Master's thesis

NTNU
Norwegian University of Science and Technology
NTNU University Museum
Department of Natural History

Marie Lajord

Effects of Red Deer (*Cervus elaphus*) on Boreal Forest Understory Plant Diversity

Master's thesis in Natural Science with Teacher Education
Supervisor: Gunnar Austrheim
Co-supervisors: Anders L. Kolstad & James D. M. Speed
June 2019

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Abstract

Understanding how large herbivores shape plant diversity patterns is an important challenge in community ecology, especially because many ungulate populations in the northern hemisphere have recently reached historically high numbers. Red deer (*Cervus elaphus*) herbivory can alter the composition and structure of forest communities by browsing shrubs and tree seedlings and grazing understory herbs and graminoids. The consequence of these changes can vary widely from positive to neutral and negative, according to variation in local deer numbers, availability of alternate food sources, and the productivity in the habitat. Thus, the determination of sustainable densities of cervids for the purpose of forest and game management is challenging.

I examined the effect of red deer browsing and grazing on vascular plant diversity using an experimental design with ten pairs of deer exclosures and open plots in Tingvoll municipality. I looked at the effect of red deer exclusion on vascular plant species alpha and beta diversity, as well as plant community composition. The results thesis showed that, contrary to my predictions, ten years after excluding the red deer, no effect on alpha or beta diversity was found. However, plant diversity decreased in both exclosures and open plots. Loss in plant diversity was associated with an extreme drought in the winter of 2013/2014 which caused severe ramet dieback of the dominant *Vaccinium myrtillus*. Understanding the impacts of large herbivores on vascular plant diversity is, however important and can help us predict the community responses and work out strategies for sustainable management of red deer herbivory for the conservation of plant biodiversity.

Keywords: *Alpha diversity, beta diversity, boreal forest, cervids, Cervus elaphus, diversity, exclosures, herbivory, heterogeneity, red deer*

Sammendrag

En viktig utfordring i økologi er og forstå hvordan hjortevilt kan påvirke plantediversitet i boreal skog, spesielt siden hjorteviltbestanden i Norge har økt til et historisk høyt nivå. Hjortens (*Cervus elaphus*) påvirkning kan føre til store endringer i artssammensetning og struktur i det økosystemet den lever i, ved å beite på busker og trearter vinterstid og urter og graminoider sommerstid. Effekten av disse påvirkningene kan variere fra positive til nøytrale eller negative, alt etter variasjon i lokal bestandstetthet, mengde og kvalitet på tilgjengelige matkilder og produktivitet i habitatet. For å kunne forutsi og forstå konsekvensene av hjortens påvirkning trengs det kunnskap om hjortebestanden, sett i samspill med økosystemet den lever i for å avgjøre hvilke tettheter av hjort som er bærekraftig.

Jeg har undersøkt effekten av hjortebeite på karplantediversitet i feltsjiktet ved å bruke et eksperimentelt studiesystem basert på ti par med uthenginger og åpne områder tilgjengelig for hjort på Tingvoll. Jeg har vurdert effekten av hjorteuthengning på alfa- og betadiversitet, i tillegg til å se på endringer i vegetasjonssammensetning. Resultatene viser, i motsetning til mine antagelser, at ti år etter ekskluderingen av hjort var det ingen effekt på alfa- eller betadiversitet. Plantediversiteten ble imidlertid redusert i både uthenginger og åpne områder. Tap av plantediversitet ble assosiert med en ekstrem tørke i løpet av vinteren 2013/2014, som førte til en uttørking av den dominante planten *Vaccinium myrtillus*. Det er viktig å forstå hvordan store beitedyr påvirker karplantediversitet. Dette kan hjelpe oss å forutse responser i vegetasjon og plantediversitet, samtidig som det kan bidra med utarbeiding av strategier for bærekraftig forvaltning av hjort.

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1.0 Introduction

1.1 Background

The boreal forest is one of the largest biomes on Earth and covers approximately 38% of the worlds forest area. It is located in the northern hemisphere (mainly in Alaska, Fennoscandia, Canada, and Russia) between the latitude of 45˚ and 70˚ north (Soja, 2007). Cold winters and deep snow-cover are common features in the boreal forest (Gauthier et al. 2015). The forest is an environment that gives habitat for many species and plays an essential role in ecosystem processing and functioning (Pohjanmies et al. 2017). In terms of plant species, Norwegian boreal forests are dominated by coniferous species such as pine *(Pinus sylvestris)*, juniper *(Juniperus communis)* and spruce *(Picea abies)*, in combination with some deciduous species such as rowan *(Sorbus aucuparia)*, aspen *(Populus tremula)*, birch *(Betula pubescens)*, willow *(Salix caprea)*, and alder *(Alnus incana)* (Moen, 1999). The understory vegetation layer consists mainly of dwarf shrubs in coniferous dominated forests (Nilsson and Wardle, 2005). In the forest with more deciduous species, herbs, and grasses are dominating the understory vegetation, and the bottom layer is dominated by bryophyte and lichen (Muukkonen et al. 2006).

The population of wild cervids (*Cervidae*) is increasing in the northern hemisphere, and in many areas, recent population increases in red deer (*Cervus elaphus*), moose (*Alces alces*) and white-tailed deer (*Odocoileus virginianus*) have created concerns about whether such large populations are sustainable (Côte et al. 2004). Red deer is now the most abundant wild large herbivore in Norway, and the population has developed from critically low to historically high numbers within the last century (Lande et al. 2014). According to Fuller & Gill (2001), there are at least six different reasons for this increase in the red deer population in Northern Europe: (1) The increase in the woodland area due to planting and neglect of cultivated land, has increased the food base for deer. (2) Changes in farming by intensifying and extensively producing grains have provided more winter food for the deer. (3) Decrease in outfield grazing by livestock influence the red deer positively, because livestock grazing influences the deer by reducing understory vegetation in woodlands, limiting both food availability and shelter opportunities. (4) More controlled and direct harvest of deer by lowering the scale of hunting as well as the impact on the population. (5) Warmer winter has been correlated with increased recruitment and overwinter survival of deer. (6) Large predators have been virtually eliminated, resulting in the removal of a significant mortality factor.

In Norway, the distribution of large herbivores has, in general, shifted from communities dominated by livestock to communities dominated by wild herbivores. The increase of browsers (moose, roe deer (*Capreolus capreolus*)) in addition to declines in livestock grazers gives changes in foraging strategy from grazing to browsing in the non-alpine area. In the coastal and alpine area, the foraging strategy is expected to maintain the same, because of the intermediate feeders (red deer, reindeer (*Rangifer tarandus*), and sheep (*Ovis aries*)) (Speed et al. 2019). The red deer have been found present in western Norway since just after the last ice age, but the population in size has varied since then because of climatic fluctuations (Rosvold et al. 2013). Red deer are classified among the intermediate and mixed feeders, as their diet changes with seasons and are affected by seasonal variation of forage quality and availability: graze graminoids and herbs during summer but browse woody species during winter (Du Toit & Olff, 2014; Hofman, 1989; Mysterud, 2010). Red deer diet and choice of plants varies during the year and among habitats (Mysterud, 2010). A summary of many studies in Europe shows that graminoids make up 29 % of the red deer diet, 23 % dwarf shrubs, 19% leaves, buds and twigs from deciduous species, 7% shots and bark from conifers, 7% herbs and the rest of the diet (34%) consists of other plant species and mushrooms (Gebert and Verheyden-Tixier, 2001). The red deer is a selective feeder that both graze and browse and can, therefore, alter the growth, reproduction, and survival of many herbs, grasses, shrubs and tree species (Côte et al. 2004, Waller and Alverson, 1997). Selectivity increase when food availability is higher (Pyke, 1984; Ceacero et al. 2012; Lande et al. 2014).

Plant species richness is often used as an indicator of plant diversity. It is useful for understanding the mechanisms behind species coexistence (Boulanger et al. 2018). Variation in biodiversity in an ecosystem can be determined by considering the species richness both at a local scale (alpha, α) and at a regional scale (gamma, γ). According to Austrheim & Eriksson (2001), the regional patterns of plant diversity is determined by, 1) the species pool, 2) the heterogeneity and fragmentation of communities, and 3) local diversity of each plant community. Beta diversity (β) is the connection between alpha and gamma diversity and illustrates the relationship between local and regional species richness (Tuomisto, 2010). To explain the species composition at the local and regional scale species evenness can be included. Species evenness is defined as the distribution of species richness weighted by the relative abundance within a defined area (Buzas, 1979). When using Shannon's diversity index differences in evenness is taken into account (Jost, 2006).

Large herbivores alter the plant community and have been found to affect species abundance and occurrence directly by herbivory (Hester et al. 2006; Olff and Ritchie, 1998). A global meta-analysis found that all types of herbivores, including insects, significantly reduced plant abundance, biomass, survival, and reproduction, and increased species evenness but not richness (Jia et al. 2018). Bernes et al. (2018) did a systematic review on the effects of large herbivores in temperate and boreal forests and found that they may alter the species abundance in forests, without changing the richness. They showed that the general effects of herbivory on abundance were negative on woody understory and dwarf shrub species, and no significant response in graminoids or herbs. Understorey abundance responded negatively to livestock and ungulates introduced into the wild, but not to native ones. Also, understorey species richness responded positively to grazers but not to browsers or intermediate feeders. Studies showed that understory species richness decreased when the abundance of understorey vegetation was reduced (Bernes et al. 2018).

Heterogeneity in space and time has been recognized as an essential feature of ecological systems (Levin, 1992). Vegetation heterogeneity can be separated into two parts: temporal- and spatial heterogeneity. Temporal heterogeneity is the term used when the community experience a disturbance, which leads to species turnover over time (Rydgren et al. 2004). Spatial heterogeneity is the variance in species composition between two sites, both at a local and regional scale (Koleff et al. 2003). Maintaining heterogeneity in habitats is important for supporting a diversity of fauna of flora (Kuijper, 2010). High spatial heterogeneity can make an ecosystem more robust to disturbance because high variation among species that will have different responses to a disturbance will level out the effects. High heterogeneity levels may play a critical role in maintaining ecosystem productivity by concentrating limiting resources, maintaining habitat diversity and influence the variety of consumers ranging from insects to birds and mammals (Adler et al. 2001).

Herbivores can maintain heterogeneity by feeding patchily and maintain the formation of open areas (Adler et al. 2001; Koleff et al. 2003; Apollonio et al. 2017). To a certain level, herbivory will increase landscape heterogeneity because each patch will be at a different stage of recovery, but if the grazing pressure is high, the landscape will become more homogenized with a selection for tolerant and resistant species (Augustine & McNaughton, 1998). Red deer can also promote homogenization by mediating seed dispersal (Albert et al. 2015) and through altering growing conditions such as micro-climate, light regimes, or soil properties (Lilleeng et al. 2016, Boulanger et al. 2018). Other mechanisms behind homogenization are likely to be a reduction of preferred species and higher growth rates of browse-tolerant and avoided plant species (Rooney, 2009). Depending on their feeding preferences, Rooney (2009) found that herbivory by white-tailed deer reduced the spatial heterogeneity, while Gaston (2006) found that black-tailed deer (*Odocoileus hemionus*) increased the spatial heterogeneity. Red deer is a mixed feeder and may have a smaller effect on spatial heterogeneity since they feed on more species than black-tailed deer (Hofmann 1989). Lilleng et al. (2016) found that vegetation, where the red deer had been excluded for the longest time, showed the highest spatial heterogeneity.

Young understory tree species like rowan and willow are favourable browsing species for cervids (Mysterud et al. 2010; van Beest et al. 2010). Deer have shown to decrease regeneration of favoured trees and other palatable species and to reduce young tree growth (Didion et al. 2009; Persson et al. 2005; Rooney & Waller, 2003). Despite the generally negative effects on woody species, increasing herbivory intensity had a weak positive effect on young trees, possibly because the removal of herbaceous vegetation by herbivores allows increased seedling establishment (Scott et al. 2000). Tree survival from juvenile to the young adult stage appears to depend on low herbivory density, and therefore, few of these trees survive to larger size classes (Hegland & Rydgren, 2016). Both Boulanger et al. (2018) and Kuijper et al. (2010) found an increase in shrub layer inside exclosures compared to open plots where the red deer had access, indicating that deer browsing limit growth of woody and shrub species. Further results showed negative effects on species richness of woody understory vegetation, whereas the richness of herbs responded positively and species richness of shrubs and graminoids showed no significant response (Bernes et al. 2018).

Herbaceous understory plant species richness in a boreal forest varies in response to red deer herbivory and may be dependent on both the density and frequency. When reviewing the literature, the findings are conflicting. Hegland et al. (2013) found that understorey plant species richness in an old-growth boreal forest followed a hump-shaped curve, increased with increasing herbivory intensity but declined at too high densities. It has also been shown that ungulates may increase plant diversity in ecosystems by removing dominant woody species (Pekin et al. 2015). According to Boulanger et al. (2018) ungulates maintained higher species richness in the herbaceous layer outside the exclosures, while the shrub layer decreased in richness. While Rooney (2001) found that when local deer herbivory increases the understory herb diversity declined, and ferns and graminoids became increasingly dominant. Further results from Rooney & Waller (2003) and Hegland & Rydgren (2016) indicates that grazing can negatively affect both growth and reproduction of individual herbs and graminoids, even though they are tolerant to a certain level. However, Speed et al. (2014) found no effect of red deer herbivory on total vegetation density and vascular plant diversity in open plots accessible to red deer or exclosed plots.

It is not always herbivory alone, causing the effects on vegetation composition. Depending on the productivity in the habitat, plants may respond differently (Olff & Ritchie, 1998; Bakker et al. 2006). At higher productivity, grazed plants can more easily compensate for grazing, and productive habitats are therefore expected to sustain plant diversity at higher herbivore densities, while less productive habitats are not (Austrheim & Eriksson, 2001). Hester et al. (2006) found that different gradients of productivity affected grazing choice and species responses to damage in non-forest vegetation. However, according to Speed et al. (2014) there was no effect of herbivore exclusion in vegetation response when the exclusions varied with productivity. Most plants have developed a type of protection against the browsing or grazing of deer. This protection can be in the form of avoidance or tolerance to herbivory (Augustine and McNaughton, 1998; Skarpe & Hester, 2008). Overcompensation is only found for plants that have a tolerance strategy. Tolerant species will react to browsing with investment in regrowth, while avoidance strategies include physical or chemical defence that causes reduced palatability (Hester et al. 2006; van der Meijden et al. 1988). Tolerant plant response may be beneficial for herbivores when plants respond by increasing vegetative production (Bergqvist et al. 2003), because such plant tissue is high in nutrient content, and contain less defence material (Volenec et al. 1996).

Rooney (2001) found that the dominance of one plant species linearly increased with local feeding intensity, indicating that abundant deer directly will reduce forest understory evenness. When the dominance of one species increases, the diversity in a community may decline as a result of competitive exclusion. According to Levy (2006) the winning plants are shade tolerant and either unpalatable to deer or able to regrow quickly after browsing. The selection by deer is a combination of availability during the seasons, palatability (food choice based on taste) and the quality of the forage. Many forests have therefore become dominated by species red deer do not find palatable, like ferns. Herbivores respond to spatial heterogeneity in vegetation (Senft et al. 1987) but can also affect the spatial heterogeneity in vegetation through impacting plant communities at different scales and in interaction with productivity and soil nutrient cycling (Austrheim & Eriksson, 2001).

Climatic stress occurs when environmental factors affect vegetation composition, such as extreme temperatures, little precipitation, and a lot of wind, etc. (Jump and Penuelas, 2005). Evergreen plants are dependent on being hardened in the fall to be able to sustain winter temperatures and to obtain enough protection from winter temperatures, it should gradually become colder. Northern ecosystems are especially exposed when warm temperatures midwinter is followed by cold temperatures the rest of the winter (Bjerke et al. 2014). In such cases, the “winter hibernation” of plants can be disrupted at the same time plants loose snow cover as protection. If the temperature fluctuates both up and down, in addition to low snow cover and a lot of wind, this climatic stress may lead to more frequent plant mortality. Climatic changes have led to warmer winters, which result in earlier melting of snow and more extended growing season for plants. These warm events will influence the amount, recruitment, and composition of plants (Bjerke et al. 2014). For the deer, high temperatures in the winter may be positive, but if this affects the availability of important grazing plants, the effect will be negative.

1.2 Objectives

With the increase in deer densities, it is essential to examine if the trend is affecting the plant diversity and whether management should be considered to regulate the red deer densities. Therefore, my aim for this thesis is to investigate how excluding red deer influenced vascular plant species alpha and beta diversity, and the species composition of ecological communities in a coastal boreal forest understory vegetation in Tingvoll, Norway.

1.3 Hypotheses

H_1: Alpha diversity will be lower within exclosures compared to open plots due to increase in dominant species preferred by red deer in the exclosures, such as dwarf shrubs and young understory trees.

H_2: Spatial beta diversity will be higher between subplots in exclosures, compared to open plots due to red deer herbivory having a homogenizing effect on the spatial distribution of plant species.

2.0 Methods

2.1 Study area

The study was conducted in the municipality of Tingvoll in the county of Møre and Romsdal, Norway (62.9˚N, 8.2˚E, Fig.2). The study area is situated in the southern to middle boreal zone and has a great variety of topographic and climatic conditions, including coastal landscapes and larger valleys and woodlands (Moen, 1999). The annual mean precipitation is 1300 mm, and mean air temperature is around –1 °C in January and 16 °C in July (Speed et al. 2013; http://www.eklima.no). Precipitation and temperature generally decrease from coast to inland, while the depth and duration of snow cover increases (Mysterud et al. 2000). Snow cover is normally present from January to March but is highly variable during winter and among years. Extreme climatic conditions in the winter of 2013/2014 with low precipitation, low snow depth, and high mean air temperature caused a drought that resulted in a large proportion of dead biomass, especially bilberry (*Vaccinium myrtillus*) (Meisingset et al. 2015).

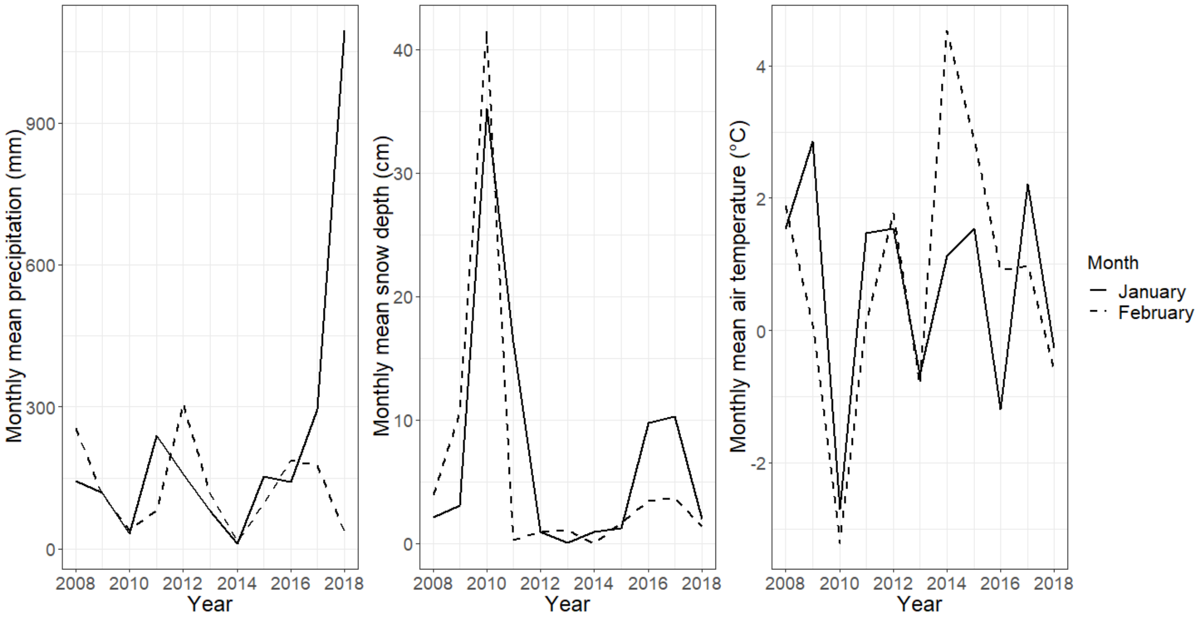

Figure 1. Monthly mean precipitation, monthly mean snow depth, and monthly mean air temperature for January (solid line) and February (dotted line) from the year 2008 to 2018. Data collected from NVE – Norges vassdrags- og energidirektorat.

Figure 2. Both pictures showing areas with dead bilberry (Vaccinium myrtillus) vegetation at one of the locations (Rottås) in Tingvoll. The picture is taken in the summer of 2014. Photo: NIBIO

Of the mainland and island, agricultural land covers 20.66 km^2; forests cover 224.58 km^2; open firm ground 50.55 km^2 and wetland 15.18 km^2 (Appendix 1, Statistics Norway (2019)). There is an active agricultural and forestry production in the study area. Agricultural areas are located on flatter and more productive areas, often in bottoms of valleys, mainly with pastures and meadows for grass production (Lande at al. 2014). These areas are surrounded by forest, which is mostly dominated by deciduous tree species, mostly rowan, birch, and alder, and pine, in addition to juniper and the heathland shrubs bilberry and heather (*Calluna vulgaris*) (Speed et al. 2013).

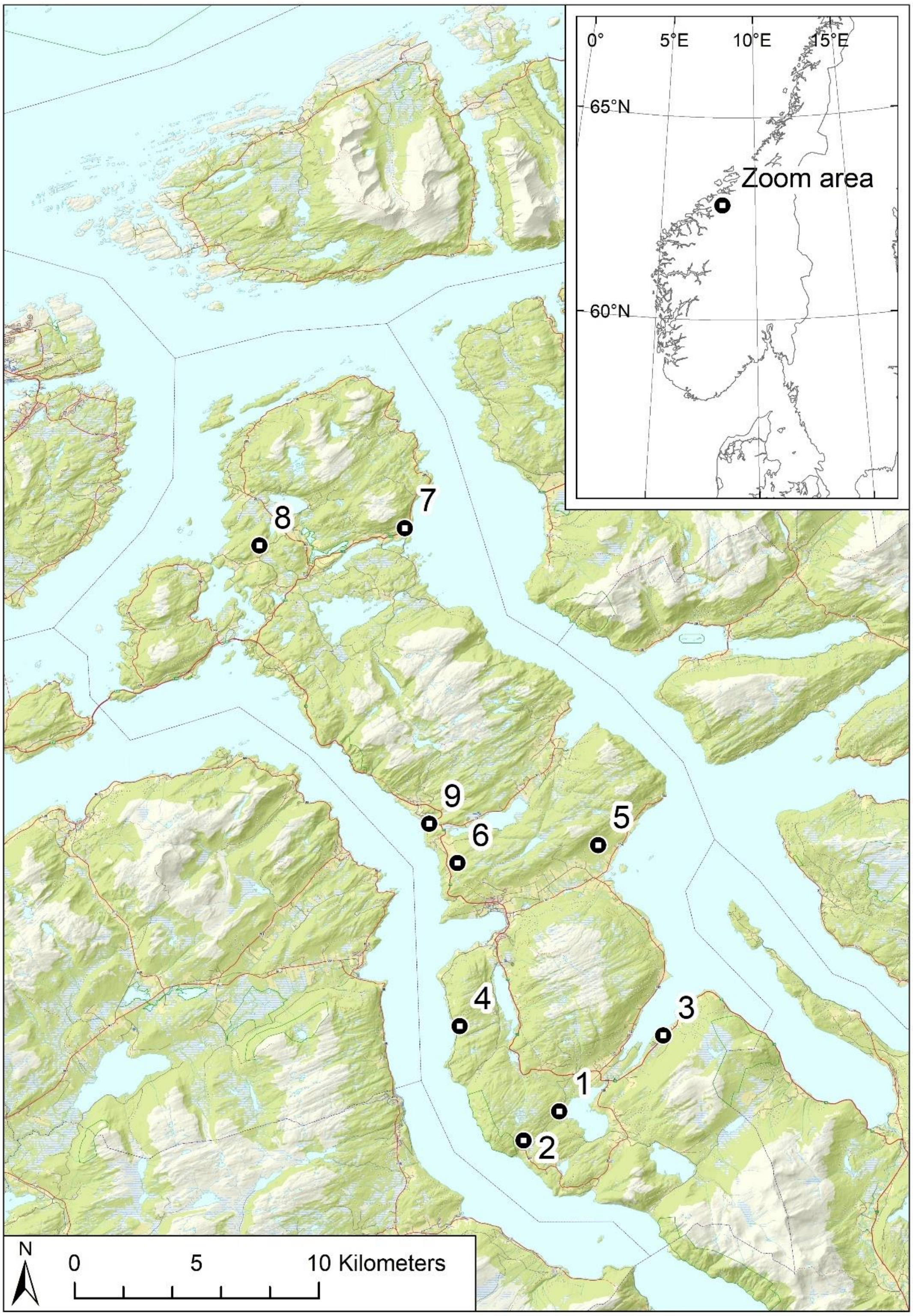

Figure 3. Map showing the geographical distribution of the 9 locations in Tingvoll county

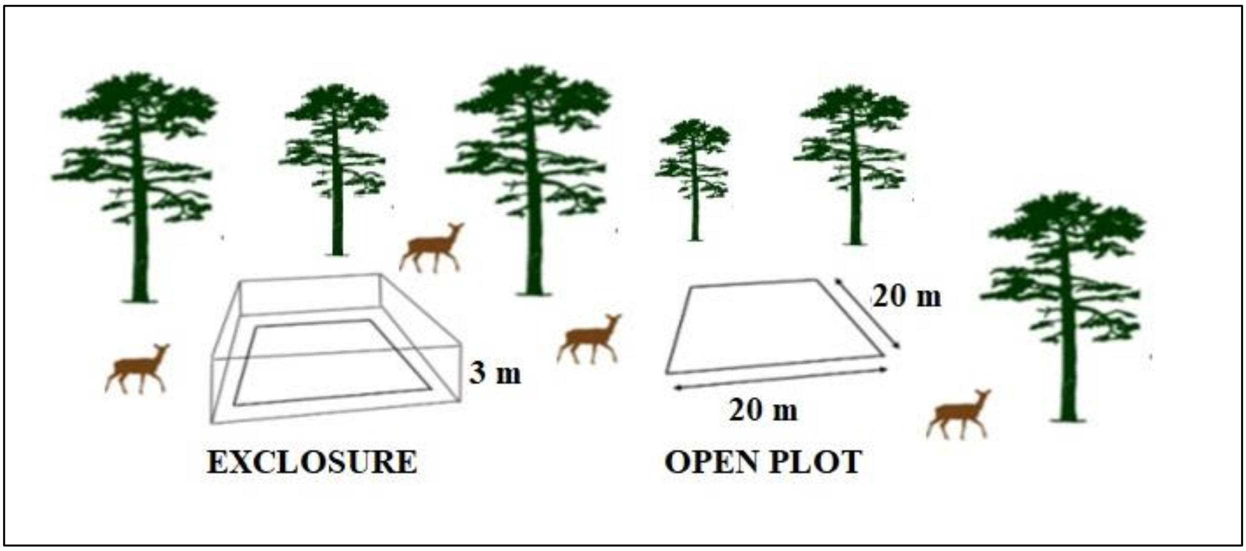

Figure 4. Figure showing the research design (reproduced with modifications and permission from Lilleeng et al (2018)).

2.2 Red deer

In Norway, the cervid metabolic biomass increased by approximately 280% from 1949 to 1999 (Austrheim et al. 2011). Absolute density estimates are not available, but is it estimated from hunting statistics that the red deer population has increased nearly 150-fold since 1900 (Statistics Norway, 2019).

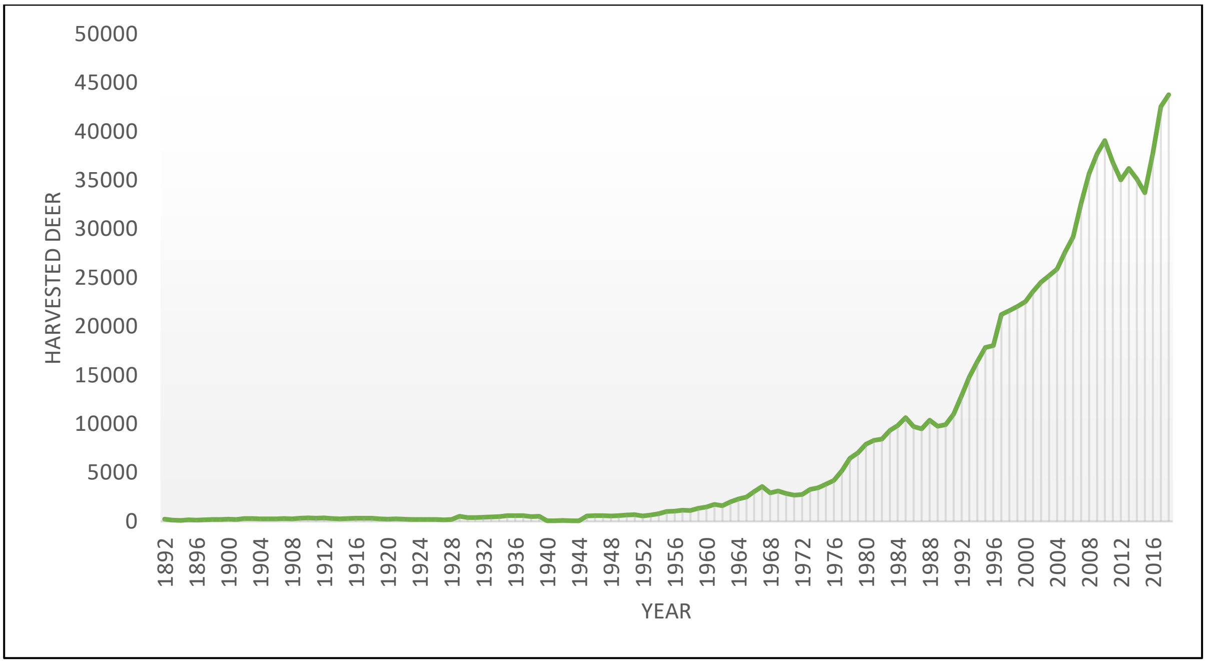

Figure 5. The number of hunted red deer in Norway from 1892-2018. The first 20 years of the time series, the average number of deer hunted was approximately 200 per year, while during the last 20 years, on average about 31 000 animals have been hunted per year. Until 1952 the statistics contain all killed deer, both hunted and killed by accident or illness. After 1952 the statistics only contains animals legally killed during hunting. Data from Statistics Norway (2019).

The red deer is the most dominant forest cervid in the municipality, and hunting statistics indicate that the red deer population has increased steadily since 1970, and the harvest yield has increased almost six-fold in the municipality during the same period of time, more than 6300 red deer were shot in 2008 (Statistics Norway, 2019). The population density is estimated to approximately 8 deer per km^^{2} (Speed et al. 2013), which is considered high for Norway, but a representative for most areas in Western Norway. In the municipality, small populations of roe deer and moose can be found but with approximately 6 and 25 times lower densities than the density of red deer, respectively (Speed et al. 2013). The red deer population is relatively stable, although some animals may migrate between summer (inland, higher elevation) and winter (coast, low elevation) foraging areas (Meisingset et al. 2013).

In Norway, the population of red deer is mainly managed by hunting during the autumn. Harvesting regimes, the degree of selectivity and harvest pressure, varies between cultures and municipalities (Mysterud & Bischof, 2010). The municipality has a management plan and goals for the different cervid populations. Hunting quotas are allocated to local management units (’vald’) consisting of smaller or larger congregations of landowners. The hunting is controlled with licenses, and the number of licenses distributed is expected to reflect habitat area and quality, in relation to population size in the municipality (Tingvoll municipality, 2019).

2.3 Study design

In the autumn of 2008, 10 sites were established at different locations in Tingvoll and included forest with conifers, mainly pine (n=7), and some richer deciduous trees, mainly birch (n=3). The locations were selected because of their difference in red deer densities during summer and winter, and to include both low and high productive sites (table 1). In the past, grazing by domestic livestock has occurred in some of the sites, but not in recent times. Therefore, red deer, and to some extent, moose and roe deer are the main herbivores on the vegetation. The exclosure in site nr. 10 was in the summer of 2016 disrupted by the livestock to a nearby farmer and had to be excluded from the study.

Table 1. Overview of the locations in Tingvoll municipality, which have been used for vegetation registering in the period 2008-2018m (Meisingset et al., 2015). H40 bonitet is the height of the dominant species at 40 years of age, and a measure on the locations ability to produce trees. F = pine and G = spruce. Feeding grounds represent which season the location is preferable for red deer.

Site nr.:	Location	H40 bonitet	Forest type	Feeding grounds
1	Haltbakken	F14	Pine	Summer
2	Rottås	F14	Pine	Winter
3	Åsprong	F14	Pine	Summer
4	Ormset	G17	Deciduous	Winter
5	Holmeid	F14	Pine	Winter
6	Bråttvika	F14	Pine	Summer
7	Kanestrøm	G17	Deciduous	Winter
8	Gjengset	F14	Pine	Winter
9	Gyl	G20	Deciduous	Winter
10	Gjørsvika	G17	Pine	Winter

Each site consists of two 20 × 20 m plots. At all sites, one plot was kept as control, which allowed deer access (hereafter ‘open plots’). In the paired plot the red deer were excluded with 3 m tall wooden poles sunk into the ground, and 10 × 10 cm mesh wiring used to exclude the red deer (hereafter ‘exclosure’). The exclosures and open plots were established in homogenous stands, with between 20-50 m apart to avoid edge effects and minimize heterogeneity. One of the two plots was randomly assigned as an exclosure, and the other one as the open plot. Henceforth, ‘treatment’ refers to exclosures and open plots. Within each exclosure and open plot, 10 permanent, fixed, subplots with quadrats of 0.5 × 0.5m were established at randomly selected locations, but edges was avoided. Birds, insects and smaller mammals could move freely in and out of the exclosures.

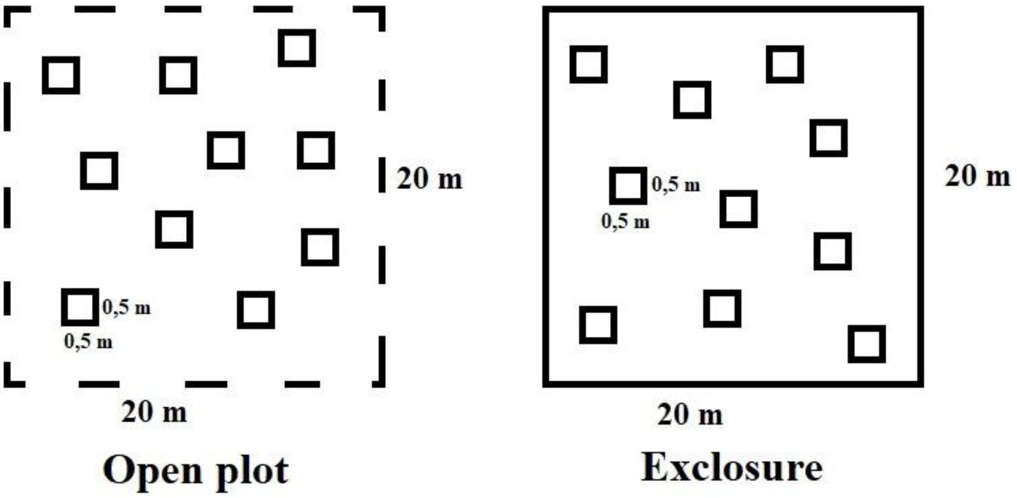

Figure 6. Illustration of the research design for monitoring vegetation. In 2008, ten permanent 0.5 × 0.5 m vegetation subplots were established in each plot (n = 180), and species richness and abundance were monitored in 2008, 2010, 2012, 2014, 2016 and 2018. N.B. the 0.5 × 0.5 m vegetation subplots are not scaled with the 20 × 20 m plots in this illustration.

2.4 Plant and herbivore data collection

Fieldwork was conducted during the summer, either late June or early August, so that herbivory that may have occurred during the spring and early summer could be examined. Vascular plant species richness was recorded and the abundance of each species in the understory vegetation in each of the ten permanent subplots per exclosure and open plot every other year from 2008 to 2018. Assessment of the field layer was carried out using a point-intercept method (e.g., Jonasson, 1988), with 16 regularly spaced pins per quadrat. All vascular plants were recorded to species level that intercepted with each pin and calculated the abundance of all species at the subplot level.

Figure 7. Figure showing how the point-intercept method was conducted out in the field. Photo: Marie Lajord.

Figure 8. Figure showing the fencing between the open and exclosed plots. Left Photo: Marie Lajord. Right photo: Ingrid Bekken Snøan.

To calculate alpha diversity within each subplot, species richness (number of species recorded in the observation unit) and the Shannon diversity index (H', which considers the species richness and the evenness of their abundance) were used for all vascular plants, including trees < 50 cm. For beta diversity between subplots, the mean within-plot Jaccard dissimilarity index was calculated for all subplots from 2008 to 2018. Since this method only considers presence-absence of species, it is a metric sensitive to the turnover of unusual species but would be limited for identifying variance in dominance (Barwell et al. 2015). Bray-Curtis index was calculated, which focusses on plant abundance values, but ended up with the same conclusion, so chose to continue with the mean Jaccard dissimilarity index. For estimating herbivory pressure, we used dung collection and hunting statistics (Appendix 2, Appendix 3).

2.5 Statistical analyses

All data processing and analyses were done in the R environment (version 3.5.1; R Core Team 2018) and Rstudio (version 1.0.153) using packages lmerTest (Kuznetsova et al. 2017), vegan (Oksanen et al. 2018), and ggplot2 (Wickham, 2009). Since the study design is nested (site, plot, and subplot), linear mixed effect models were used with random intercepts for each site. Effect of exclosure treatment, year and their interaction, in addition to quadratic terms of year and interaction with treatment were tested on species richness, Shannon's diversity index, and Jaccard dissimilarity. Including dung counts and deer density estimates from hunting statistics did not improve the models (Appendix 2, Appendix 3). Model reduction was done by starting with full models including all fixed variables and their interactions and then applying backward elimination of non-significant ($p < 0.005$) fixed effects. Explored using quadratic terms for year since exclosure and the quadratic interaction with treatment. Residuals were visually checked for normality and homoscedasticity of variance within all levels of explanatory variables. If model assumptions were violated, the response variable was log transformed. Some of the species from the original dataset were merged if there was uncertainty that the species was classified right. This was the case for Common Cow-wheat (*Melampyrum pratense*) and Small Cow-wheat (*Melampyrum sylvaticum*), which was merged to Cow-wheat (*Melampyrum sp*).

Differences in species composition between open plots, and exclosures were analyzed with principal components analysis (PCA). The abundance of each plant species for every subplot were used as variables in the analyses (log+1 transformed values). All species, including the rare, was included in the ordination solution. The PCA was run for both treatments all ten years and indicated how the species composition between years differed between the open plots and exclosures. The area of the polygons is related to beta diversity estimate.

3.0 Results

3.1 Alpha diversity

We recorded a total of 77 plant species across all ten sampling years, and 34 of the recorded species occurred in both treatments. Overall, the mean number of species per subplot was 4.4 (± 0.2 SE). Bilberry and wavy hair-grass (*Avenella flexuosa*) were the most common and occurred in almost all plots all years (Appendix 4). In exclosures, the species that increased in abundance from 2008 to 2018 was chickweed wintergreen (*Trientalis europaea*), cow-wheat, and wood anemone (*Anemone nemorosa*). Species that decrease during that period was common bent (*Agrostis capillaris*), dwarf cornel (*Chamaepericlymenum suecicum*), heather, purple moor-grass (*Molinia caerulea*), and twinflower (*Linnaea borealis*). In open plots species that increased in abundance from 2008 to 2018 was common couch (*Elytrigia repens*), dwarf cornel, sweet vernal grass (*Anthoxanthum odoratum*), wavy hair-grass, and wood anemone. Species that decreased during that period was cow-wheat, heather, lingonberry (*Vaccinium vitis-idaea*), purple moor-grass, twinflower, and violet (*Viola sp*). No species showed any apparent change in relative density outside the exclosures than inside the exclosures, but this was not statistically assessed.

The ordination plot (Appendix 5) allows us to visualize how alike the sites are to one another in terms of species composition. The polygons, based on the plots, are quite similar in the end as they were at the beginning of the study. The left plot are positioned in relation to species composition. The right plot shows that the exclosures were, to some extent, getting more diverse over time (darker reds have larger area), while the open plots are quite stable (darker blues have slightly larger area).

Species richness in both exclosure and open plot increased from yse = -1 to yse =1, decreased from yse = 1 to yse = 5 and increased from yse = 5 to yse = 9 (Fig. 9). The difference in species richness between treatments was greater between the plots at the beginning of the experiment (yse = -1) than at the end (yse = 9). Open plots started with more species than exclosures, but in yse = 2 a shift resulted in exclosures having more species. Ten years after excluding red deer, treatment did not significantly affect the species richness in (Fig. 9; Table 2, Appendix 6).

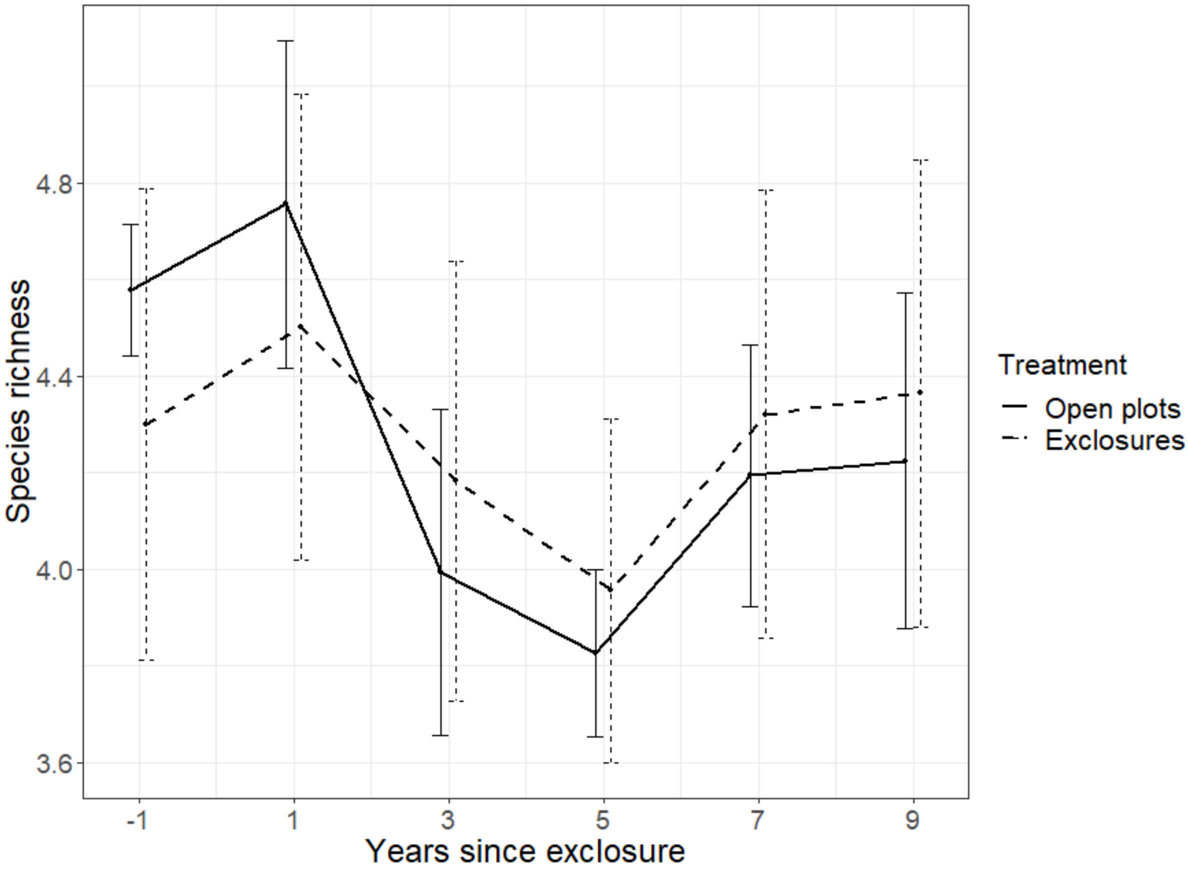

Figure 9. The relationship between year since exclosure and species richness (mean and SE) in a deer excluding study in Tingvoll. Recorded diversity within plots for vascular plants in the boreal forest. Year since exclosure = 0 is 2009. Either exclosed (dotted line) or open (solid line) to red deer during 10 years of experiment. The sample units are 20 × 20 m plots (n=9 locations).

Table 2. Output from linear mixed effect model that predicted species richness (log +1 transformed) as a function of year since exclusion (yse) and treatment. The treatment factor reference level is the exclosure. SE = standard error, Df = degrees of freedom.

Variable	**Estimate**	**SE**	**Df**	**T-value**	**P-value**
Intercept	1.652e+00	8.458e-02	1.740e+01	19.534	2.81e-13
Yse	-2.814e-02	9.057e-03	1.049e+03	-3.107	0.00194
I(Yse^2)	2.311e-03	1.007e-03	1.049e+03	2.295	0.02191
Treatment Exclosure	-6.138e-02	1.195e-01	1.731e+01	-0.514	0.61389
Yse:Treatment Exclosure	7.302e-03	5.880e-03	1.049e+03	1.242	0.21455

Excluding red deer gave no effect on Shannon diversity (alpha diversity or within subplot diversity). Shannon diversity decreased over time, in both exclosures and open plots, but the difference between treatments showed no significant effect after 10 years of the experiment (Fig. 10; Table 3, Appendix 7).

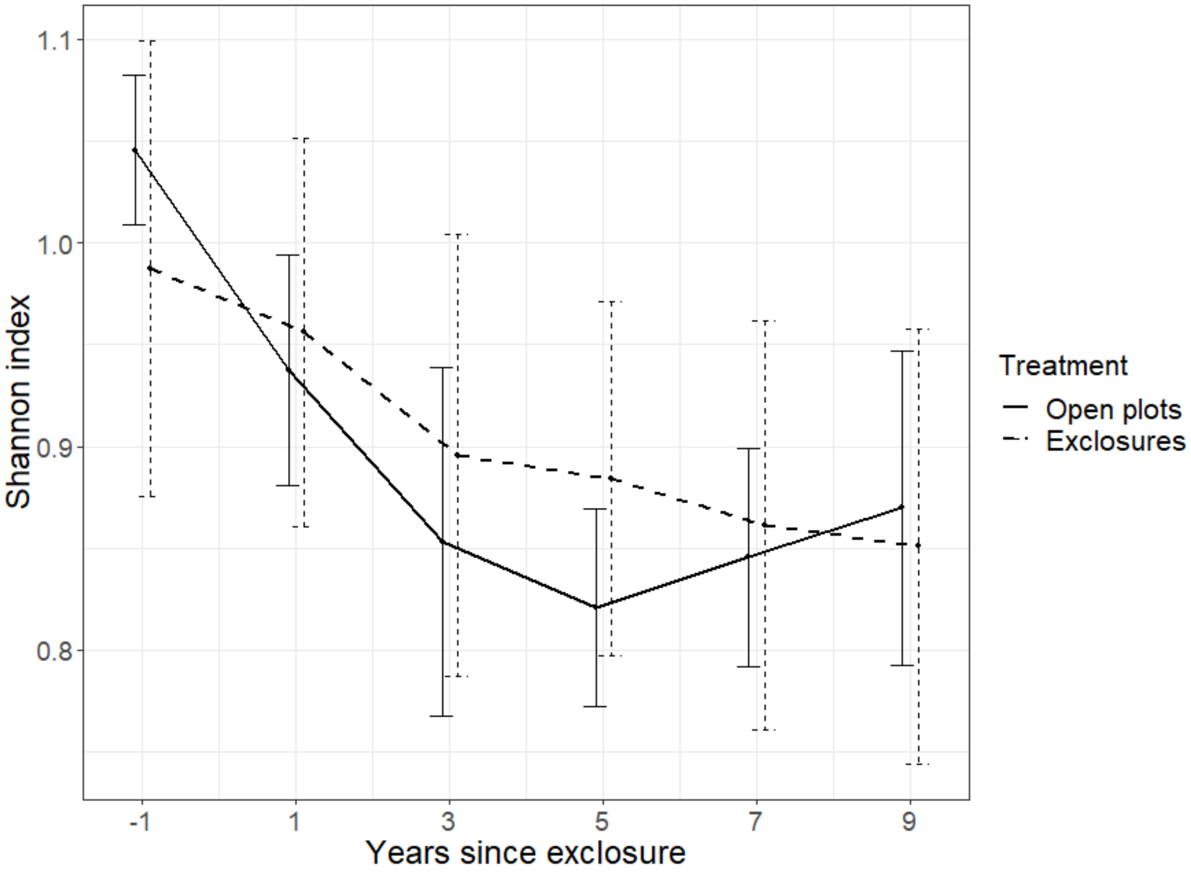

Figure 10. The relationship between year since exclosure and mean (± SE) Shannon diversity within plots for vascular plants recorded in the boreal forest in Tingvoll. Either exclosed (dotted line) or open (solid line) to red deer. The sample units are 20 × 20 m plots (n=9 locations).

Table 3. Output from linear mixed effect model that predicted Shannon's diversity index (log+1 transformed) as a function of year since exclusion (yse) and treatment. The treatment factor reference level is the exclosure. SE = standard error, Df = degrees of freedom.

Variable	Estimate	SE	Df	T-value	P-value
Intercept	6.585e-01	4.727e-02	1.782e+01	13.932	5.11e-11
Yse	-2.136e-02	5.720e-03	1.049e+03	-3.734	0.000199
I(Yse^2)	1.525e-03	6.359e-04	1.049e+03	2.399	0.016628
Treatment Exclosure	-8.228e-03	6.674e-02	1.770e+01	-0.123	0.903271
Yse:Treatment Exclosure	1.259e-03	3.714e-03	1.049e+03	0.339	0.734754

3.2 Beta diversity

The analysis of mean Jaccard dissimilarity found no effect of red deer browsing. The mean Jaccard dissimilarity decreased steadily over time in the exclosure and remained stable in open plots, but no significant effect between treatments after 10 years (Fig.11; Table 4). Bray-Curtis dissimilarity (within subplots, between years) was also calculated and showed similar effects.

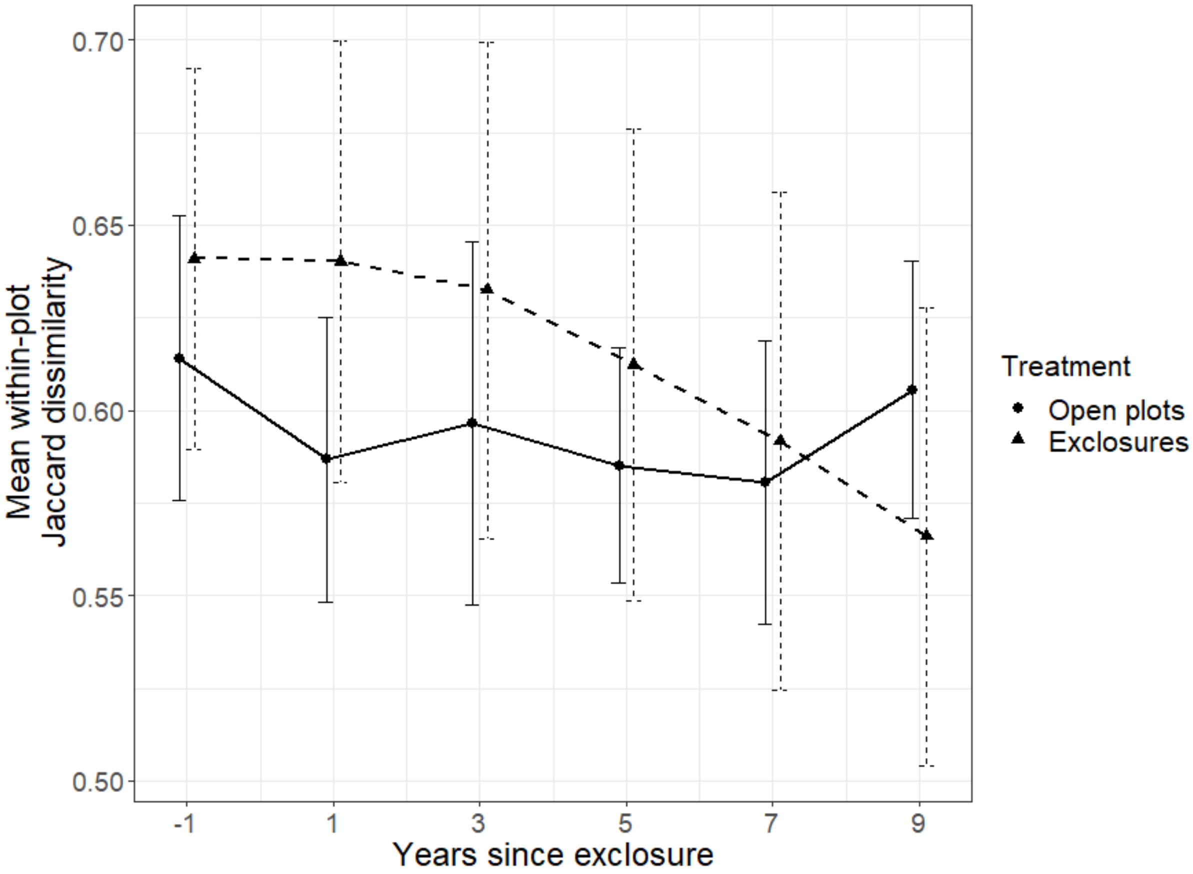

Figure 11. Year since exclosure and mean (± SE) within-plot Jaccard dissimilarity for vascular plants recorded in the boreal forest in Tingvoll either exclosure (triangle) or open (dots) to red deer. The sample units are 20 × 20 m plots (n=9 locations).

Table 4. Output from linear mixed effect model that predicted Mean within-plot Jaccard dissimilarity (log+1 transformed) as a function of year since exclusion (yse) and treatment. The treatment factor reference level is the exclosure. SE = standard error, Df = degrees of freedom.

Variable	Estimate	SE	Df	T-value	P-value
Intercept	0.598871	0.045249	10.098024	13.235	1.05e-07
Yse	-0.001035	0.003265	91.974824	-0.317	0.7520
TreatmentExclosures	0.054041	0.024743	92.002252	2.184	0.0315
Yse:TreatmentExclosures	-0.005535	0.004742	91.991815	-1.167	0.2462

4.0 Discussion

4.1 Status on effects of herbivory on vegetation and diversity

Studies have found red deer to decrease alpha diversity in preferred shrubs and understory tree species (Hegland & Rydgren, 2016; Rooney & Waller, 2003), and both increase (Hegland et al. 2013; Boulanger et al. 2018) and decrease (Rooney, 2001) alpha diversity in herbaceous and graminoids species. Studies have also found red deer herbivory to both increases (Adler et al. 2001; Gaston, 2006; Augustine & McNaughton, 1998) and decreases (Lilleeng et al. 2016; Rooney, 2009) spatial heterogeneity.

4.2 Main findings

In this project, using the SustHerb (https://www.ntnu.no/museum/sustherb) system of multiple paired exclosures and open plots in Tingvoll municipality and with their recordings every second year on understory vascular plants, we were able to test if excluding the red deer affected the alpha and spatial beta diversity in coastal boreal forests. We found no effects of red deer herbivory on plant species alpha or beta diversity, which was opposite to my predictions. Most of the plant species recorded, 34 out of 77, in the study were found in both open plots and exclosures and was therefore not affected that strongly by herbivory of the red deer. In 2018, six more species were found in the exclosures than in the open plots, but the differences were not statistically assessed. After ten years of excluding the red deer, both measures of alpha diversity decreased in both treatments. Also, both models were tested with a quadratic response curve over time but did not change the response values. The beta diversity in open plots are stable during the ten years, while it decreases in exclosures. However, the difference between the treatments was not significant. I hypothesized that excluding the red deer would lead to more heterogeneous vegetation in the exclosures, due to red deer promoting a homogenized landscape. This was not the case, as the model shows that excluding the deer after ten years did not significantly affect plant species beta diversity.

4.3 Effects of red deer herbivory on alpha diversity

After ten years of excluding the deer, I found no significant effect on alpha diversity. Species richness or evenness are parameters expected to respond on a longer time scale to herbivore exclusion, since herbivores affect overall plant species diversity by modifying local colonization and extinction processes (Olff & Ritchie, 1998). Several studies have found positive effects of red deer herbivory on alpha diversity in their forest ecosystem. Hegland et al. (2013) used an exclosure study in an old-growth boreal forest at Svanøy to test if the species richness increased with an increasing red deer herbivory gradient. They found that species richness followed a unimodal peaked curve, meaning that the species richness was highest at intermediate red deer levels. Boulanger et al. (2018) assessed the effect of ungulates on plant species richness in European temperate forests and found that by controlling the shrub layer in the forest, ungulates increased herbaceous species richness by increasing the light reaching the ground. Inside the exclosure, they found the opposite effect, and the increase in shrub cover lead to a decrease in species richness. On the other hand, Côte et al. (2004) found negative effects of deer herbivory on plant species richness, but these conclusions are often drawn from studies with high population densities and do not investigate the full gradient of herbivory impacts.

Shannon's index account for both abundance and evenness of the species present and, since both species richness and Shannon diversity index decreases, it is possible that the evenness also decrease. This indicates dominance of a few species in both exclosures and open plots. By preventing deer to access vegetation, it is predicted that fence treatment modifies the abundance of dominant plants. Pekin et al. (2015) found that when red deer browse on the more competitive tree species, plant species richness increased because of reduced competition from these species in the open plots. However, Beguin et al. (2011) found no evidence that the increase in white birch (*Betula papyrifera*), a highly preferred species by deer, was the direct cause of a decrease in herb richness in exclosures. They did, however, find that higher abundance of dominant browse-tolerant species, both in open plots and exclosures, increased the herb layer richness. This shows that the interactions between plant species are complex, and how the abundance of one species may have cascading effect on another. Rooney (2001) shows that understory herb diversity declined because of ferns and graminoids becoming increasingly dominant when exposed to red deer herbivory. This indicates that when the dominance of one plant species linearly increases because of local feeding intensity, abundant deer indirectly reduce forest understory vegetation diversity. When the dominance of one plant increases, the diversity in a community may decline as a result of competitive exclusion, this may be due to plant species that are dominant and resistant against herbivory, like ferns, or tolerate high grazing pressure, as graminoids.

I hypothesized that removing herbivory as a disturbance in the exclosure, after ten years the species alpha diversity would decrease, and we would get increased species richness of the species normally limited by the red deer. In accordance with Speed et al. (2014) I found no effect of excluding the red deer in mature forest exclosures in the understory vegetation layer. I found species dominating the exclosure plots after removing the red deer were chickweed wintergreen, cow-wheat, and wood anemone, and species dominating the open plots were common couch, dwarf cornel, wavy hair-grass, wood anemone, and but the statistical difference between the treatments was not assessed. Species having a high frequency in both treatments were bilberry, wavy hair-grass, and wood anemone. In an exclosure experiment, Boulanger et al. (2018) found that the species dominating in exclosure differed from the species dominating the open plots.

The reason why the diversity between the open plots and exclosure are not significantly different may be due to the plant resilience abilities, meaning how long it takes for a plant to recover after a disturbance (Elmqvist et al. 2003). Austrheim & Eriksson (2001) suggest that local changes in community composition depend both on the local grazing frequency and how long the plant community needs to recover after a grazing session. They suggested that when grazing continued over time, the shift in community composition would become permanent. Even though red deer herbivory as disturbance has been removed, once another stable species composition has been accomplished in the presence of herbivory, the probability of the community to return to its original state is low (Russell et al. 2001). This may imply that more time is needed in these exclosures before the effect of excluding red deer will be detectable. The responses of plant communities to increased or decreased herbivory may not be symmetric, with a slower response observed when herbivory is decreased than increased (Olofsson 2006).

4.4 Effects of red deer herbivory on beta diversity

I hypothesized that excluding the red deer for ten years would lead to more heterogeneous exclosures, due to red deer promoting a homogenized landscape. This was not found in this study. The decrease in spatial beta diversity in exclosures indicates increased homogenization without any disturbance from red deer, which is the opposite of what we expected. There may be several reasons for why exclosures have not become more heterogeneous. After removing a disturbance as herbivory, the response rate to the plant community may not be symmetric (Beschta and Ripple, 2009). As some species will establish quickly after removing the herbivores, while others will not. The effects of increased herbivory depended on the herbivores ability to reduce the abundance of the most palatable plants, while the effect of reducing herbivore intensity depended on the capacity of herbivore-intolerant species to recover and establish in the habitat (Olofsson, 2006). Further, Olofsson (2006) suggests that the direct effect of increasing herbivory pressure, is likely more dramatic than the indirect effect of decreasing the pressure as palatable or sensitive species are often depleted more quickly than they can re-establish.

My study was conducted in a boreal forest with relative homogenous vegetation. Although red deer uses many different areas for foraging, productive boreal forest is the habitat red deer uses the most (Godvik et al. 2009). The red deer is a selective feeder, based on the availability of forage plants, and by eating patchily and a variety of vascular plant species, the red deer are able to maintain open areas, and thereby increase the spatial heterogeneity (Adler et al. 2001; Koleff et al. 2003; Apollonio et al. 2017). Red deer may also increase the turnover rates of nitrogen by defecation and thus sustain plant production if the intensity of grazing frequency is not too high. So, by eating in patches and feeding selectively, when preferred plant species are unevenly distributed, herbivory will increase landscape heterogeneity because each patch will be at a different stage of recovery (Augustine & McNaughton, 1998). Gaston (2006) found that island with less disturbance by black-tailed deer had the most alike vegetation composition, indicating that deer increased heterogenized on this island.

In contradiction with my findings, many studies have found deer to homogenize the vegetation (Lilleeng et al. 2016; Austrheim & Eriksson, 2001). Lilleng et al. (2016) found that the vegetation where the red deer had been excluded for the longest time showed highest spatial heterogeneity, and that red deer herbivory decreased the spatial species turnover outside the exclosures, thus homogenizes the forest floor. The findings are supported by Austrheim & Eriksson (2001), which found that when grazing intensities were high in productive areas, herbivores homogenized the vegetation. Other mechanisms that may promote homogenization by red deer herbivory, but were not tested for in my thesis, are mediating seed dispersal (Albert et al. 2015). Boulanger et al. (2018) found that ungulates disperse non-forest species seeds more often than forest species, and thereby leading to homogenizing the plant community between forest and non-forest habitats.

4.5 Reasons for reduction in diversity over time

The response of vegetation to herbivory in forest will depend on several factors such as successional state, productivity and climate. The extreme weather occurring in Tingvoll during the winter of 2013/2014, may be an explanation for why the effect of red deer in this study was non-significant on vascular plant alpha and beta diversity. Several studies have shown that plant diversity not always change in response to grazing, but that environmental variation also can affect vegetation composition (Stohlgren et al. 1999). The extreme weather included high temperatures, little precipitation, little moisture and a lot of wind, and led to a heavy dry out of several evergreen plants. It was observed large areas with dry and dead vegetation, especially for the species with evergreen leaves, for example, Lingonberry, as well as deciduous dwarf-shrubs such as Bilberry and Heather. Coniferous trees (pine, spruce) and tall shrubs were also affected by the dry out. Such phenomenon is often referred to as climatic stress (Jump and Penulas, 2005) and shows that many plants in northern areas can be vulnerable for extreme weather, especially high temperatures in winter (Meisingset et al. 2015). Meisingset et al. (2015) found that the reduction in relative bilberry biomass was around 60%. Bilberry decreased both in open plots and exclosures. The decrease in biomass was therefore not affected by the amount of red deer browsing in that period and thus showed that extreme weather conditions might change vegetation density and composition considerably in a short period. The weather effect may also alter the feeding preferences of the deer. The composition of red deer winter diet, especially the ratio between graminoids and woody species, are often depended on the snow conditions, and the availability of the different plants (Mysterud, 2010). In periods with high snow cover, the deer is dependent on browsing in the forest area.

The red deer densities have increased massively in the last decades, also in our study area. There is also some information on the variation within the study region (number of deer given for the different "hunting area") although the variation among study sites is more difficult to quantify. I tried to test if the variation in deer density between the different areas was a relevant covariable, but it did not affect the model. Without knowing how often deer are frequently visiting the different sites, our results cannot serve as a conclusive result for the impact of different density measurements, but rather a general examination of the Tingvoll study site. Rooney and Waller (2003) found that the relation between plant species diversity and deer density is complex since the plant response on herbivory often is non-linear. Meaning that the diversity of some plants will increase, while others decrease. Studies conducted in both North America and Europe have shown changes in species diversity as an effect of grazing and browsing by deer (Fuller & Gill, 2001; Hegland et al. 2013).

4.6 Limitations of the study

Regarding the experimental design, the red deer exclusions are not a real-life situation, but changes in the forest understory vegetation and composition within the exclosures can identify some of the changes occurring when excluding the deer. Unfortunately, we are unable to obtain a specific density of red deer at each site. To add, it is important to remember that the exclosures function as a contrast to the open plots with access to deer rather than a representation of natural succession. Measures such as species richness are easy to interpret and may provide important information about ecosystems. However, using only a few univariate measures on diversity to investigate how specific factors affect an ecosystem or ecological community implies a risk of drawing incomplete conclusions. In this study, the sampling and data recording was conducted by different researchers almost every year.

5.0 Conclusion

The relatively long-term nature of the study presented here suggests that the densities of red deer in northern forest ecosystems may not affect the plant diversity aspect of biodiversity. While the effects of deer herbivory on vascular plant alpha and beta diversity has been shown in numerous sites (Hegland et al. 2013; Rooney and Waller, 2003; Boulanger et al. 2018; Lilleeng et al. 2016), my results show little evidence for this at Tingvoll. After ten years of excluding the red deer, both measures of alpha diversity decreased in both exclosures and open plots with access to red deer. In addition, beta diversity decreased in exclosures, while remained stable in the open plots. Still, none of the results were statistically significant and, therefore, no effects of red deer herbivory on plant species alpha or beta diversity was found, which was opposite to my predictions.

Understanding how management can influence the effects of large herbivores on plant communities is critical for a good conservation. For successfully monitoring deer effects on plant communities, long-term studies and evaluating the performance indicators of habitat productivity and ecosystem responses are necessary. An important observation from this study is that climatic effects may mediate herbivory effects on plant diversity and need to be monitored in addition to plant-herbivore interactions. Effective management of red deer should therefore also be seen in connection with the ecosystem.

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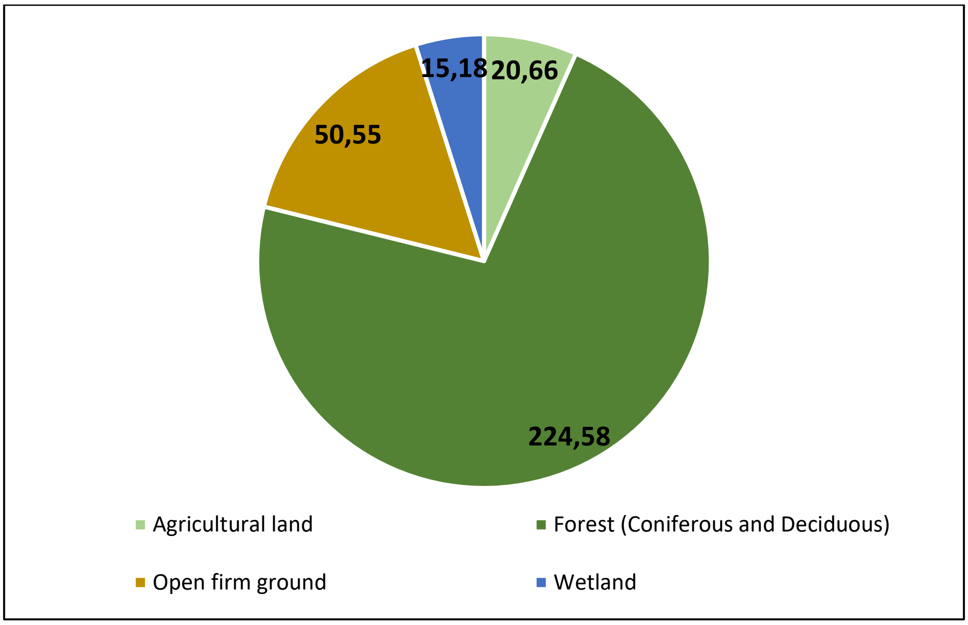
Appendix

Appendix 1: Area division in Tingvoll municipality. The area measure in km^2. Data from Statistics Norway (2019).



Appendix 2: Dung per m^2 in 2018 in open plots where red deer had access. 0.00 means that no dung has been accounted for.

Locality/Year	**2018**
Åsprong	0.16
Bråttvika	0.00
Gjengset	0.16
Gyl	0.04
Haltbakken	0.00
Holmeid	0.16
Kanestrøm	0.00
Ormset	0.06
Rottås	0.14

Appendix 3: Table of observed deer statistics from Tingvoll. One management unit ('Vald') represents different study sites. Hogheia Vetten = Haltbakken, Ormset and Rottås, Melsaasen Varfjellet = Gjengset, MTH = Bråttvika, Holmeid and Gyl, Nordre Straumsnes = Kanestrøm and Torsknuken = Åsprong. Data from Hjorteviltregisteret (2019).

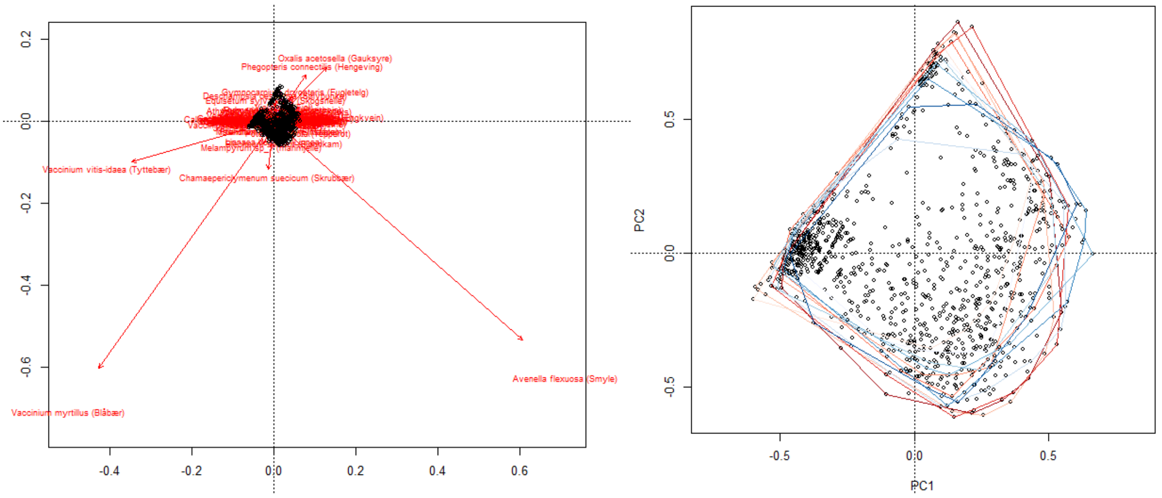
Management Unit/Year	**2008**	**2010**	**2012**	**2014**	**2016**	**2018**
Hogheia Vetten	901	534	672	942	774	1028
Melsaasen Varfjellet	1818	1393	784	988	1126	1105
MTH	1704	2093	1282	1878	1987	2418
Nordre Straumsnes	676	372	355	714	456	619
Torsknuken	444	578	447	207	331	589
Sum	5543	4970	3540	4729	4674	5759

Appendix 4: Table showing frequency of all plots where the species were abundant/occurred, based on presence/absence in subplot; n = 90 for 2008 and n = 89 for 2018 for both treatments in a red deer exclosure study in Tingvoll. Species is bold are the ones changing the most in abundance from 2008 to 2018.

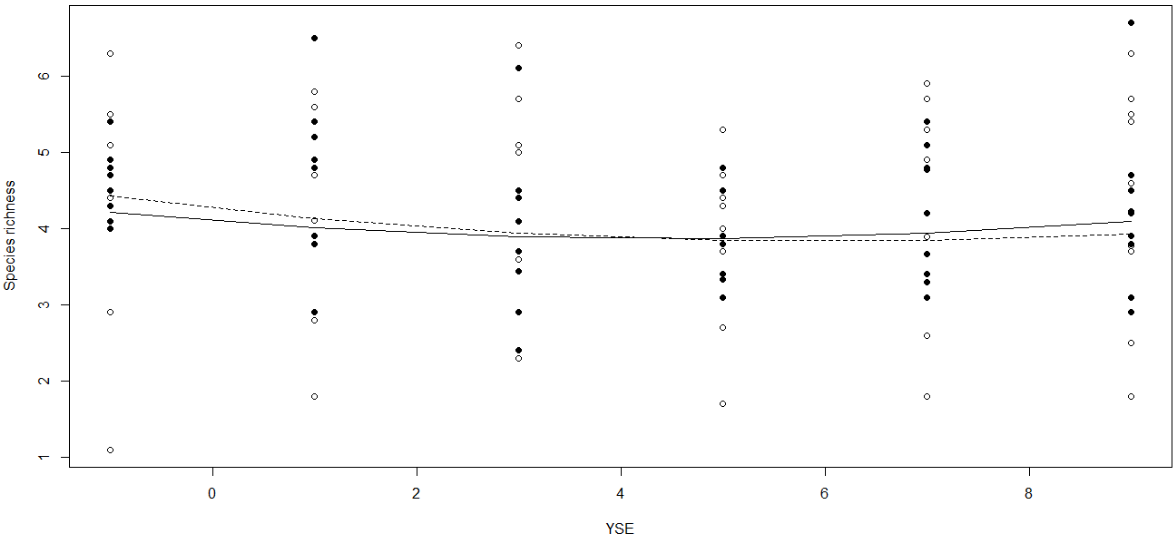
	2008		**2018**	
Species/Treatment	Open Plot	Exclosure	Open Plot	Exclosure
Agrostis capillaris	13	11	14	7
Alnus incana	4	0	0	0
Anemone nemorosa	1	1	11	16
Anthoxanthum odoratum	1	1	9	1
Athyrium filix-femina	0	0	0	2
Avenella flexuosa	63	48	68	46
Betula pubescens	0	0	0	0
Blechnum spicant	4	8	7	9
Bromus hordeaceus	0	0	0	0
Calluna vulgaris	13	14	0	1
Carex bigelowii	0	0	0	0
Carex echinata	0	0	0	0
Carex nigra	1	0	2	0
Carex nigra var_ juncea	0	0	0	0
Carex pallescens	0	0	4	0
Carex pilulifera	0	0	0	0
Carex sp.	8	3	4	4
Carex vaginata	0	0	0	0
Chamaepericlymenum suecicum	9	16	17	12
Chrysosplenium alternifolium	0	0	0	0
Circaea alpina	0	0	0	0
Convallaria majalis	1	0	1	0
Corylus avellana	1	0	0	0
Deschampsia cespitosa	1	5	2	8
Dryopteris expansa	0	0	0	0
Elytrigia repens	0	0	6	0
Empetrum nigrum	6	5	7	2
Epilobium angustifolium	0	1	0	0
Equisetum sylvaticum	0	2	0	2
Eriophorum vaginatum	0	0	0	0
Festuca sp.	0	0	1	0
Filipendula ulmaria	0	0	0	0
Fragaria vesca	0	0	0	0
Frangula alnus	0	0	0	0
Fraxinus excelsior	0	0	1	1
Galium odoratum	0	0	0	2
Geranium sylvaticum	0	1	0	1

Gymnocarpium dryopteris	9	13	9	11
Hypericum montanum	0	0	1	0
Hypericum perforatum	0	0	0	0
Juniperus communis	4	2	0	2
Linnaea borealis	26	28	9	18
Luzula pilosa	7	7	8	8
Luzula sp.	1	0	0	0
Maianthemum bifolium	9	11	9	13
Melampyrum sp.	23	18	15	25
Melica nutans	0	0	0	0
Milium effusum	0	0	0	2
Molinia caerulea	5	7	0	1
Narthecium ossifragum	1	0	0	0
Orthilia secunda	0	0	0	0
Oxalis acetosella	19	14	18	17
Phegopteris connectilis	7	11	8	10
Pinus sylvestris	1	0	0	0
Poa nemoralis	0	0	0	0
Poa pratensis	1	1	0	0
Poaceae	0	0	0	2
Populus tremula	0	1	3	2
Potentilla erecta	13	10	9	7
Prunus padus	0	0	0	1
Pteridium aquilinum	3	4	3	3
Pyrola sp.	0	0	1	0
Rubus chamaemorus	0	0	2	1
Rubus idaeus	0	2	0	3
Rubus saxatilis	0	1	0	4
Rumex acetosa	0	0	0	0
Salix caprea	0	0	0	0
Salix sp.	5	2	0	0
Solidago virgaurea	2	0	2	1
Sorbus aucuparia	4	7	6	4
Succisa pratensis	2	2	1	1
Trientalis europaea	8	7	7	20
Vaccinium myrtillus	80	71	72	69
Vaccinium uliginosum	3	7	3	10
Vaccinium vitis-idaea	43	37	31	35
Veronica officinalis	0	3	0	1
Viola sp.	10	5	5	4

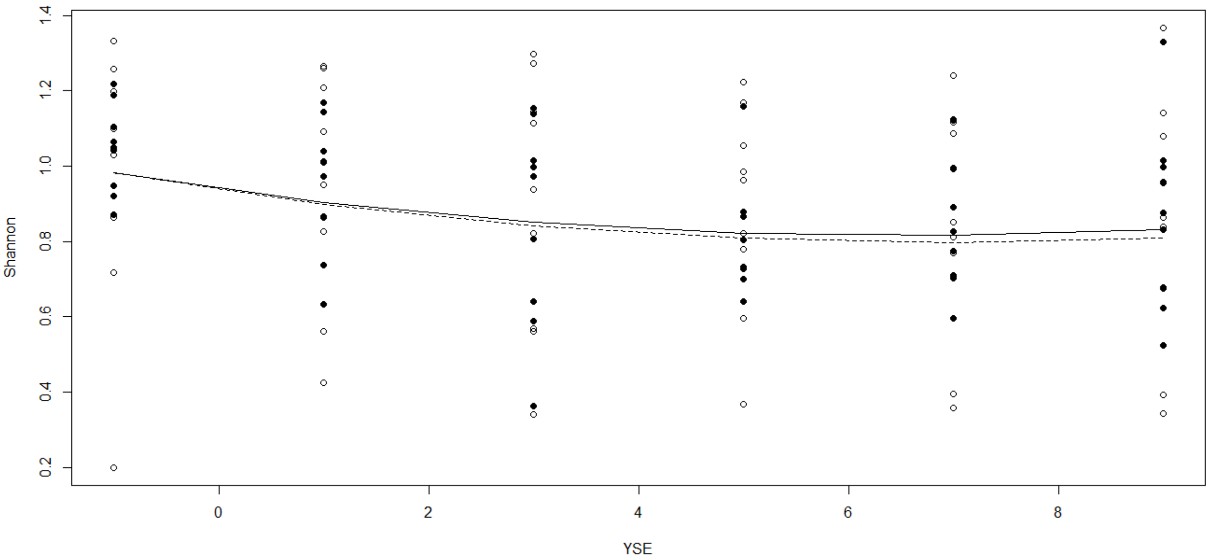
Appendix 5: To the left: PCA-ordination bi-plot showing the plots (small grey dots) and species loading (arrows). To the right: Ordination plot based on Bray-Curtis dissimilarities for vascular plant species composition. Dots are plots. Plots within each treatment and year are connected and arranged into transparent polygons, visualizing the different treatments over the years. Blue colour gradient represents the open plots over the years (light blue are 2008, while dark blue are 2018), and the red colour gradient represent the exclosure over the years (light red are 2008, while dark red are 2018).



Appendix 6: Scatterplot of species richness (SR) vs year since exclosure with regression line in a 10-year exclosure study of red deer in Tingvoll. Year since exclosure = 0 is 2009. The regression line is back transformed. Recorded species richness within plots for vascular plants in either exclosed (open circles and solid line) or open (filled circles and dotted line) plots to red deer. The sample units are 20 × 20 m plots (n=9 locations).



Appendix 7: Scatterplot of Shannon's diversity vs. year since exclosure with regression line in a 10-year exclosure study of red deer in Tingvoll. Year since exclosure = 0 is 2009. The regression line is back transformed. Recorded species richness within plots for vascular plants in either exclosed (open circles and solid line) or open (filled circles and dotted line) plots to red deer. The sample units are 20 × 20 m plots (n=9 locations).



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