaceus	Carabidae	Predator	41	37
Carabus granulatus	Carabidae	Predator	18	16
Carabus hortensis	Carabidae	Predator	3	2
Carabus nemoralis	Carabidae	Predator	116	143
Carabus problematicus	Carabidae	Predator	31	55
Carabus violaceus	Carabidae	Predator	304	283
Cychrus caraboides	Carabidae	Predator	192	211
Loricera pilicornis	Carabidae	Predator	21	0
Patrobus atrorufus	Carabidae	Predator	176	70
Trechus obtusus	Carabidae	Predator	52	34
Trechus secalis	Carabidae	Predator	127	54
Pterostichus diligens	Carabidae	Predator	0	1
Pterostichus melanarius	Carabidae	Predator	123	113
Pterostichus niger	Carabidae	Predator	864	1104
Pterostichus oblongopunctatus	Carabidae	Predator	58	19
Pterostichus rhaeticus/nigrita	Carabidae	Predator	18	5
Pterostichus strenuus	Carabidae	Predator	3	0
Calathus micropterus	Carabidae	Predator	29	32
Agonum fuliginosum	Carabidae	Predator	46	29
Dicheirotrichus placidus	Carabidae	Predator	2	1
Calodromius spilotus	Carabidae	Predator	2	0
Dromius agilis	Carabidae	Predator	1	0
Dromius angustus	Carabidae	Predator	1	0
Anacaena globulus	Hydrophilidae	Omnivore	4	10
Cercyon lateralis	Hydrophilidae	Herbivore	1	0
Megasternum concinnum	Hydrophilidae	Detritivore	496	638
Myrmetes paykulli	Histeridae	Predator	1	0
Acrotrichis cognata	Ptiliidae	Detritivore	1	1
Acrotrichis intermedia	Ptiliidae	Detritivore	0	4
Agathidium atrum	Leiodidae	Fungivore	5	2
Agathidium laevigatum	Leiodidae	Fungivore	3	4
Nargus wilkini	Leiodidae	Omnivore	1	0
Choleva fagniezi	Leiodidae	Detritivore	1	9
Sciodrepoides fumatus	Leiodidae	Detritivore	1	2
Sciodrepoides watsoni	Leiodidae	Detritivore	45	30
Catops coracinus	Leiodidae	Detritivore	1	0
Catops nigricans	Leiodidae	Detritivore	2	8
Catops nigrita	Leiodidae	Detritivore	1	0
Catops tristis	Leiodidae	Detritivore	8	4
Stenichnus collaris	Scydmaenidae	Predator	15	5
Phosphuga atrata	Silphidae	Predator	73	116
Nicrophorus vespilloides	Silphidae	Detritivore	55	82
Omalium rivulare	Staphylinidae	Predator	5	8
Omalium rugatum	Staphylinidae	Predator	0	1
Anthobium atrocephalum	Staphylinidae	Predator	1	0
Olophrum piceum	Staphylinidae	Predator	0	3
Acidota crenata	Staphylinidae	Predator	1	0

Species	Family	Feeding guild	Open plots	Exclosure plots
Lesteva longoelytrata	Staphylinidae	Predator	2	8
Megarthrus nitidulus	Staphylinidae	Predator	0	6
Proteinus atomarius	Staphylinidae	Omnivore	5	0
Proteinus brachypterus	Staphylinidae	Predator	22	13
Mycetoporus lepidus	Staphylinidae	Predator	2	0
Ischnosoma splendidum	Staphylinidae	Predator	9	12
Lordithon exoletus	Staphylinidae	Predator	9	32
Lordithon thoracicus	Staphylinidae	Predator	6	4
Bolitobius cingulatus	Staphylinidae	Predator	1	2
Bolitobius inclinans	Staphylinidae	Predator	5	4
Tachinus laticollis	Staphylinidae	Predator	12	10
Tachinus marginellus	Staphylinidae	Predator	3	2
Tachinus pallipes	Staphylinidae	Predator	0	1
Tachinus proximus	Staphylinidae	Predator	14	6
Tachinus signatus	Staphylinidae	Predator	162	181
Aleochara moerens	Staphylinidae	Predator	1	0
Oxypoda alternans	Staphylinidae	Predator	4	7
Oxypoda annularis	Staphylinidae	Predator	6	1
Oxypoda brevicornis	Staphylinidae	Predator	4	1
Acrostiba borealis	Staphylinidae	Predator	1	0
Ocalea picata	Staphylinidae	Predator	9	9
Liogluta micans	Staphylinidae	Predator	1	1
Liogluta microptera	Staphylinidae	Predator	21	7
Geostiba circellaris	Staphylinidae	Predator	36	17
Atheta castanoptera	Staphylinidae	Predator	2	3
Atheta cinnamoptera	Staphylinidae	Predator	11	3
Atheta crassicornis	Staphylinidae	Predator	35	21
Atheta excellens	Staphylinidae	Predator	1	0
Atheta fungi	Staphylinidae	Predator	2	0
Atheta hypnorum	Staphylinidae	Predator	0	2
Atheta incognita	Staphylinidae	Predator	0	2
Atheta intermedia	Staphylinidae	Predator	6	4
Atheta nigricornis	Staphylinidae	Detritivore	2	2
Atheta picipennis	Staphylinidae	Predator	2	0
Atheta procera	Staphylinidae	Predator	1	0
Atheta sodalis	Staphylinidae	Predator	5	3
Atheta subtilis	Staphylinidae	Predator	1	0
Amischa analis	Staphylinidae	Predator	1	0
Drusilla canaliculata	Staphylinidae	Predator	12	0
Zyras humeralis	Staphylinidae	Predator	14	6
Gyrophaena affinis	Staphylinidae	Predator	0	1
Leptusa pulchella	Staphylinidae	Predator	2	1
Leptusa ruficollis	Staphylinidae	Predator	7	2
Autalia impressa	Staphylinidae	Predator	3	4
Syntomium aeneum	Staphylinidae	Herbivore	1	0
Oxytelus laqueatus	Staphylinidae	Omnivore	13	3
Stenus impressus	Staphylinidae	Predator	12	30
Lathrobium brunnipes	Staphylinidae	Predator	3	2
Lathrobium fulvipenne	Staphylinidae	Predator	8	5
Xantholinus tricolor	Staphylinidae	Predator	10	3
Othius myrmecophilus	Staphylinidae	Predator	87	52
Othius punctulatus	Staphylinidae	Predator	14	15

Species	Family	Feeding guild	Open plots	Exclosure plots
Bisnius puella	Staphylinidae	Predator	0	1
Philonthus decorus	Staphylinidae	Predator	514	510
Philonthus marginatus	Staphylinidae	Predator	1	1
Staphylinus erythropus	Staphylinidae	Predator	218	276
Quedius fuliginosus	Staphylinidae	Predator	49	34
Quedius fulvicollis	Staphylinidae	Predator	0	1
Quedius mesomelinus	Staphylinidae	Predator	0	1
Quedius molochinus	Staphylinidae	Predator	8	5
Quedius nigriceps	Staphylinidae	Predator	4	2
Quedius picipes	Staphylinidae	Predator	3	3
Geotrupes stercorosus	Geotrupidae	Detritivore	113	54
Aphodius depressus	Scarabaeidae	Omnivore	1	0
Potosia cuprea	Scarabaeidae	Herbivore	2	0
Cyphon coarctatus	Scirtidae	Detritivore	0	2
Athous subfuscus	Elateridae	Omnivore	12	7
Selatosomus impressus	Elateridae	Herbivore	4	2
Dalopius marginatus	Elateridae	Omnivore	1	1
Dictyoptera aurora	Lycidae	Omnivore	0	1
Podabrus alpinus	Cantharidae	Omnivore	8	3
Absidia schoenherri	Cantharidae	Omnivore	1	0
Malthodes fuscus	Cantharidae	Omnivore	3	0
Malthodes mysticus	Cantharidae	Predator	1	1
Epuraea marseuli	Nitidulidae	Omnivore	1	0
Epuraea pygmaea	Nitidulidae	Omnivore	0	1
Omosita depressa	Nitidulidae	Detritivore	1	0
Rhizophagus dispar	Rhizophagidae	Undefined	4	5
Rhizophagus ferrugineus	Rhizophagidae	Undefined	0	7
Cryptophagus dorsalis	Cryptophagidae	Fungivore	3	3
Cryptophagus setulosus	Cryptophagidae	Omnivore	93	117
Atomaria bella	Cryptophagidae	Fungivore	0	3
Atomaria hislopi	Cryptophagidae	Omnivore	0	2
Cerylon fagi	Cerylonidae	Predator	1	0
Sphaerosoma pilosum	Alexiidae	Fungivore	2	0
Aridius nodifer	Latridiidae	Fungivore	1	1
Cis lineatocribratus	Ciidae	Fungivore	0	1
Sphaeriestes castaneus	Salpingidae	Predator	1	0
Otiorhynchus nodosus	Curculionidae	Omnivore	7	1
Otiorhynchus porcatus	Curculionidae	Herbivore	1	0
Otiorhynchus scaber	Curculionidae	Omnivore	110	69
Otiorhynchus singularis	Curculionidae	Omnivore	13	8
Polydrusus undatus	Curculionidae	Herbivore	0	1
Strophosoma melanogrammum	Curculionidae	Herbivore	3	4
Hylobius abietis	Curculionidae	Omnivore	35	27
Rhyncolus ater	Curculionidae	Saproxylic	26	6
Hylurgops palliatus	Curculionidae	Omnivore	2	0
Hylastes brunneus	Curculionidae	Omnivore	10	17
Tomicus minor	Curculionidae	Herbivore	1	1
Total number of individuals			**4913**	**4820**

Note: Feeding guild was determined by Sindre Ligaard, and mainly according to Freude, H., Harde, K.W. & Lohse, G.A. 1964-79. *Die Käfer Mitteleuropas. Band 1-12.* Krefeld.

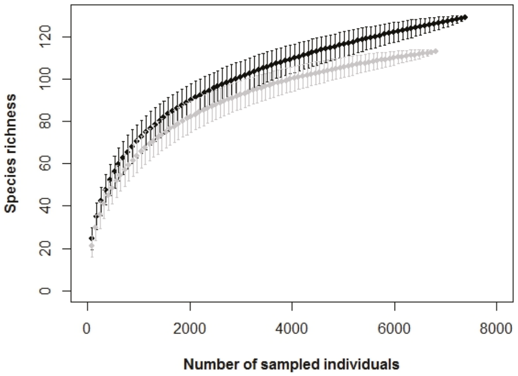
Online Resource 3 Kendall rank correlation coefficients between all explanatory variables. Significant correlations ($p \leq 0.05$) in bold. Altitude, and Historical Herbivory Intensity (HI_H); n = 12, Current Herbivory Intensity (HI_C) and young tree abundance; n = 24, other variables; n = 168.

	Moisture	Total N	pH	Veg. height	Heather ab.	Herb ab.	Grass ab.	Fern ab.	Bryophyte ab.	Young tree ab.	HI_C	HI_H
Altitude	-0.058	0.047	0.098	0.064	0.018	0.076	0.094	0.023	**-0.137**	-0.098	-0.021	-0.076
Moisture		0.063	-0.099	0.016	-0.009	0.079	0.085	-0.054	**0.188**	-0.056	0.036	**0.167**
Total N			**0.440**	**-0.174**	**-0.426**	**0.307**	**0.283**	**0.181**	**0.235**	-0.036	**0.145**	**0.386**
pH				**-0.124**	**-0.398**	**0.331**	**0.249**	**0.126**	**0.104**	-0.018	**0.127**	**0.295**
Vegetation height					**0.207**	**-0.147**	0.008	0.028	**-0.244**	-0.100	**-0.576**	**-0.152**
Dwarf shrub abundance						**-0.393**	**-0.426**	**-0.129**	-0.033	0.026	**-0.237**	**-0.385**
Herb abundance							**0.432**	0.055	0.061	-0.078	**0.143**	**0.279**
Grass abundance								**0.123**	-0.012	**0.142**	0.083	**0.156**
Fern abundance									0.030	0.058	0.090	0.051
Bryophyte abuncance										**0.136**	**0.247**	**0.230**
Young tree abundance											0.070	**0.118**
HI_C												**0.280**

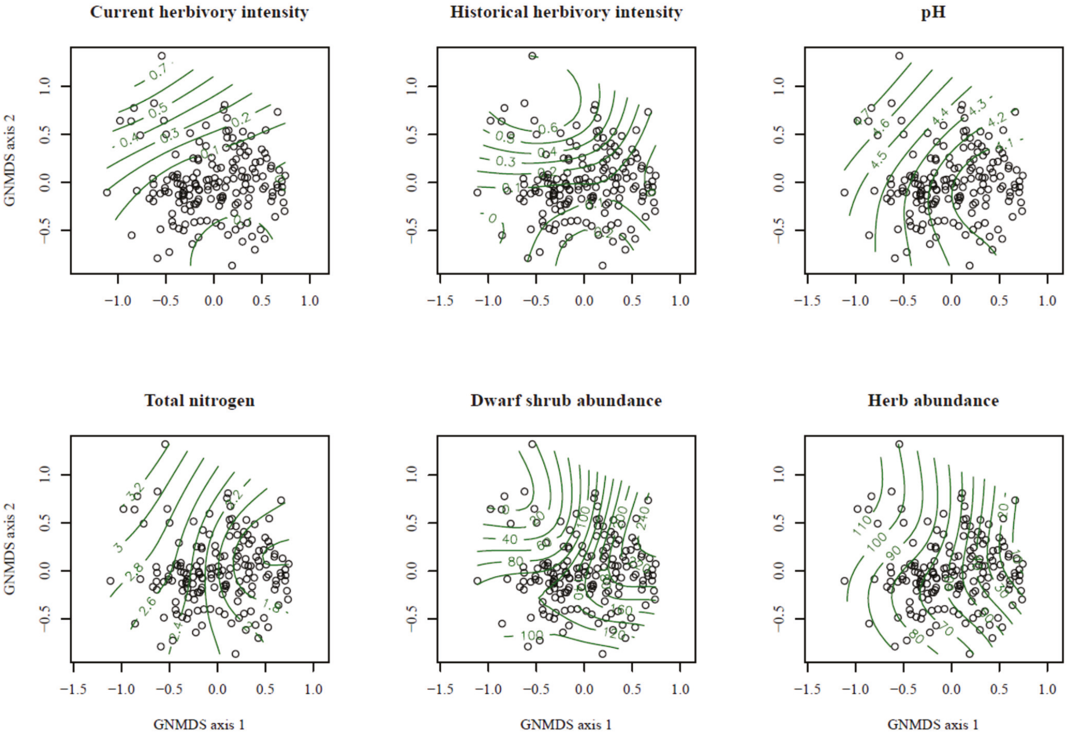
Online Resource 4 Parameter estimates from negative binomial generalized linear mixed effects models with macroplot nested in block as random factors for exclosure-models and random factor block for current herbivory intensity-models. We validated each final model by visually investigating normality in model residuals with quantile-quantile-plot and plots of residuals versus fitted values, in addition to comparing it with the null model. We report model estimates with explanatory variable treatment or herbivory intensity also for models were there were no significant effect of these variables, i.e. when the null model were the most parsimonious, to provide information for the reader. Significant effects (p ≤ 0.05) in bold.

Species	Estimate	SE	Z	P		Estimate	SE	Z	P
Pterostichus niger									
Intercept	2.213	0.145	15.230	< 0.001	*Intercept*	2.267	0.209	10.840	< 0.001
Exclosure vs open	0.278	0.163	1.710	0.088	*Herbivory intensty*	-0.365	0.862	-0.420	0.670
Megasternum concinnum									
Intercept	0.725	0.510	1.420	0.155	*Intercept*	1.050	0.680	1.550	0.120
Exclosure vs open	0.455	0.193	2.360	**0.018**	*Herbivory intensty*	-2.070	2.780	-0.750	0.460
Philonthus decorus									
Intercept	-0.606	1.099	-0.550	0.580	*Intercept*	0.438	1.106	0.400	0.690
Exclosure vs open	-0.402	0.402	-1.000	0.320	*Herbivory intensty*	-3.783	4.496	-0.840	0.400
Carabus violaceus									
Intercept	1.170	0.163	7.180	< 0.001	*Intercept*	1.195	0.230	5.200	< 0.001
Exclosure vs open	-0.054	0.174	-0.310	0.760	*Herbivory intensty*	-0.222	0.950	-0.230	0.820
Staphylinus erythropus									
Intercept	-0.421	0.594	-0.710	0.480	*Intercept*	0.669	0.763	0.880	0.380
Exclosure vs open	0.426	0.388	1.100	0.270	*Herbivory intensty*	-7.801	4.326	-1.800	0.071
Cychrus caraboides									
Intercept	0.652	0.204	3.200	0.001	*Intercept*	0.894	0.256	3.500	< 0.001
Exclosure vs open	0.119	0.161	0.740	0.459	*Herbivory intensty*	-1.480	1.074	-1.380	0.168
Tachinus signatus									
Intercept	-2.657	1.761	-1.510	0.130	*Intercept*	-1.805	1.612	-1.120	0.260
Exclosure vs open	-0.339	0.439	-0.770	0.440	*Herbivory intensty*	-0.299	5.543	-0.050	0.960
Carabus nemoralis									
Intercept	0.144	0.222	0.650	0.520	*Intercept*	0.156	0.261	0.600	0.550
Exclosure vs open	0.195	0.211	0.930	0.350	*Herbivory intensty*	0.134	1.042	0.130	0.900
Cryptophagus setulosus									
Intercept	-0.222	0.266	-0.830	0.400	*Intercept*	0.600	0.310	1.930	0.053
Exclosure vs open	0.296	0.196	1.510	0.130	*Herbivory intensty*	-5.850	1.910	-3.060	**0.002**
Phosphuga atrata									
Intercept	-0.440	0.252	-1.750	0.081	*Intercept*	0.305	0.307	0.990	0.320
Exclosure vs open	0.628	0.274	2.300	**0.022**	*Herbivory intensty*	-6.094	2.092	-2.910	**0.004**
Nicrophorus vespilloides									
Intercept	-0.424	0.464	-0.910	0.360	*Intercept*	0.336	0.566	0.590	0.552
Exclosure vs open	0.399	0.654	0.610	0.540	*Herbivory intensty*	-7.281	3.599	-2.020	**0.043**
Patrobus atrorufus									
Intercept	-4.293	2.302	-1.860	0.062	*Intercept*	-4.780	1.540	-3.110	0.002
Exclosure vs open	-1.767	0.862	-2.050	**0.040**	*Herbivory intensty*	10.790	4.280	2.520	**0.012**
Otiorhynchus scaber									
Intercept	-1.867	0.817	-2.290	0.022	*Intercept*	-0.865	1.049	-0.820	0.410
Exclosure vs open	-0.130	0.310	-0.420	0.674	*Herbivory intensty*	-7.666	5.721	-1.340	0.180
Trechus secalis									
Intercept	0.328	0.192	1.710	0.088	*Intercept*	0.444	0.262	1.690	0.091
Exclosure vs open	-0.859	0.232	-3.700	**< 0.001**	*Herbivory intensty*	-0.362	1.024	-0.350	0.724
Geotrupes stercorosus									
Intercept	-10.112	3.286	-3.080	0.002	*Intercept*	-9.527	3.759	-2.530	0.011
Exclosure vs open	-0.681	0.306	-2.230	**0.026**	*Herbivory intensty*	0.167	11.243	0.010	0.988

Othius myrmecophilus									
Intercept	-0.176	0.248	-0.710	0.480	*Intercept*	0.183	0.308	0.600	0.550
Exclosure vs open	-0.489	0.335	-1.460	0.140	*Herbivory intensty*	-2.265	1.427	-1.590	0.110
Nebria brevicollis									
Intercept	-8.283	2.821	-2.940	0.003	*Intercept*	-7.620	2.880	-2.640	0.008
Exclosure vs open	-2.403	0.434	-5.540	**< 0.001**	*Herbivory intensty*	17.090	5.460	3.130	**0.002**



Online Resource 5 Cumulative numbers of beetle species from individual-based rarefaction curves for open (black) and exclosure (grey) plots (1000 permutations). Error bars indicate ± 2 standard deviations.



Current herbivory intensity

Historical herbivory intensity

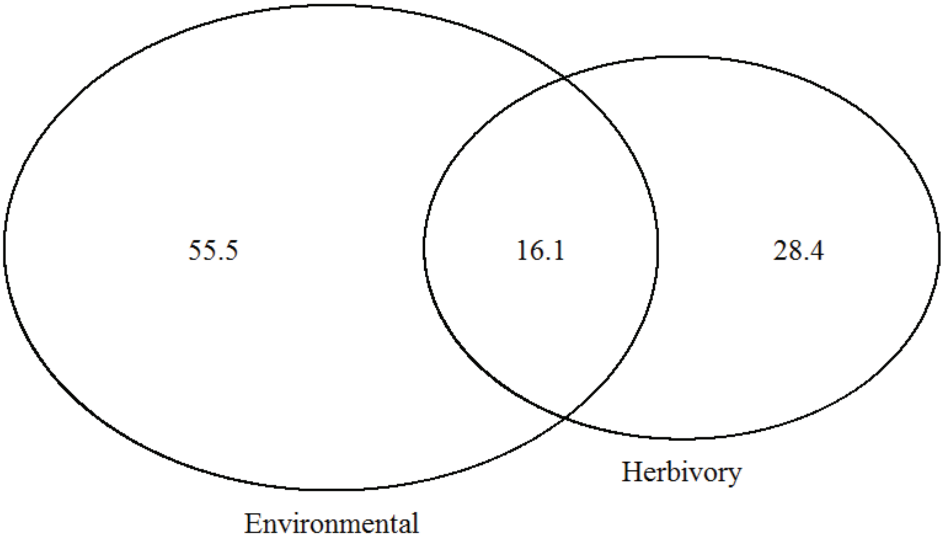
pH

Total nitrogen

Dwarf shrub abundance

Herb abundance

Online Resource 6 Variation of explanatory variables in the plots is shown for variables that are significantly related to at least one ordination axis (global non-metric multidimensional scaling ordination, axes 1 and 2, $p \leq 0.05$), analyzed with split-plot GLM. Models use ranged and zero-skewness transformed variable values; raw values are written onto the isolines. Axes are scaled in half-change units.



Online resource 7 Venn diagram for partitioning the variation explained by two sets of explanatory variables, Environmental (E) and Herbivory intensity (H). E consisted of altitude, soil moisture, pH, total nitrogen and vegetation height, whereas H consisted of Current and Historical Herbivory intensity. We performed a sequence of (partial) CCA analyses to quantify the variation explained by H not shared with E (H | E), E not shared with H (E | H), and the variation shared by the two groups (H ∩ E). All variation components are expressed as fractions of the total variation explained (Økland 1999).

Paper IV

Red deer limit the number of herbivorous larvae on bilberry in boreal forest

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Submitted manuscript

Abstract

By browsing, ungulates may limit other herbivores with which they share food plants. Browsing can induce trophic cascades by removing plant biomass and by altering chemical composition of plants. In Northern Europe, many ungulates like red deer (*Cervus elaphus*), have reached historically high densities, causing biodiversity concern. We investigated the effect of red deer browsing on the abundance of herbivorous larvae (Lepidoptera and Symphyta) living on the key species bilberry (*Vaccinium myrtillus*) in a Norwegian boreal forest ecosystem. We combined experimental exclusion of red deer with a gradient in browsing intensity. During 15 years (2001 to 2016), we recorded the number of larvae feeding on bilberry leaves, and related this to bilberry biomass and deer browsing intensity. Browsing reduced larvae abundance in the forest understory, as exclosure plots contained twice as many larvae compared to deer-access plots. Plant biomass in deer-access plots was much lower (one ninth) compared to biomass in exclosures and likely explains the difference in larvae abundance. We show an additional effect of browsing on plant quality, as the larvae density was lower on average deer-access ramets than on exclosure ramets. Interestingly, the larval densities were highest at relatively high browsing intensities but declined on the most heavily browsed ramets. Our study indicates that deer browsing may increase nutritional value in bilberry, which can cause a quality-quantity trade-off for herbivorous larvae. Our study underpins red deer as a potential trigger of trophic cascades, by for example altering food availability for insectivorous forest-dwelling birds.

Keywords: Competition, herbivory, insects, plant-animal interaction, trophic cascade

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Author contribution: SJH originally formulated the idea. MSL, SJH, KR, SRM designed the study, MSL and SJH conducted the field work. MSL performed the statistical analyses. MSL wrote the first draft of the manuscript, MSL, SJH, KR, SRM edited the subsequent drafts.

Introduction

Vertebrate herbivores can trigger ecological cascades by affecting the insect herbivores with which they share food plants. Wild ungulates in the northern hemisphere have reached historically high densities after centuries of very low abundance (Austrheim et al. 2011; Côté et al. 2004; Fuller and Gill 2001) because of increased food availability, a warmer climate, regulation of hunting, and strict predator control (Chollet et al. 2016; Kuiters et al. 1996). The increasingly high densities of deer can cause difficulties for nature management and conservation as they may affect ecological interactions across trophic levels. Ungulates alter plant community composition and structure (Augustine and McNaughton 1998; Lilleeng et al. 2016) and may limit other herbivore guilds that feed on the same plant species (Pedersen et al. 2011) by reducing plant biomass or inducing plant defense mechanisms (Gomez and Zamora 2002; Karban 2011). However, some plant species respond to herbivory by compensatory growth (McNaughton 1983). The new tissue may have lower levels of defense compounds, and consequently be more palatable to ungulate and insect herbivores (Hrabar and du Toit 2014; Mathisen et al. 2017). Thus, herbivore pressure may be either reduced or increased following ungulate herbivory events.

Ungulate-induced changes in food plants can affect herbivorous insect larvae and thus induce trophic effects. Insect larvae are protein-rich and can be critical for chick survival in many bird species. Globally, 60% of all bird species depend on insects as a food source (Morse 1971). Insects in Northern Europe are declining dramatically in biomass and diversity (Brooks et al. 2012; Conrad et al. 2006; Hallmann et al. 2017; Thomas et al. 2004), with a concomitant decrease in bird abundance (Inger et al. 2015). Ungulate herbivory may be one factor that is contributing to the decline in abundance and diversity of forest birds that depend on insects and understory vegetation (Allombert et al. 2005a; Chollet et al. 2016; deCalesta 1994). Thus, ungulate herbivory can play a part in trophic shifts in forests.

Studies of food plants used by both ungulates and insect larvae can improve understanding of the mechanisms underlying interactions between these herbivores. Bilberry (*Vaccinium myrtillus*) is a key resource in the boreal ecosystem (Nilsson and Wardle 2005) and is widely distributed throughout Eurasia. Many species from several taxa, including birds, carnivorous mammals, rodents, ungulates, insects and even humans (Dahle et al. 1998; Hancock et al. 2011; Hegland et al. 2005; Kidawa and Kowalczyk 2011; Pedersen et al. 2011), use bilberry as a food plant, and forage on different plant parts at different times of the year. Insect larvae feed mainly on the plant leaves during the growing season, whereas ungulates mostly feed on bilberry in winter but may exploit it throughout the year (Hegland et al. 2005; Latham et al. 1999). In addition, large herbivores can unintentionally consume insect larvae while foraging, which may affect the size of insect larvae populations (Ben-Ari and Inbar 2013; Gish et al. 2017). Insects and ungulates may thus compete both directly and indirectly for the same food plant.

The most abundant leaf-chewing insects on bilberry are Lepidoptera (Geometridae and Tortricidae*)* and Hymenoptera (Symphyta) larvae (Atlegrim 1989). These larvae are important prey for insectivorous birds. For example, black grouse (*Lyrurus tetrix*) and capercaillie (*Tetrao urogallus*, Jahren et al. 2016), both of which are declining, time their breeding so that the chicks hatch just before larval numbers peak (Wegge et al. 2010). Later in the season, the bilberry plants themselves are a key food source for the chicks (Wegge and Kastdalen 2008). The imago stage of several bilberry-feeding larvae may provide important ecosystem services, such as pollination. As ungulate population densities increase, they may thus affect several ecological guilds via browsing on bilberry.

Red deer prefer herbs and young trees and show an intermediate preference for bilberry (Mysterud et al. 2010), feeding on the evergreen stems mainly in winter. Bilberry is assumed to be important for deer winter survival in areas with long winters (Hegland et al. 2005; Mysterud et al. 2010). Red deer remove entire shoots when feeding on bilberry, whereas insect larvae feed selectively on leaves. Bilberry seems to be one of the most browsing-tolerant of the boreal forest dwarf shrubs (Hegland and Rydgren 2016). Nevertheless, even low deer densities reduce the plant size and population growth rate (Hegland et al. 2010; Hegland et al. 2005). The central role of bilberry in the boreal ecosystem makes it a good model species for investigating the ecological consequences of red deer browsing in more detail, for example through their impact on insects. Studies on how the current high densities of red deer in Northern Europe (Fuller and Gill 2001) affect population densities of insect larvae can shed light on cascading effects that might be induced by increased ungulate populations.

We used a deer exclosure experiment along a browsing intensity gradient to explore long-term effects of red deer herbivory on bilberry ramets and populations of leaf-chewing insect larvae that use bilberry as their food plant. We analyzed the impact of deer browsing on 1) *number of larvae*, the most relevant measure for species that depend on larvae as a food source, and 2) *bilberry biomass*, i.e. the size effects of browsing. Further, we investigated whether browsing had an effect on 3) *larval density* per ramet, measured as the proportion of leaves chewed by larvae on each ramet, which can reveal more about the mechanisms regulating changes in larvae populations. Based exclusively on our expectation that deer browsing would reduce biomass, we predicted 1) that we would find fewer herbivorous larvae where deer had access than in exclosures, and that larval numbers would decrease with increasing deer browsing intensity, because red deer reduce both plant cover and the amount of plant tissue available for larvae to feed on (Baines et al. 1994). We used biomass estimation to control the quantities of plant tissue actually available. We also predicted 2a) to find the highest food quantity (bilberry biomass) in the exclosures, and that food quantity outside the exclosures would be negatively related to increasing deer browsing intensity (Hegland and Rydgren 2016; Lilleeng et al. 2016). Reproductive effort in bilberry can affect e.g. moth population sizes (Selås et al. 2013), and the number of flowers gives an indication of the year's berry production. The number of flowers is dependent on bilberry ramet size (Hegland et al. 2005). We therefore predicted 2b) that there would be fewer bilberry flowers on browsed ramets. Further, browsing may either increase or decrease the quality of bilberry as food. Herbivory may trigger defense mechanisms, so that plants produce substances that are toxic or reduce digestibility (Cipollini and Sipe 2001; Sampedro et al. 2011; Seldal et al. 1994). On the other hand, plants under stress may reallocate resources from plant defense, so that their nutritional value for insect larvae increases (plant-stress hypothesis, White (1978)). In these circumstances, stressed plants are expected to host a higher density of herbivores per area than non-stressed plants. If red deer browsing does not affect the quality of bilberry as food, the proportion of the leaves chewed by insect larvae should be the same on all ramets. However, if browsing modifies food quality, insect density should be higher on ramets with a higher nutritional value for insects than on those with a lower nutritional value. Winter herbivory is hypothesized to be less likely to induce plant defense responses than summer herbivory (Hegland et al. 2016; Strengbom et al. 2003). As red deer browse bilberry mainly in winter, we expect that up to a point, stress caused by deer herbivory is more likely to increase the nutritional value of bilberry ramets (White 1978). However, the optimal habitat for insect herbivores is a function of both food quality and food quantity. Given our expectation that bilberry quantities will be reduced as browsing intensity increases, we therefore predict that 3) larval density should be highest on ramets exposed to intermediate levels of browsing intensity, in a trade-off between quality and quantity.

Material and methods

Study area

We conducted our study in an old-growth boreal forest on the 11-km^2 Svanøy island, situated approximately 2 km from the mainland of Sogn og Fjordane county, Western Norway (61°30'N, 5°05'E). The forest is dominated by Scots pine (*Pinus sylvestris)*, with *Vaccinium* species and to some extent heath (Ericaceae) as the major understory species (Skogen and Lunde 1997). The forest floor is covered with lichens and mosses. Throughout Europe, many areas with high deer density have a similar dwarf shrub-dominated understory (Baines et al. 1994; Pato and Obeso 2013). The climate is relatively mild and wet, with a mean annual temperature of 8° C and precipitation of 2000 mm (https://www.met.no). The overall density of red deer on the island is approximately 7.5 animals km^{-2}, which is considered high in Norway (e.g. Hegland et al. 2013), and intermediate on the European scale (Milner et al. 2006). Western Norway is the region of the country with the highest densities of red deer, and only small populations of other forest-dwelling ungulates found elsewhere in Norway such as moose (*Alces alces*) and roe deer (*Capreolus capreolus*). The latter are not present in the study area. There is a red deer farm on the island with approximately 30 deer km^{-2}, well separated from the wild animals by a game fence. The deer farm consists partly of forest types similar to those on other parts of the island, and we established two of the experimental blocks here (see Experimental setup). There are also some free-ranging domestic sheep (*Ovis aries)* on the island, mainly during summer months.

Experimental setup

We established twelve experimental blocks in pine-bilberry forest at altitudes ranging from 20–140 m in December 2000. Two of these blocks were in the deer farm. Each block comprised one deer-access and one exclosure macroplot, each measuring 9 × 9 m. The exclosures were fenced with 3 m high wire mesh (10 × 10 cm mesh size), leaving a 0.5 m buffer around each macroplot to avoid edge effects (Fig. 1). Within each macroplot, we randomly distributed seven plots (each of 1 x 1 m), and restricted their placement to flat terrain more than 0.5 m from the closest large tree (height > 2 m). We recorded plant species composition as subplot frequency in 100 subplots (10 x 10 cm) in each plot (n = 168) in June 2001, 2006 and 2011 (Lilleeng et al. 2016). Average (± SE) bilberry subplot frequency was 74% (± 3%, 2001), 82% (± 3%, 2006), and 80% (± 3%, 2011) in deer-access plots, and 68% (± 3%, 2001) and 79% (± 3%, 2006 and 2011) in exclosure plots. One of the deer-access macroplots on the red deer farm differed from the other macroplots in having lower bilberry cover and several plots without any bilberry ramets.

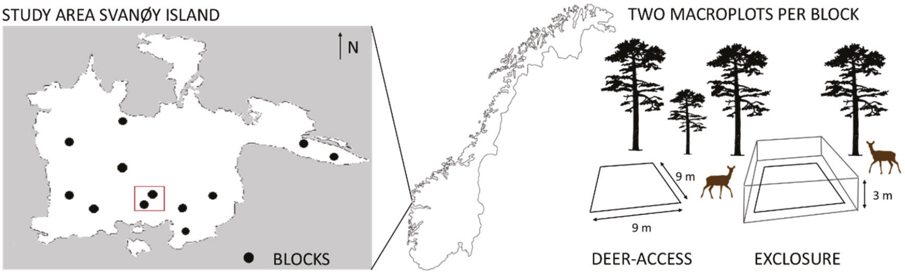

Figure 1. Twelve experimental blocks (black dots) were established on Svanøy island, Western Norway, each containing one exclosure and one deer-access macroplot, with seven plots within each macroplot. The two deer-farm blocks are indicated by a square on the map. Illustration based on Lilleeng et al. (2018).

Bilberry measurements

Bilberry is a shade-tolerant perennial clonal dwarf shrub with an extensive rhizome system and ramets as orthotropic aerial shoots (Flower-Ellis 1971). To estimate biomass, reproduction and herbivory, we surveyed randomly selected bilberry ramets: five ramets from each plot in June 2001; three ramets from four out of seven plots in each macroplot in 2006; and three ramets from each plot in 2011, 2012, 2013 and 2016. For each ramet, we recorded ramet height (cm), canopy diameter (cm), number of annual shoots, and number of flowers, as well as insect and deer browsing (see below for details, Fig. 2). In 2001 and 2012, we also counted the total number of leaves on each ramet.

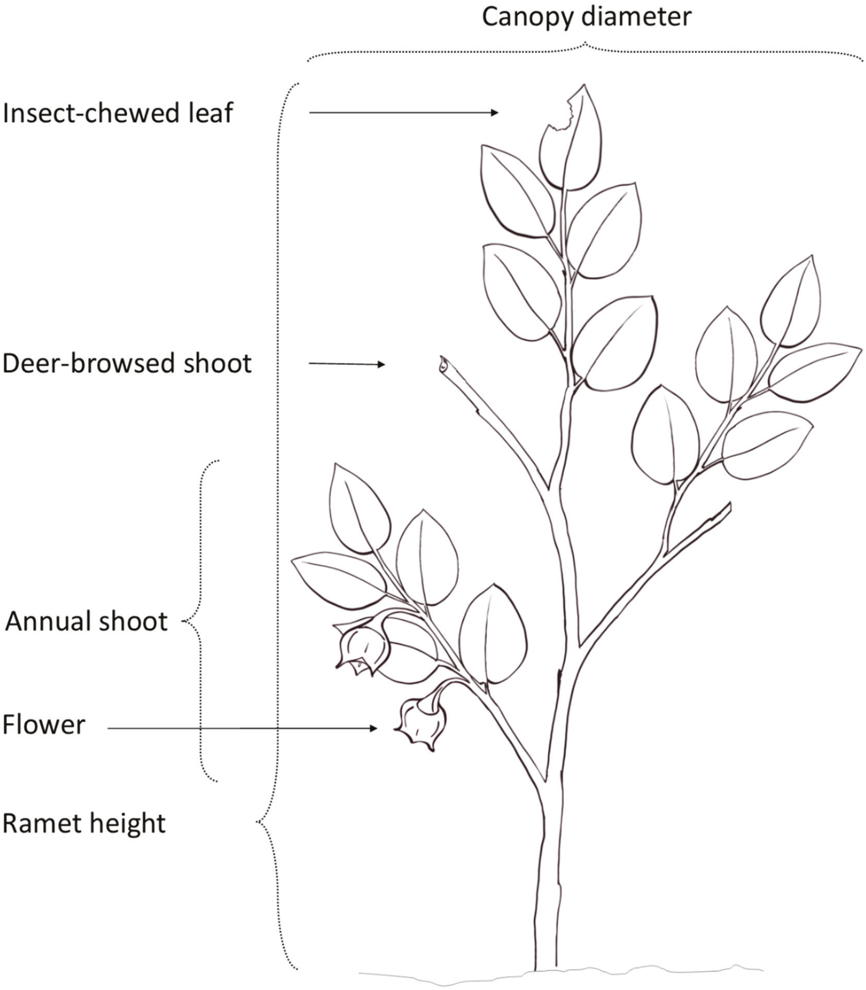

Figure 2. Bilberry ramet with traces of chewing by insect larvae and red deer browsing. Traits included in analyses are indicated. Illustration by Ronny Steen.

Number of larvae

We used two approaches to estimate the number of herbivorous insect larvae. First, we performed a direct count (a): We recorded the number of Lepidoptera and Hymenoptera (Symphyta) larvae at macroplot scale in early and late June 2012 and late June 2013 by sweep netting (25 cm diameter canvas sweep net) through the understory vegetation once and counting the larvae caught ('Sweep netting method'). The vegetation in the two deer-access macroplots in the red deer farm was too short for sweep netting. We swept the exclosure macroplots within the red deer farm in 2012 only, so that the total sample size was 72 - 8 = 64. We did all insect sampling in dry weather between 0900 and 1800, stored the larvae in 70% ethanol, and counted the individuals of Lepidoptera and Symphyta. Second, we performed an indirect count (b): In all six censuses, from 2001 to 2013, we recorded browsing by leaf-chewing insect larvae by counting the number of insect-chewed leaves on each monitored bilberry ramet ('Bilberry-recording method', Fig. 2; Hegland et al. 2005). We used the number of larva-chewed leaves as an indirect estimate and a proxy for the number of larvae. The advantage of this method is that it reflects larval abundance over a longer time period, but it does not provide specific information on taxon level. We always conducted sweep netting prior to ramet monitoring to avoid biased sampling caused by disturbance.

Red deer browsing

To describe the gradient in browsing intensity, we recorded red deer browsing intensity on each ramet (Fig. 2), based on the proportion of shoots browsed by deer. In all cases except the direct counts (2012 and 2013), we transformed the proportion browsed to a five-level index (Hegland et al. 2013), as we had recorded browsing intensity directly using this index in 2001. Cutoff-levels for the proportion of shoots browsed by deer for each level were 0 (0%; hereafter termed 'No'), 1 (1–24%; 'Low'), 2 (25–49%; 'Moderate'), 3 (50–74%; 'High'), 4 (75–100%; 'Heavy'), sensu Frelich and Lorimer (1985). In all, we surveyed bilberry performance and insect and red deer herbivory on 3001 ramets in the period 2001–2016.

Data analysis

We used R version 3.4.2 (R Core Team 2017) for all statistical analyses. We analyzed the effect of treatment (i.e. deer-access versus exclosure), time (years as factors) and browsing intensity (i.e. the deer-browsing index) on the responses with generalized linear mixed effects models fitted with maximum likelihood (glmer, package lme4 Bates et al. 2015; and glmmadmb, package glmmADMB Skaug et al. 2016) and linear mixed effects models (lmer, fit by REML, package lmerTest Kuznetsova et al. 2016). We accounted for random effects caused by the spatial and temporal dependence between observations. We evaluated our models for normality of residuals by quantile-quantile plots. For all models, we started with the most complex structure of fixed effects and did backward model selection using Aikake's information criterion (AIC) as our model selection criterion to find the most parsimonious model (Crawley 2013).

We investigated prediction 1) using both measures for number of larvae: For 1a) *number of sweep-netted larvae*, we specified Poisson glmer models with treatment (all macroplots) or proportion of deer-browsed shoots (deer-access macroplots) as fixed factor and *block* as random factor. To investigate whether there was a unimodal effect of deer-browsing on the number of insects, we included proportion of deer-browsed shoots as a quadratic term in the full model, but this term was not significant. Similarly, we fitted negative binomial glmmadmb models for 1b) *number of insect-chewed leaves* on the bilberry ramets with treatment × year (five-year intervals; 2001, 2006, 2011, 2016) as fixed factors and random factor *plot* nested in *macroplot* nested in *block*, and deer browsing intensity as fixed factor (deer-access plots) with random factor *plot* nested in *block* and *year*. We used a negative binomial family because a priori Poisson models were overdispersed.

To identify the effect red deer browsing had on bilberry biomass, prediction 2a, we estimated ramet size (dry mass, grams) non-destructively using a multiple regression model with ramet height and number of shoots developed from the same data source as Hegland et al. (2010) (SM1). We fitted lmer models for 2a) *bilberry biomass* (= ramet size) with treatment × year (2001, 2006, 2011, 2016) as fixed factors and random factor *plot* in *macroplot* in *block*, and deer browsing intensity as fixed factor with random factor *plot* in *block* and *year*. We investigated the relationship between the total number of leaves on the ramet and our estimate of ramet size with glmer, random factor *plot* in *macroplot* in *block* on 2001 and 2012 data. In parallel, we applied a linear regression to achieve the estimated R^2_{adj}, although this method does not account for our nested sampling regime (i.e. no random effect). For prediction 2b), we analyzed the number of flowers in exclosures vs deer-access plots with Poisson glmer, and *plot* in *macroplot* in *block* and *year* as random factor.

To estimate whether the proportions of insect-chewed leaves were affected by browsing, we estimated the effect of red deer browsing on 3) *larval density* per ramet in 2001 and 2012 by using number of insect-chewed leaves as a response, and total number of leaves on ramet as an offset value, as recommended by Reitan and Nielsen (2016), in negative binomial glmmadmb models that were otherwise the same as in 1b. As 2001 and 2012 were the only years for which we had data on the total number of leaves per ramet, we also modelled the data from 2001 and 2012 without offset. The results were in line with the models including the 2001, 2006, 2011 and 2016 data, and are not reported here.

Results

1) Number of larvae

Deer exclosures had twice as many insect larvae as deer-access macroplots (Direct count: $\beta = 0.73 \pm 0.22$ SE, $n = 64$, $p = 0.001$, TableA1A, Fig. 3A). Across the macroplots accessible to red deer, there was no relationship between browsing intensity and the number of insect larvae ($\beta = -1.58 \pm 1.36$ SE, $n = 30$, $p = 0.246$, TableA1B, Fig. 3B).

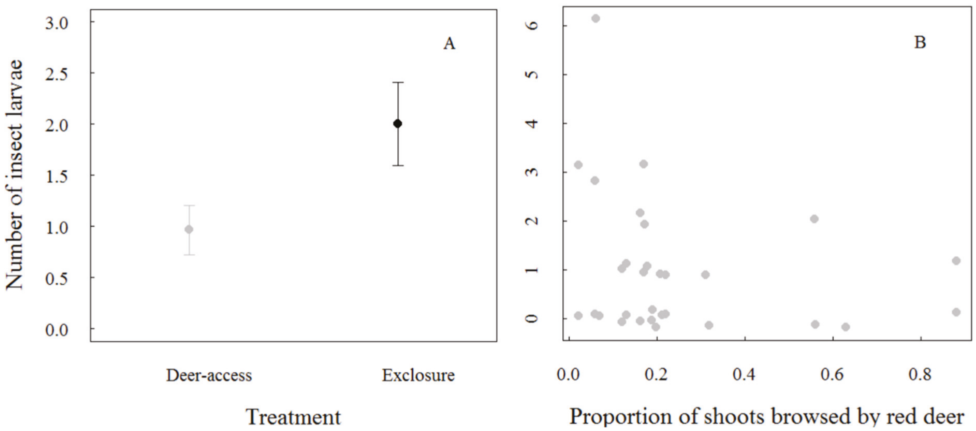

Figure 3. Mean (± SE) number of insect larvae collected on Svanøy island in A) exclosures (black) and deer-access (grey) macroplots (81 m^2, n = 64), and B) in deer-access macroplots (jittered for visualization purposes) related to the intensity of red deer browsing, measured as the proportion of bilberry ramet shoots browsed (n = 30). All larvae were collected by sweep netting in 2012 and 2013.

We found up to three times more insect-chewed bilberry leaves inside exclosures than in deer-access plots, and the difference increased with time since the establishment of exclosures (Indirect count: β (± SE); 2006 = 0.78 (0.19), 2011 = 0.73 (0.14), 2016 = 1.23 (0.15), all $p < 0.001$, Fig. 4A, Table A2). Insect herbivory also fluctuated between years, and the trends were the same for both exclosure and deer-access plots, with 2011 as the peak year in our study (Fig. 4A). In plots accessible to deer, ramets exposed to intermediate (i.e. low to high) deer browsing intensities had more insect-browsed leaves (β (± SE); Low = 0.67 (0.12), Moderate = 0.57 (0.13), High = 0.58 (0.13), all $p < 0.001$, Fig. 4B, Table A2) than unbrowsed or heavily browsed ramets. Heavily browsed ramets had fewer insect-chewed leaves than those exposed to intermediate browsing intensities, but did not differ from the unbrowsed ramets (β (± SE) = 0.10 (0.14), p = 0.47 (Table A2).

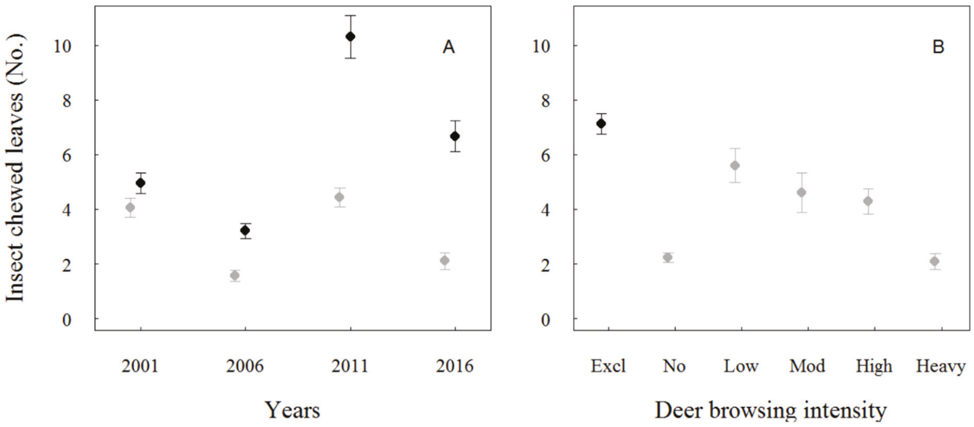

Figure 4. Mean (± SE) number of insect-chewed leaves on bilberry ramets on Svanøy island in A) deer-access (grey) and exclosure plots (black) measured at five-year intervals and on B) ramets in deer-access plots exposed to different browsing intensities. In B) we include 'Exclosure' (mean for 2006–2016, while other categories are represented by the mean for 2001-2016, to ensure that this point represents the treatment effect), to show that unbrowsed ramets in deer-access plots differ from exclosure ramets. Categories for deer browsing intensity were 'No' (0% of shoots browsed), 'Low' (1–24%), 'Moderate' (25–49%), 'High' (50–74%), and 'Heavy' (75–100%).

2) Bilberry biomass

Both exclusion of deer and the intensity of red deer browsing affected bilberry biomass. Ramets were nine times larger in exclosures than in deer-access plots ($p < 0.001$, estimated biomass (dry mass (± SE)) 2016 in deer-access vs exclosure plots; 0.12 (0.01) vs 1.07 (0.16) grams, respectively), and most of this change occurred during the first five years ($p < 0.001$, Fig. 5A, Table A3). In deer-access plots, ramets exposed to intermediate deer browsing intensities were larger than unbrowsed and heavily browsed ramets (lmer β (± SE); Low = 0.98 (0.10), Moderate = 0.57 (0.11), High = 0.48 (0.10), all $p < 0.001$, Fig. 5B, Table A3). Heavily deer-browsed ramets did not differ in size from unbrowsed ramets ($p = 0.91$, Table A3). Bilberry biomass corresponded well with the total number of leaves on ramets, i.e. the availability of leaves for insect browsing (2001: lmer $t = 46.87$, $p < 0.001$, linear regression $R^2_{adj} = 0.75$; 2012: $t = 30.58$, $p < 0.001$, $R^2_{adj} = 0.72$). Ramets in exclosures had more flowers than ramets in deer-access plots (estimated median number (±SE) of flowers in deer-access plots; 0.24 (0.08) vs 0.05 (0.02) in exclosure plots, Poisson glmer, z-value = 5.51, $p < 0.001$).

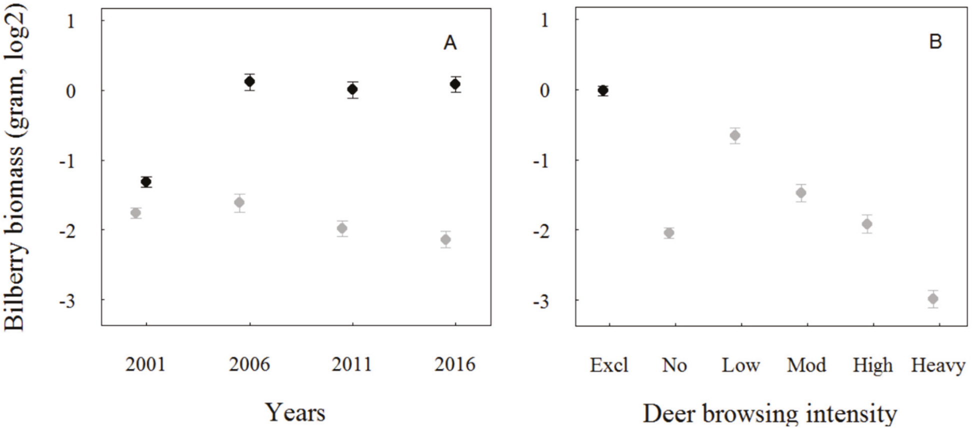

Figure 5. Mean (± SE) bilberry biomass (grams, expressed as log2, per ramet) on Svanøy island in A) exclosure (black) and deer-access (grey) plots measured at five-year intervals, and on B) ramets in deer-access plots exposed to different browsing intensities. In B) we include 'Exclosure' (the mean for 2006-2016, while other categories are represented by the mean for 2001-2016, to ensure that this point represents the treatment effect), to show that unbrowsed ramets in deer-access plots differ from exclosure ramets.

3) Larval density

Red deer browsing reduced the larval density per ramet (proportion of insect-chewed leaves on the bilberry ramets, β (± SE); Exclosure $_{2012}$ = -2.39 (± 0.15) vs deer-access $_{2012}$ = -2.64 (± 0.11), z = 2.40, p = 0.016, Fig. 6A, Table A4). The intensity of browsing did not alter larval density on the ramets in the deer-access plots (p-values >> 0.05), except on ramets exposed to high-intensity browsing, where the larval density was higher than for any other browsing intensity (β_{diff} (± SE): 0.37 (± 0.14), z = 2.63 p = 0.009, Fig. 6B, Table A4).

Discussion

Red deer browsing significantly reduced the abundance of bilberry-feeding larvae, indicating that browsing has the potential to trigger ecological cascades in our study area. The negative abundance effect is mainly a result of a strong deer-induced reduction in plant biomass. The larval density per ramet was highest on plants exposed to high browsing intensity (50 to 75% of the shoots browsed by red deer), and on exclosure plants protected from red deer, suggesting that food quality is also dependent on deer browsing.

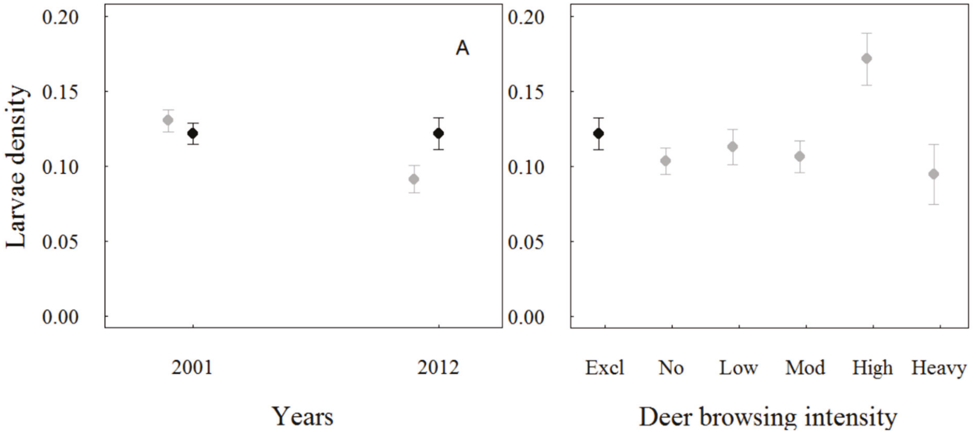

Figure 6. Mean (± SE) larval density per ramet (number of insect-chewed leaves / total number leaves on ramet) of bilberry on Svanøy island in A) deer-access (grey) and exclosure plots (black) measured in 2001 and 2012 (the only years for which data on total number of leaves per ramet is available), and B) on ramets in deer-access plots exposed to different browsing intensities. In B) we include 'Exclosure' (the mean for 2012 to ensure that this point represents the treatment effect, while other categories are represented by the mean for 2001 and 2012), for comparison of unbrowsed ramets in deer-access plots and exclosure ramets.

The effects of browsing on bilberry-feeding larvae confirmed our first prediction: red deer herbivory strongly reduced the abundance of insect larvae in the boreal understory vegetation, as indicated by a 50% reduction in the number of insects outside the exclosures (Fig. 3A, 4A). This is consistent with Baines (1994), who found four times as many larvae in exclosures than in areas where red deer had access Scottish pine forest. Although most insect larvae were found on plants in exclosures, there were marked differences between the numbers of larvae on ramets that were accessible to deer. Bilberry plants that were exposed to low to high browsing intensity (1–74% of shoots removed) had more insect-chewed leaves than heavily browsed plants (≥ 75 % of shoots removed, Fig. 4B). A likely explanation for the uneven distribution of herbivorous larvae on the deer-browsed plants is that heavy browsing leaves fewer leaves for insect larvae to feed on. Sweep netting of larvae did not confirm the same pattern of decrease in larval numbers with increasing intensity of deer browsing in the deer-access plots (Fig. 3B) as was indicated by the number of leaves chewed (Fig. 4B). However, there was a negative trend also here, but with high variation between the macroplots (Table A1). We made the direct measurement of abundance (sweep netting) at macroplot scale, whereas indirect abundance measurements (number of leaves chewed) were made at ramet scale. Moreover, sweep netting only gives a snapshot of larval numbers, which may vary during the season in response to various factors such as weather conditions, whereas the number of insect-chewed leaves on ramets gives information on insect herbivory over a longer period. We argue that the indirect count at ramet scale therefore gives a very precise estimate of browsing effects in insect abundance, and we give more weight to these results in the followings.

Our results showed that on average, deer browsing reduced bilberry biomass in the forest understory to about one ninth of the original level, in support of our second prediction. Bilberry plants responded quickly to exclusion of red deer by growing larger, as also shown in pine forest in Scotland (Baines et al. 1994) and in moorland (Welch 1998), which may be a general adaptation to disturbance. In our study, the change in size occurred within the first five years after exclusion, which is line with other observed vegetational changes (Lilleeng et al. 2016). After five years, the bilberry biomass remained relatively stable in exclosures, and did not reflect the inter-annual fluctuations in abundance of insect larvae. Our results indicate that a relatively short period without deer-browsing is sufficient for bilberry to return to their optimal size, even after decades of red deer herbivory. Several other studies have shown that bilberry is relatively browsing-tolerant (Dahlgren et al. 2007; Hegland et al. 2010; Hegland and Rydgren 2016), especially when browsing occurs in winter and in areas where productivity is low to intermediate. The reduction in plant size caused by red deer browsing became greater as increasing browsing intensity increased, except that unbrowsed plants that were accessible to deer were smaller than those browsed at low to high intensity. This could suggest that bilberry has a unimodal response to herbivory and shows strong regrowth after intermediate browsing intensities, so that the plants become larger than both unbrowsed and heavily browsed plants. However, this is unlikely, as unbrowsed plants that were accessible to deer were much smaller than plants in the exclosures. We conclude that red deer either do not browse the smallest plants because they are less accessible in the field layer than the taller plants, or they avoid the small plants because their nutritional value is lower.

Our third prediction, that larval density would be highest on plants exposed to intermediate browsing intensity, was partly met. Insect herbivory can be used as a proxy for ecologically effective plant defenses (Hegland et al. 2016). Thus, the larval density per ramet can reveal whether the pattern of insect herbivory mainly coincides with food quantity (here: plant biomass), or whether red deer browsing also induces plant defenses that further limit herbivorous larvae populations. Unexpectedly, larval density per ramet was lower on plants in deer-access plots than in exclosure plots. The additional larval preference for leaves of exclosure plants indicates that red deer herbivory in general reduces the food quality of bilberry for other herbivores. Alternatively, the higher biomass in exclosures may attract more insects and thus have an additive effect (Price 1991). However, larval density was higher on ramets where browsing intensity was high (50 to 75 % of the annual shoots browsed) than for all other browsing categories where plants were accessible to deer (Fig. 6B). This may indicate that bilberry plants exposed to relatively intense browsing by deer have lower levels of plant defense compounds, but that when many (here: > 75 %) shoots are browsed, the available biomass is no longer sufficient for the herbivorous larvae, and they therefore avoid the heavily browsed shoots. This supports the plant-stress hypothesis (White 1978), which involves a quality-quantity trade-off. However, in a cafeteria-trial experiment with standardized size bilberry leaves from the same study area, herbivorous larvae avoided the leaves from ramets that were heavily browsed by red deer and preferred the lightly browsed (Moe et al. 2018), and selection should therefore be based on quality alone. This unimodal relationship between browsing intensity and larval preference concurs with results in our study, although we found a preference for more browsed ramets (50-75%). Our study showed that browsing had the greatest effect on larval abundance through biomass removal, but there was also an additional impact beyond this, probably because nutritional quality was affected.

Plants that were accessible to but not browsed by red deer had as few larvae as heavily browsed plants (Fig. 4B). Larval abundance appears mainly to reflect available biomass, as the unbrowsed accessible plants were one tenth of the size of the exclosure plants, and approximately one third of the size of those exposed to low browsing intensity, but nonetheless larger than the heavily browsed plants (Fig. 5B). Larval density was similar for all plants accessible to deer, except where browsing intensity was high (as discussed above, Fig. 6B), which indicates that the nutritional quality for larvae is similar where browsing intensity is moderate to low. Red deer feed selectively (Dumont et al. 2005), and as the nutritional quality of the plants they avoid appears to be similar (as reflected by larvae density), 'avoidance' may simply mean that red deer choose the most easily accessible or larger plants. Kuijper et al. (2010) showed that tree performance was mainly dependent on vegetation cover until the trees grew taller than 50 cm, when ungulate herbivory drastically reduced their performance, indicating that the field layer vegetation can have a protective effect on smaller plants. Similarly, small bilberry plants in our study may be protected by taller vegetation. Strengbom et al. (2003) found that root voles *Microtus oeconomus* also avoided the smallest bilberry plants, and explained this by optimization of food handling time. There is probably no universal pattern, with different responses depending on the species involved. For example, Stephan et al. (2017) found a lower density of insect herbivores on *Sasa palmata* protected from sika deer, although the total leaf area consumed was higher, indicating a decrease in plant nutritional value. Since both plant growth and plant defenses increased in the absence of sika deer (Stephan et al. 2017), the cause of the lower density of insects remains unclear. However, another possible reason why deer browse less on the smaller bilberry plants is that their shoots have lower nutritional quality in winter for red deer than their leaves have for herbivorous larvae in summer. Ungulate browsing may increase plant nutritional value (Danell and Huss-Danell 1985), and therefore trees with browsing history are often re-browsed (Mathisen et al. 2017). Neither browsing by grey-sided vole (*Myodes rufocanus*) nor clipping experiments to simulate ungulate browsing increase phenolic tannin levels in bilberry (Strengbom et al. 2003). We did not analyze the nutritional value or the plant defenses caused by browsing on bilberry ramets in this study, but an earlier study revealed that winter browsing by red deer on bilberry did not result in the same systematic responses indicative of induced defenses as did chemical treatment (Hegland et al. 2016). The abundance and density of larvae on bilberry appear as the ultimate measure of which effect red deer browsing can have on bilberry-dependent insects and also thereby for understanding the red deer's potential for causing ecological cascades.

In addition to the browsing-induced difference in larval abundance, we also found a strong temporal pattern in the co-fluctuations of larval numbers (Fig. 4A). Our results indicated that red deer browsing reduced the amplitude of population fluctuations of herbivorous larvae, as the differences between years were much larger in exclosures than in browsed plots. Multi-annual cycles in population densities are common in northern latitudes (Berryman 1996). General fluctuations in moth populations depend mainly on climate and the trade-off between plant defense and plant reproduction strategies (Selås et al. 2013). The population peaks of the northern spinach *Eulithis populata,* which feeds mainly on bilberry leaves, correlates with bilberry seed production peak years and summer temperature (Selås et al. 2013). Without the peak years in berry production, there are no cyclicity in moth population peaks (Selås et al. 2013). We showed that red deer reduced the number of bilberry flowers, thus reducing bilberry fruit production. Red deer may therefore play a part in dampening population fluctuations in herbivores with overlapping diet requirements, such as rodents.

The observed reduction in larval numbers may induce cascades in boreal forest ecosystems. On islands in British Columbia, Allombert et al. (2005b) showed that the abundance of vegetation-dwelling invertebrates was eight times lower on islands where black-tailed deer were present than on deer-free islands. Furthermore, deer browsing led to a strong reduction in the songbird population (Allombert et al. 2005a). The deer density on these islands was high (~30 deer/km^2), but similar effects have also been found in hardwood forests at lower deer densities (8 and 14 white-tailed deer per km^2, deCalesta 1994), and this is the general pattern in North America (Chollet and Martin 2013). In our study, red deer (overall density ~7.5 deer/km^2) clearly reduced the number of insect larvae. This indicates that birds and other organisms that depend on vegetation-dwelling invertebrates may be affected by red deer browsing in our study area as well. Thus, ungulate herbivory has a strong potential for causing cascading effects when ungulates coexist with sympatric herbivores with which they share food plants.

Overall, we found consistent evidence that red deer browsing had indirect limiting effects on herbivorous insect larvae populations living on the dominant boreal plant bilberry. The main mechanism behind this is the reduction of bilberry biomass by deer. The fast recovery of bilberry plants after exclusion of red deer shows that the system is highly resilient to browsing-induced disturbance. Forests with a diversity of host plants are likely to be more resilient to high ungulate densities, as they can maintain more generalists and other herbivore specialists, thus making for example songbirds more resilient to ungulate overbrowsing (Godfrey et al. 2018). Also, as there is considerable seasonal and spatial variation in Norwegian red deer area use (Bischof et al. 2012), the effective browsing intensity is relatively low in many areas for large parts of the year. It is therefore important to manage forests in a way that maintains their biodiversity, and to protect and maintain deer migration routes between winter and summer ranges to avoid overbrowsing. In areas of conservation concern for sensitive insect species (Brousseau et al. 2013), limitation of ungulate browsing may be considered. Combining local and landscape scale impacts when studying large changes in wildlife populations is an important future challenge for researchers and nature managers.

Acknowledgements

This study is part of the EcoDynDeer project, funded by the Research Council of Norway, MILJO 2015 program (project number 204403/E40) and the Norwegian Environment Agency. We are grateful to Carolin Tröger and Agnes Kammerhofer for field assistance, to Ronny Steen for the bilberry illustration, and to Sam Steyaert for helpful comments on the manuscript. Alison Coulthard did copy editing.

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Appendix

Supplementary material 1 (SM1): Supplementary material to the methods:

We constructed a multiple regression model to estimate the dry mass of bilberry ramets using the same data source as Hegland et al. (2010). We only included the variables recorded every time we took measurements during the 15 years of the present study (i.e. ramet height and number of shoots).

$$Ramet\ size_{\text{[Dry mass]}} = -9.268 + 1.575 \log_2(Ramet\ height) + 0.743\ \log_2(No.annual\ shoots)$$

The model explained 88 % of the dry mass variation, and we therefore consider that it gives an appropriate non-destructive estimate of ramet size.

Table A1. Effects of A) treatment, n = 64 and B) red deer browsing intensity (n = 30) on the number of sweep-netted insect larvae on Svanøy island in 2012 and 2013. Parameter estimates from Poisson generalized linear mixed effects models fitted with random factor block.

	Estimate	SE	z	P
A) Treatment				
Intercept	-0.047	0.194	-0.240	0.810
Exclosure vs deer-access	0.729	0.222	3.281	**0.001**
B) Red deer browsing intensity				
Intercept	0.159	0.408	0.389	0.697
Proportion of shoots browsed by red deer	-1.582	1.363	-1.161	0.246

Table A2. Numbers of insect-browsed leaves on bilberry ramets on Svanøy island: differences between A) treatments (exclosure vs deer-access plots) and years (change in effect between sampling events), and B) various levels of deer browsing intensity index in deer-access plots. We present this as parameter estimates from generalized linear mixed effects models with negative binomial error structure, log link. We used data from five-year intervals in the period 2001 to 2016. The browsing index is based on the percentage of annual shoots browsed by red deer: 'No' (0%), 'Low' (1–24%), 'Moderate' (25–49%), 'High' (50–74%), 'Heavy' (75–100%), sensu Frelich and Lorimer (1985). Reference levels are A) 'deer-access plots' in 2001 and B) 'No' deer browsing. We fitted the models with random effect a) plot in macroplot in block and b) plot in block and year.

	Estimate	SE	z	P
A) Treatment × time				
Intercept	1.20	0.17	6.92	< 0.001
Exclosure vs deer-access	0.14	0.14	0.99	0.320
Year 2006 vs 2001	-1.03	0.14	-7.43	< 0.001
Year 2011 vs 2001	0.16	0.10	1.56	0.120
Year 2016 vs 2001	-0.81	0.11	-7.32	< 0.001
Exclosure × year 2006	0.78	0.19	4.17	< 0.001
Exclosure × year 2011	0.73	0.14	5.11	< 0.001
Exclosure × year 2016	1.23	0.15	8.25	< 0.001
B) Red deer browsing intensity				
Intercept	0.48	0.31	1.54	0.120
Low deer browsing (1–24%) vs No	0.67	0.12	5.61	< 0.001
Moderate deer browsing (25–49%) vs No	0.57	0.13	4.42	< 0.001
High deer browsing (50–74%) vs No	0.58	0.13	4.63	< 0.001
Heavy deer browsing (75–100%) vs No	0.10	0.14	0.72	0.470

Table A3. Bilberry ramet sizes on Svanøy island: differences between A) treatments (exclosure versus deer-access plots) and years (change in effect between sampling events), and B) deer browsing intensity, measured as a 0-4 index in deer-access plots. We present this as parameter estimates from linear mixed effects models with Gauss error structure. We used data from five-year intervals in the period 2001 to 2016. The browsing index is based on the percentage of annual shoots browsed by red deer: 'No' (0%), 'Low' (1–24%), 'Moderate' (25–49%), 'High' (50–74%), 'Heavy' (75–100%), sensu Frelich and Lorimer (1985). Reference levels are A) 'deer-access plots' in 2001 and B) 'No' deer browsing. We fitted the models with random effect A) plot in macroplot in block and B) plot in block and year.

	Estimate	SE	z	P
A) Treatment × time				
Intercept	-1.77	0.32	-5.61	< 0.001
Exclosure vs deer-access	0.42	0.24	1.78	0.098
Year 2006 vs 2001	0.15	0.12	1.23	0.219
Year 2011 vs 2001	-0.22	0.10	-2.18	0.029
Year 2016 vs 2001	-0.37	0.10	-3.72	< 0.001
Exclosure × year 2006	1.28	0.18	7.35	< 0.001
Exclosure × year 2011	1.43	0.14	9.98	< 0.001
Exclosure × year 2016	1.79	0.14	12.65	< 0.001
B) Red deer browsing intensity				
Intercept	-2.17	0.35	-6.21	< 0.001
Low deer browsing (1–24%) vs No	0.98	0.10	9.35	< 0.001
Moderate deer browsing (25–49%) vs No	0.57	0.11	5.11	< 0.001
High deer browsing (50–74%) vs No	0.48	0.10	4.59	< 0.001
Heavy deer browsing (75–100%) vs No	-0.01	0.11	-0.11	0.914

Table A4. Larval density per bilberry ramet (i.e. number of insect-browsed leaves when number of available leaves is accounted for with an offset, 2001 and 2012) on Svanøy island: differences between A) treatments (exclosure vs deer-access plots) and years (change in effect between sampling events), and B) deer browsing intensity, measured as a 0-4 index in deer-access plots. We present this as parameter estimates from generalized linear mixed effects models with negative binomial error structure, log link. The browsing index is based on the percentage of annual shoots browsed by red deer: 'No' (0%), 'Low' (1–24%), 'Moderate' (25–49%), 'High' (50–74%), 'Heavy' (75–100%), sensu Frelich and Lorimer (1985). Reference levels are A) 'deer-access plots' in 2001, and B) 'No' deer browsing. We fitted the models with random effect A) plot in macroplot in block and B) plot in block and year.

	Estimate	SE	z	P
A) Treatment × time, family Negative binomial				
Intercept	-2.12	0.13	-16.81	< 0.001
Exclosure vs deer-access	-0.07	0.12	-0.56	0.577
Year 2012 vs 2001	-0.45	0.11	-4.18	< 0.001
Exclosure × year 2012	0.35	0.15	2.40	0.016
B) Red deer browsing intensity				
Intercept	-2.42	0.19	-13.10	< 0.001
Low deer browsing (1–24%) vs No	0.04	0.13	0.31	0.757
Moderate deer browsing (25–49%) vs No	-0.01	0.14	-0.09	0.927
High deer browsing (50–74%) vs No	0.37	0.14	2.63	0.009
Heavy deer browsing (75–100%) vs No	0.09	0.23	0.38	0.706

ISBN: 978-82-575-1534-8
ISSN: 1894-6402

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