Master's thesis

NTNU
Norwegian University of Science and Technology
Faculty of Natural Sciences
Department of Biology

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Plant Species Responses to Moose (*Alces alces*) and Red Deer (*Cervus elaphus*) Herbivory in Successional Boreal Forests

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Supervisor: Gunnar Austrheim, James Speed, Anders Kolstad, Erling Solberg
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Abstract

Large herbivores are an important driver in regulating the composition of species in forest understory. The manner in which they regulate ecosystem properties vary among different herbivore species and is to a large extent dependent on their feeding strategy. The herbivore community in Norway is dominated by moose (*Alces alces*) and red deer (*Cervus elaphus*). Their densities in Norway have changed temporally, with increased red deer densities in the south, and stable and reduced moose densities in central and southern Norway respectively. In this study I investigated the temporal changes in moose and red deer densities in focal municipalities located in two regions with contrasting cervid densities; Trøndelag and Telemark og Vestfold. Furthermore, density of red deer and moose was used to explore variations in plant species responses to herbivores. I have used data from 31 paired exclosures in these regions to examine the impact of herbivores on species in the field layer. The effect of herbivores was examined by comparing exclosed and open plots. This was also done per region and year to investigate temporal variations and variations among regions. The analysis of the impact of herbivores in 2019 for all sites showed that *Chamerion angustifolium* and *Gymnocarpium dryopteris* were negatively affected by herbivores, while *Potentilla erecta* became more abundant in the presence of herbivores. There were both temporal trends and regional variations in plant responses to herbivory. This was particularly apparent in *Rubus ideaus* which became more abundant in open plots relative to exclosed in Trøndelag, while it showed a distinct U-shape over time in Telemark og Vestfold. Moreover, an effect of proportion of red deer in the herbivore community on species response to herbivory was demonstrated for *Vaccinium ulignosum, Dryopteris expansa* and *Trientalis europea*. Relative abundance of *T. europea* was lower when the ratio of red deer in the herbivore community increased, while relative abundance increased for *V. ulignosum* and *D. ryopteris*. If the trend of increasing red deer populations relative to moose continues this might shift the plant species composition in the field layer and *T. europea* could become less common while the opposite might happen for *V. ulignosum* and *D. expansa*.

Sammendrag

Store beitedyr er en viktig regulerende faktor for artssammensetningen i feltsjiktet i skogsøkosystemer. Hvordan de regulerer ulike økosystemegenskaper varierer blant ulike beitedyr og avhenger i stor grad av deres beitestrategi. Samfunnet av beitedyr i Norge er dominert av elg (*Alces alces*) og hjort (*Cervus elaphus*). Tettheten deres har gjennomgått tidsmessige endringer som har innebåret en økning av hjort i Sør-Norge, mens tettheten av elg har vært stabil i Midt-Norge og synkende i Sør-Norge. I denne studien har jeg undersøkt tidsmessige endringer i tettheten av hjort og elg i utvalgte kommuner tilhørende to regioner med ulike tettheter av hjortedyr; Trøndelag og Telemark og Vestfold. Tettheten av elg og hjort ble også brukt for å undersøke variasjon i planteresponser på utstenging av beitedyr. Jeg har jeg brukt data fra 31 parede uthegninger i disse to regionene for å granske hvilken effekt beiting har på arter i feltsjiktet. Dette ble gjort per region og år for å undersøke temporære variasjoner og variasjoner blant regionene. Analyser av data fra 2019 viste at *Chamerion angustifolium* og *Gymnocarpium dryopteris* ble negativt påvirket av beitedyr, mens *Potentilla erecta* ble vanligere når beitedyr var til stede. Det ble funnet både temporære og regionale variasjoner i planteartenes respons på tilstedeværelse av beitedyr, særlig tydelig for *Rubus ideaus* som ble vanligere i åpne plot relativt til uthegningene i Trøndelag, mens i Telemark og Vestfold var det en tydelig U-form over tid. Det ble også demonstrert at andelen hjort i beitedyrsamfunnet hadde en innvirkning på responsen på beitedyr for *Vaccinium ulignosum*, *Dryopteris expansa* og *Trientalis europea*. Relativ abundans for *T. europea* var lavere når andelen hjort økte relativt til elg, mens det motsatte ble funnet for *V. ulignosum* og *G. dryopteris*. Dersom trenden med økende andel hjort relativt til elg vedvarer kan dette endre artssammensetningen i feltsjiktet. *T. europea* kan bli mindre vanlig, mens det motsatte kan skje for *V. ulignosum* og *D. expansa*.

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1 Introduction

Herbivory is an important force in shaping the structure and composition of forest ecosystems (Hester et al., 2006, Pastor et al., 1988, Augustine and McNaughton, 1998). There exists large variation among plant species in where they grow, their structure and nutrient content. This variation creates a basis for diversification among herbivores, allowing them to specialize on different plant species based on certain plant characteristics (Clauss et al., 2008). A large part of variation in the diet of herbivores relate to the browser-grazer spectrum (Hofmann, 1989). Herbivore species with a diet that consists of more than 90% grasses are considered grazers, while species with more than 90% dicotyledons such as trees and shrubs are considered browsers, and species somewhere in the between (10-90%) are considered mixed feeders (Fritz and Loison, 2006). The two herbivores covered in this study, moose (*Alces alces*) and red deer (*Cervus elaphus*) are browsers and mixed-feeders respectively (Hofmann, 1989). Large herbivores such as these is expected to have substantial effects on their ecosystems (Milchunas and Lauenroth, 1993, Hester et al., 2006, Augustine and McNaughton, 1998). These manifest themselves in direct effects such as herbivory and trampling, but also indirect effects such as changing competitive interactions and community structure and altering the nutrient supply (Molvar et al., 1993, Pastor et al., 1988, McInnes et al., 1992).

Herbivory can be described as a series of hierarchically ordered decisions. This ranges from which plant (and plant part) to forage on and patches to feed in, to which landscapes to migrate to. At each scale a decision must be made in order to maximise food intake. At community level this means selecting nutrient rich plants and minimizing intake of toxins, while at larger scales other factors such as rainfall or spatial structure of available forage in the landscape will determine patch selection and in which landscape to forage (Senft et al., 1987). This is illustrated by seasonal migrations of grazing herds in Serengeti (Frank et al., 1998). Scale dependence in forage selection by moose in boreal systems has also been demonstrated. At landscape scale, moose select for habitat of lower quality, but high quantity forage, while at smaller spatial scale moose select for areas with high quality forage (van Beest et al., 2010). Similarly, landscape level variations in availability of pastures can moderate red deer habitat selection, where selection for pastures increase when availability decreases (Godvik et al., 2009).

Plant properties affecting herbivore preference relate to different defensive strategies by plants (Burghardt and Schmitz, 2015). Roughly, plant defence traits can be organized in the following two groups; herbivore avoidance and herbivore tolerance (Rosenthal and Kotanen, 1994). As such, plant species can be separated depending on their strategies. Typical tolerance traits are modular growth and meristems located close to the ground which allow continued growth despite herbivore pressure. Avoidance traits are traits such as spikes, hiding or secondary metabolites which makes them less attractive to herbivores (Hester et al., 2006). Where plant species are located on this spectrum is important for how the plant community will be structured in the presence of herbivores. Grasses are typically quite grazing tolerant, with rapid annual growth and meristems close to the ground which in turn means that grasses can persist even at high grazing pressure (Burghardt and Schmitz, 2015, Hester et al., 2006). The concept of the grazing lawn is a prime example of coevolution of organisms from different trophic levels and how herbivory might induce increased grass abundance through compensatory growth and positive feedback (McNaughton, 1984). Presence of grazers can maintain grassland and decelerate or inhibit forest expansion in this manner. Similar dynamics can also occur from browsing in forest systems, a concept which has been termed “browsing lawn” (Cromsigt and Kuijper, 2011).

Selective foraging by herbivores can alter multiple ecosystem properties and characteristics in forest ecosystems. Multiple studies have documented how browsing can shift the level of dominance between species (Côté et al., 2004, Horsley et al., 2003, Russell et al., 2001). If herbivores forage selectively on dominant species, high densities of herbivores can facilitate dominance by other more herbivory resistant species. Because herbivores in boreal forest systems feed selectively, they will naturally impact different species in different ways. For example, multiple studies have shown how increasing densities of herbivores can have positive effects on graminoids. Both from browsing through improved light conditions, but also from grazing through feedback dynamics such as grazing lawns (Tremblay et al., 2006, Mathisen et al., 2010, McNaughton, 1984). The exact mechanism for how herbivores affect species in the field layer is not necessarily obvious, as simulated moose herbivory increased light availability in addition to reducing *Vaccinium myrtillus* performance (Mathisen et al., 2010). Rooney (2009) illustrated a strong effect of browsing by white tailed deer on ecosystem characteristics and species composition. By documenting effects of browsing over 16 years he showed that with white tailed deer present grasses and sedges accounted for 83% of relative cover compared to <10% when deer were absent. Not only did the relative cover of grasses and sedges decrease, but total cover by ground-layer vegetation quadrupled. The presence of white-tailed deer has driven the community from one dominated by forbs and herbs to one dominated by herbivory tolerant grasses and sedges.

The effect of herbivores on plants differs depending on their functional characteristics. As covered by Rooney (2009), graminoids seem to benefit from the presence of white tailed deer, while forbs, ferns and woody browse perform worse when compared to unbrowsed exclosures. Bernes et al. (2018) conducted a systematic review on the effects of ungulate herbivory on different aspects of the plant communities. Among their findings they demonstrated that shrubs were negatively affected by ungulate herbivory, while there was no significant effect on graminoids or forbs. However, there are studies that have documented positive effects of moderate and high red deer density on forb abundance (Hegland and Rydgren, 2016). Furthermore, they investigated the effect on certain focal species. Among them, both *Calluna vulgaris* and *Vaccinium vitis-idaea* were negatively affected by ungulate herbivory. Moreover, Bernes et al. (2018) highlight that much of the variation among the studies included in their analysis can be attributed to variations among forest systems. Soil rich coniferous forests and broadleaved deciduous forests were the only ones that showed significant negative effects from ungulate herbivory on understory abundance.

Deer herbivory can have multiple effects on the ecosystem which extend beyond their direct effects on palatable and unpalatable plant species. In addition, they can cause shifts in the composition of plants and the structure of the community. Furthermore, this can have an impact on both insects and small mammals (Côté et al., 2014, McInnes et al., 1992). Moreover, in successional systems where many herbivory studies have been conducted, the initial effect of herbivores can alter successional trajectories in the ecosystem and have long lasting legacy effects (Côté et al., 2014, Kolstad et al., 2018, Hidding et al., 2013). Such effects can for example be a shift in domination between functionally different groups such as from palatable forbs to less palatable ferns (Nuttle et al., 2014, De La Cretaz and Kelty, 2002). The duration of such legacy effects can be quite substantial, and Nuttle et al. (2014) have shown that variations among areas of different deer densities has maintained for at least 20 years after equalization of deer densities. Even short periods of herbivory can create alternative successional trajectories by extirpating browsing intolerant species, and thus create trajectories that favors browsing resistant species (Hidding et al., 2013).

1.1 Moose and red deer in Norwegian forests

Norway is to a large extent dominated by managed boreal forest distributed over many different private forest owners (Gauthier et al., 2015, Yrjölä, 2002). Only a small proportion of the forests are protected as reserves, while the rest is managed and used for forestry. The most common species are the conifers Norway spruce (*Picea abies*), and pine (*Pinus sylvestris*), in addition to birch (*Betula* spp) and patches of aspen (*Populus tremula*) and alder (*Alnus* spp). Most of the forest in Norway is younger than 80 years. The primary method of felling is mechanized clear cutting, followed by planting of seedlings. Young stands are typically tended, and unwanted species are removed (Yrjölä, 2002). Present practice of clear-cutting large areas emerged in the first half of the 20th century and succeeded a period of more conservative and selective harvesting of trees. The introduction of clear-cuts combined with seedling planting has led to both younger and more homogenous forests (Yrjölä, 2002, Nygaard and Øyen, 2020).

As mentioned, the two dominant herbivores in Norway and the focal herbivores in this study are the moose and the red deer, both of which have a long history in Norway (Rosvold et al., 2013). The cervids has increased in density in Norway during the latter part of the 20th century, with the numbers of moose increasing the most. Its population growth between the 60s and 2000 has been close to exponential (Austrheim et al., 2008). This dramatic growth can be ascribed to low carnivore populations combined with change in habitat from cultivated land to forest and a reduction in livestock grazing. However, the main reason for this population growth has been a change in hunting regulations. The change in forestry practice to extensive use of clear-cutting has also possibly contributed to the population growth (Nygaard and Øyen, 2020).

Despite both moose and red deer having a long history in Norway, their ranges have been largely separated. Moose has high cold tolerance and is adapted to withstand low temperatures, while the red deer is less tolerant to cold and snow. Hence, their ranges in Norway to a large extent reflect these differences, with the red deer located along the coast, which is milder, while the moose is distributed more inland (Rosvold et al., 2013).

In 1968 the hunting policy shifted to sex and age-specific quotas, which relaxed the hunting pressure on female moose and likely allowed the population to increase. This policy seemed to be effective, and at the turn of the century the density of moose had increased from 3.1 kg km^{-2} in 1949 to 25 kg km^{-2} in 1999, measured in metabolic biomass (MBA) (Austrheim et al., 2008, Austrheim et al., 2011). More recently moose densities have stabilized in central and northern Norway, while decreasing in southern Norway. The red deer densities have generally increased throughout its range in Norway (Solberg et al., 2017). The increasing densities of wild herbivores and decrease in cattle densities represent a functional shift in herbivore assemblages, from one dominated by livestock to one dominated by wild cervids. This trend is particularly noticeable in the warmer regions of Norway (Speed et al., 2019).

Moose tend to forage on deciduous trees with a diet dominated by birch, aspen and rowan (*Sorbus aucuparia*), in addition to *Vaccinium myrtillus* (Wam and Hjeljord, 2010, Mysterud, 2000, Månsson et al., 2007). The ecological effect of moose will naturally be strong on preferred species. Kolstad et al. (2018) found that moose exclusion in successional boreal forests shifted the ratio of deciduous and coniferous trees in the canopy cover in an herbivore exclusion study. Indeed, moose browsing is known to have negative effects on palatable deciduous trees such as sallow and rowan (Myking et al., 2013). The proportion of deciduous trees in the canopy was higher inside exclosures, while conifers dominated the canopy in the open plots. In fact, moose preference for early successional deciduous tree species has the potential to accelerate the ecosystem towards a climax state dominated by less preferred conifers (Pastor et al., 1988, Speed et al., 2013). Exclusion of moose had a positive effect on both large herbs and ferns. Graminoids are grazing tolerant and light demanding species and were subsequently expected to be negatively affected by herbivore exclusion. Yet, graminoids showed only a weak negative effect of exclusion in Kolstad et al. (2018), although other studies have found negative effects of herbivore exclusion on graminoids, and the general consensus is that graminoids are tolerant to herbivory compared to other groups (Tremblay et al., 2006).

The red deer is one of the most dominant herbivores in northern Europe, and multiple studies have investigated their ecological impact. Being a mixed-feeder the red deer has the potential to affect a large number of species in the community, feeding on both trees and shrubs, but also graminoids (Gebert and Verheyden-Tixier, 2001). Lilleeng et al. (2016) found that increased herbivore intensity by red deer had a strong positive effect on temporal heterogeneity in boreal forest. Temporal heterogeneity favors successional species and increases an ecosystems susceptibility to invading species and can have a destabilizing effect on the ecosystem. Furthermore, increased herbivory had a weak positive effect on spatial heterogeneity. The hypothesized mechanism for increased temporal heterogeneity was that red deer herbivory will increase light availability which could facilitate recruitment of new species.

Hegland and Rydgren (2016) identified plant species that benefit and suffer from increased intensity of red deer herbivory in western Norway. Tree species such as rowan and the shrub *Calluna vulgaris* benefitted from exclosures, while other shrubs such as *Vaccinium ulignosum* and *Vaccinium vitis-idaea* were classified as low impact benefitters of exclosures, in addition to *Trientalis europea* and *Linnea borealis*. *Vaccinium myrtillus* performed better up to intermediate levels of herbivory. Contrary to the authors expectations, graminoids showed no response and were classified as neutrals. Graminoids tend to benefit from herbivory by browsers such as moose, but this effect might not be present under red deer herbivory as it is a mixed feeder. Studies have also shown that increased grazing intensity can have negative effects on multiple performance related traits such as size and number of berries in *V. myrtillus* (Tolvanen et al., 1994, Hegland et al., 2005).

Many of these studies have looked at the effect of herbivory in systems with only one herbivore. However, in addition to describing effects of a single herbivore it is also relevant to look at systems where there is more than one herbivore present. Several of the studies mentioned above have described the effect of red deer herbivory in forest systems (Lilleeng et al., 2016, Mysterud et al., 2010, Hegland et al., 2013, Hegland and Rydgren, 2016), describing how they can promote abundance of graminoids and inhibit shrubs such as *Vaccinium myrtillus*. Similarly studies on moose have shown that they can alter tree composition from deciduous to coniferous (Kolstad et al., 2018) and in some cases promote species in the field layer by indirectly increasing light conditions (Mathisen et al., 2010). Moreover, it has been demonstrated that red deer has expanded its range in Norway and has thus increased the degree of coexistence between red deer and moose (Austrheim et al., 2011, Speed et al., 2019).

Because of this increased coexistence it is increasingly more useful to investigate the effects of an herbivore community consisting of both, and how this effect varies with different proportions of red deer and moose. The isolated effects of these species in forest systems are well established already, but their combined effect is not. Naturally there are some caveats to investigating effects of multiple herbivores in a single system, such as herbivores potentially altering their diet or behavior in the presence of another herbivore. As Mysterud (2000) showed there is some degree of diet overlap between red deer and moose which may indicate presence of exploitative competition.

Given their differing feeding strategies their effect on the plant community will also differ. Speed et al. (2014) found that *Vaccinium myrtillus* became more dominant in moose dominated spruce forests, while the opposite happened in red deer dominated deciduous forest. Both the forest type and stand age differed between these systems and the authors do point out that they are not comparing effects of moose and red deer. Yet, it is possible that red deer, as a mixed feeder, to a greater extent forage on *V. myrtillus* than the moose does (Mysterud, 2000). It could be that the effect of herbivores on *V. myrtillus* is dependent on herbivore species and that in moose dominated forests *V. myrtillus* gains a competitive advantage over more heavily browsed species in the field layer.

A subject particular interest is the coexistence of different functional types. Grazers forage close to the ground, in the herbaceous layer. By doing this they can regulate competition between herbaceous and woody vegetation which in turn affect food availability for browsers. Changing ratios of browsers and grazers can shift the relationship between them in terms of facilitation and inhibition (Hester et al., 2000).

Given the substantial impact large herbivores have on their surrounding ecosystem and the potentially differing effects among browsers and grazers combined with the shifting densities of moose and red deer in Norway, knowledge of how they affect the plant community and in turn the ecosystem is of great interest. No doubt, the high densities of moose during recent decades has had a big impact on the ecosystem through trampling, nutrient deposits and selection pressure from browsing. However, with the increasing densities of red deer and increasing degree of coexistence of moose and red deer this impact might change.

Red deer, being a mixed feeder with a higher tendency to graze than moose, are therefore expected to reduce the abundance of preferential plant species such as *Vaccinium myrtillus* in the field layer of successional boreal forests. However, presence of red deer might also prevent regrowth of vegetation and keep the landscape more open and thus facilitate better growing conditions in the field layer. The possibility of these two effects regulating species responses can make the impact on different species unpredictable.

The aim of this study is to investigate the herbivore community in focal municipalities in two regions in Norway with contrasting cervid densities and describe the species-specific plant responses to herbivory. Furthermore, to investigate what extent proportion of red deer and moose in the herbivore community shapes the response to herbivory. Knowledge not only about the effect of herbivory in a general sense, but also how variations among herbivores can affect plant species differently will be useful for forest and cervid management. Particularly as the composition of herbivores in the community has undergone prominent changes, information about how such changes might affect the plant community is vital.

I will therefore attempt to answer the following research questions: First (Q1), how has the cervid densities changed temporally in focal municipalities? Secondly (Q2), what effect do large herbivores have on field layer species abundance in successional boreal forests? And finally (Q3), how does this effect vary with varying red deer to moose ratio?

Q1 is exploratory and will be used to contextualize the findings for Q2 and Q3. For Q2 I expect that graminoid species will perform better outside exclosures (Tremblay et al., 2006, Rooney, 2009). I also expect ferns to perform better inside exclosures (Kolstad et al., 2018). Furthermore, I have expectations for selected focal species (Table 1). For Q3 I expect that *Vaccinium myrtillus* will be increasingly more negatively affected by herbivory when the proportion of red deer increases (Table 1) (Speed et al., 2014, Hegland et al., 2005). In general I expect that higher ratio of red deer will increase the negative impact on species in the field layer that are susceptible to red deer herbivory (Hegland and Rydgren, 2016).

I have selected four focal species to pay particular attention to (Table 1). *Avenella flexuosa*, which is the most common graminoid in the study area, the two dwarf shrubs *Vaccinium myrtillus* and *Calluna vulgaris,* both of which are common in the study area and *Chamerion angustifolium* which has been documented to be strongly affected by herbivory.

Table 1: Expected response for four focal species. “Browsing 2019” is the expected herbivore effect (Open – exclosed) from all sites in 2019. “Red deer ratio” represents the expected direction of the effect of red deer ratio on plant species effect size. Upward arrow represents a positive effect, downward arrow represents a negative effect and a dash represents no expectation.

Focal species	**Browsing 2019 (Q2)**	**Red deer ratio (Q3)**	**Reference**
Avenella flexuosa	↑	-	(Tremblay et al., 2006, Hegland and Rydgren, 2016)
Calluna vulgaris	↓	-	(Bernes et al., 2018, Hegland and Rydgren, 2016, Speed et al., 2014)
Chamerion angustifolium	↓	-	(Kolstad et al., 2018, Tremblay et al., 2006)
Vaccinium myrtillus	-	↓	(Hegland et al., 2005, Speed et al., 2014)

2 Methods

2.1 Study area

The data was collected in Trøndelag and Telemark og Vestfold (from here referred to only as "Telemark") region (Figure 1) as part of the SustHerb project (Sustainable management of moose https://www.ntnu.no/museum/sustherb). Telemark is located in southern Norway and, while Trøndelag is located in central. Both regions are dominated by spruce and pine, with some patches of deciduous trees (Yrjölä, 2002). Moose is the predominant herbivore in both regions, but in Telemark the red deer has increased in abundance in recent years.

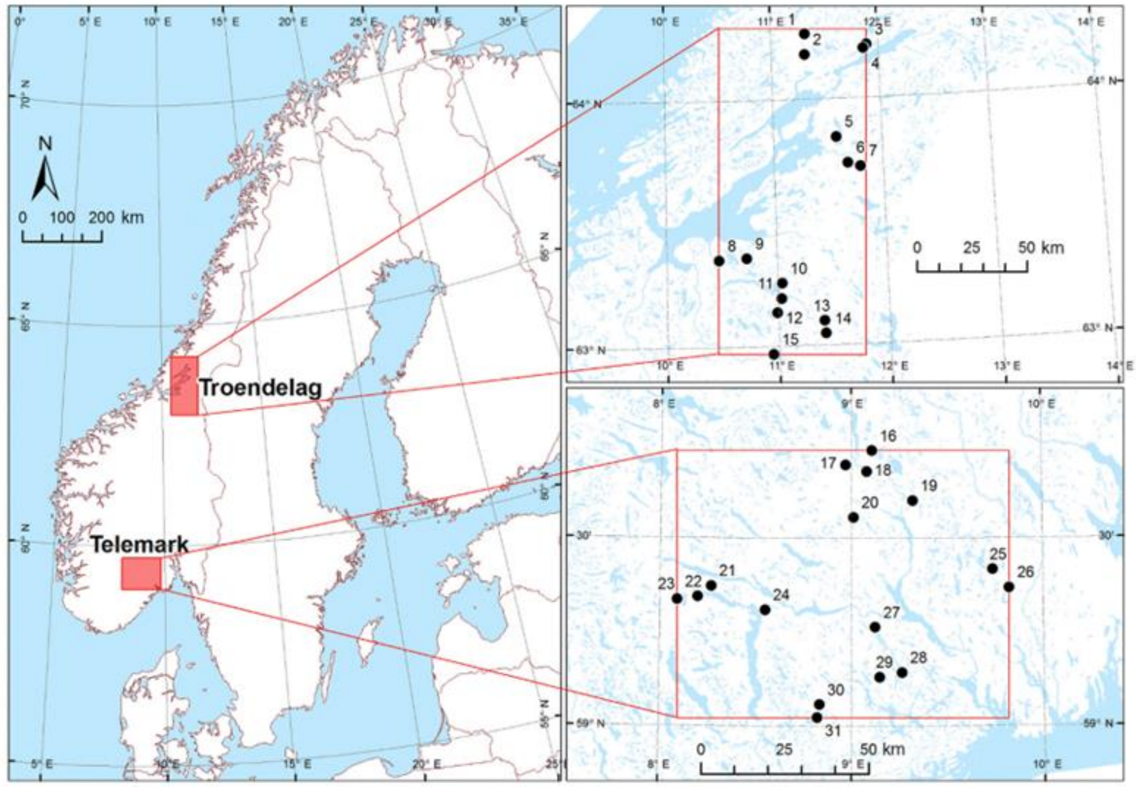


Figure 1: Study area indicated by red squares, paired exclosure and open plots indicated with black dots within the red rectangles.

Both regions contain 20x20 meter paired exclosure and open plots. There are 15 paired plots in Trøndelag and 16 in Telemark, located across municipalities with varying herbivore densities and historical trends. Exclosure plots were surrounded with three-meter-tall fences with approximately 10x10 cm openings in the wire allowing smaller animals such as hare

(*Lepinus timidus*) and rodents to access the plots whilst keeping out large animals, primarily moose and red deer. Roe deer (*Capreolus capreolus*) were also common in some municipalities, while livestock rarely is expected to use the open plots. The fences were erected in 2008 and 2009 in Trøndelag and Telemark respectively, in recently clear-cut boreal forests. All sites were clear-cut between 2002 and 2007. Data has been recorded every other year with the exception of the most recent recording in Trøndelag, which was done in 2019, three years after the last recording.

Within each exclosed and open plot are ten randomly selected 50x50 cm subplots (Figure 2). These were selected when the exclosures were erected and marked for future recording with wooden pieces in the bottom left corner, numbered 1 to 10 in addition to metal cylinders in each corner. The cylinders enabled us to locate the subplot and assemble the equipment used for the recording of vegetation properly.

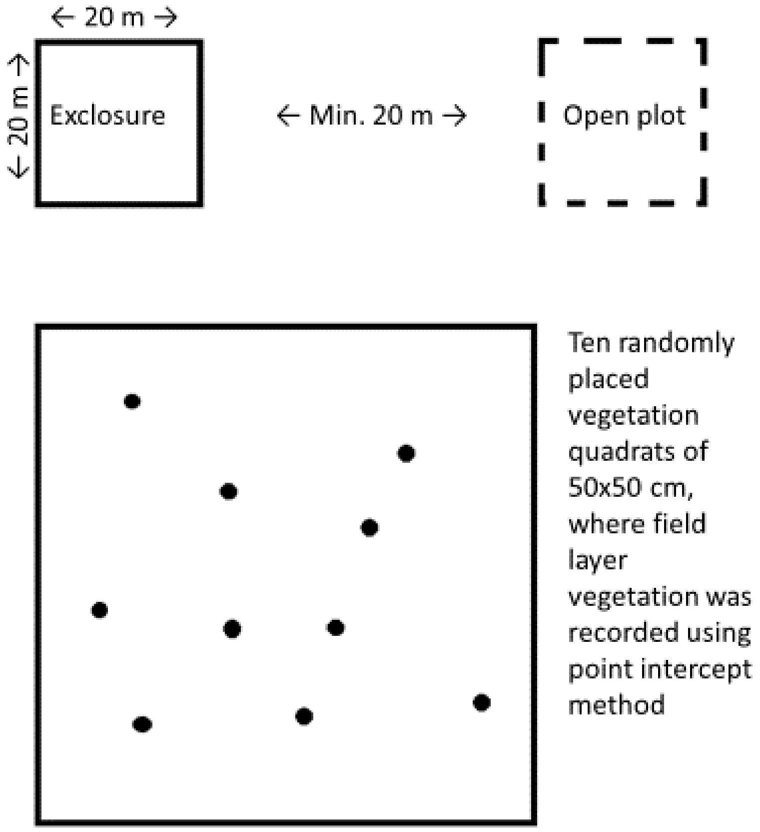


Figure 2: Schematic representation of exclosed and open plots and the structure of each plot.

2.2 Data collection

The data for the understory vegetation was collected for all exclosed and open plots. Vegetation data was collected with the use of point intercept method (Jonasson, 1988). For each subplot 16 systematically placed pins were used to record all species present in the field layer. All vascular plant species were recorded at species level if possible following Lid & Lid (2005). If determination of species was impossible, it was recorded at genus or family level, this was done for some recordings of *Carex* species. The number of contact points per species was recorded for each of the 16 pins in addition to ground cover (litter, moss or lichen). All recordings were done in the period late June to late July. For some sites not all subplots were found in a given year of recording. In these cases, this was accounted for in the analysis, as all species abundances were averaged on plot level.

Temporal and spatial changes in moose and red deer biomass were calculated at the municipality level using an existing dataset on metabolic biomass of different herbivore species throughout Norway and runs back to 1949 (Austrheim et al., 2011, Austrheim et al., 2008, Speed et al., 2019). Data is based on hunting statistics, and allometric scaling was used to convert number of individuals to metabolic biomass per species prior to this study (Austrheim et al., 2011). Metabolic biomass of moose, red deer and roe deer per municipality was divided by the area of unenclosed land (*utmark* in Norwegian) of the municipality to acquire the density of each species per year. Spatial differences in herbivore densities among regions were investigated, in addition to temporal changes within the municipalities of each region.

2.3 Statistical analysis

Species effect sizes were calculated using Standardized Mean Difference (SMD). Effect sizes were based on the difference in mean abundance for a species between exclosed and open plots and divided by the pooled standard deviation. Calculations for species observations within *Carex* and *Salix* genus were all done on genus level rather than species, as there was a substantial number of *Carex* sp and *Salix* sp observations without specified species within the genus.

When calculating effect size per year and region, the plant abundances (number of pin-point intercepts) was averaged per plot in order to get an average from all ten subplots. These averages were then used to calculate the mean and standard deviation for each species which was used in the calculation of the effect sizes. Rare species (present in <5 sites) were excluded from the analysis. This threshold of 5 sites was used for both for analysis per region and for the analysis of both regions together in 2019.

Effect sizes were also calculated per plot, using the data from 2019. This made it possible to compare effect size among sites with varying composition of herbivores.

Herbivore data calculated as metabolic biomass per municipality was used to calculate proportion of red deer (from here referred to as “red deer ratio”) in the herbivore community (Austrheim et al., 2008, Speed et al., 2019). This data is available on municipality level, which means that sites in the same municipality will have the same value of red deer ratio. These values were acquired by first calculating the densities of moose and red deer from the total metabolic biomass of each species in the municipality. Then the density of red deer was divided by the sum of the densities of moose and red deer, yielding a value between 0 and 1 which gives an indication of the proportion of red deer in the community. Values close to zero will be moose dominated, while values closer to one will be red deer dominated.

This red deer ratio was used as explanatory variable in a linear (fixed effects) meta-regression with effect size per site as response variable. One model was created for each species present in at least five of the 31 sites. The model coefficients would explain to what extent an increased proportion of red deer would increase or decrease the effect size for individual plant species. A positive coefficient would mean that the abundance of a species will increase more inside exclosures relative to outside with an increased proportion of red deer.

The data was analyzed in R statistical environment. Effect size of herbivory treatment was calculated on plant species abundances. All values for all species were the sum of all contact points for one species per subplot (Jonasson, 1988). Both calculation of effect sizes (SMD) and meta-regression analysis using the “rma” function with “fixed effect” method, were done using the package “metafor” (Viechtbauer, 2010). For graphical representation of temporal trends in effect size “ggplot2” was used for plotting and “MBESS” for calculation of confidence intervals around effect sizes (Wickham, 2016, Kelley, 2017).

3 Results

Since 1949, moose has been the most dominant herbivore in all focal municipalities. The Trøndelag municipalities show a steady increase in moose densities (Figure 3). Some municipalities in Trøndelag show strong fluctuations, most noticeable in Namdalseid and Steinkjer. Red deer densities were generally quite low, although with a slight recent increase in Midtre Gauldal, Selbu and Steinkjer.

The Telemark municipalities Drangedal, Kviteseid, Nome, Notodden and Siljan show a strong increase in moose densities up to the year 1999 before a rapid decline in the following years. At the same time red deer densities have increased in all five Telemark municipalities. In Nome the densities of moose and red deer were close to equal in 2015 (moose density=11.02 kg km^{-2}, red deer density=10.31 kg km^{-2}) (Figure 3, Table A1).

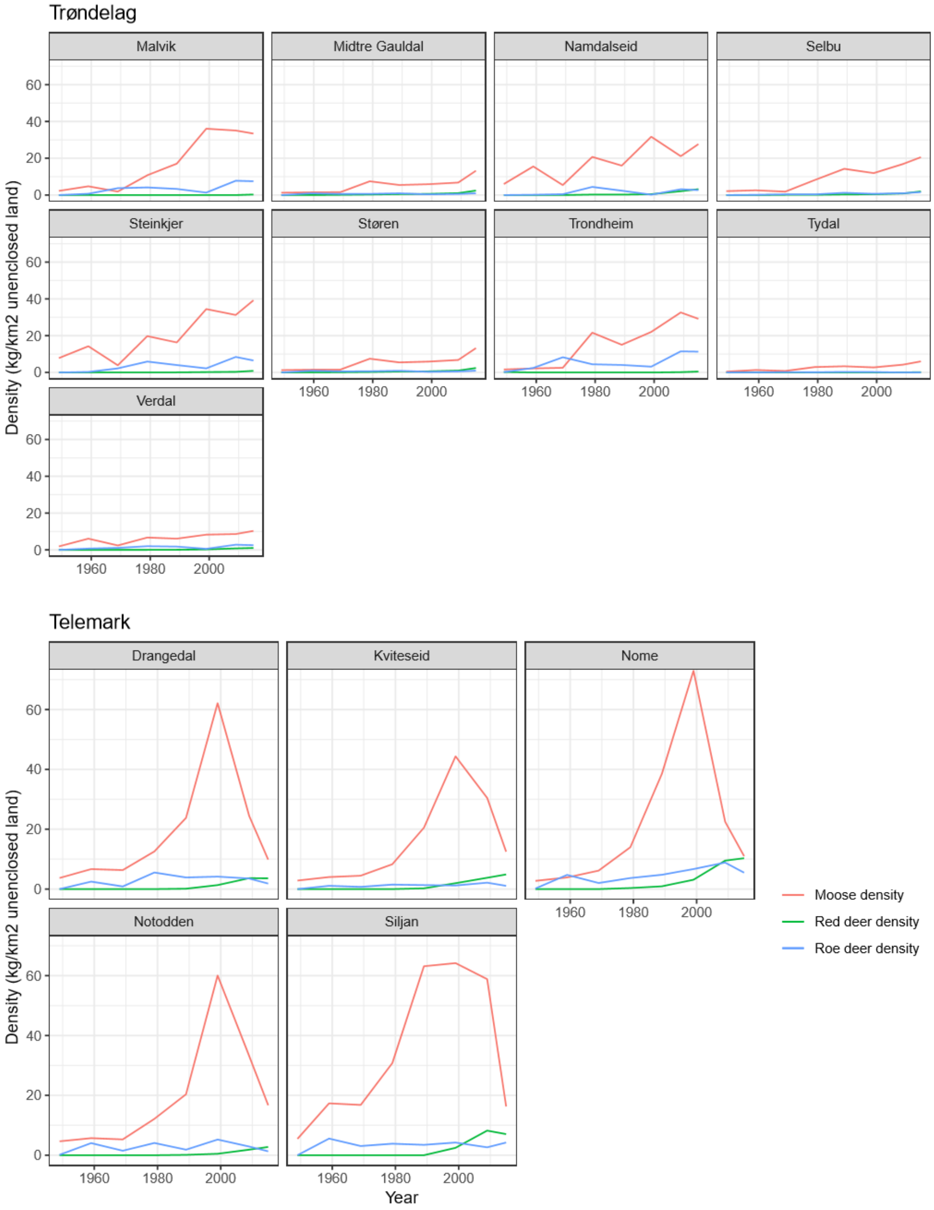


Figure 3: Temporal changes in cervid densities (measured in kg metabolic biomass per km^2 unenclosed land) in municiaplities containing SustHerb sites

An overall analysis on the plant effect of exclosure treatment in 2019 showed a negative herbivore effect on six species. These were *Chamerion angustifolium*, *Gymnocarpium dryopteris*, *Athyrium filix-femina*, *Rubus idaeus*, *Phegopteris connectilis* and *Melampyrum sylvaticum* (Figure 4), with *Chamerion angustifolium* the species most negatively affected by herbivores (SMD -1.23857) (Table A2).

Two species showed a positive herbivore effect, these being *Calamagrostis phragmitoides* and *Potentilla erecta*. Both were significantly more abundant in the open plots than inside exclosures (Figure 4). The remaining 21 species (including *Salix* sp and *Carex* sp) showed no significant response from herbivores.

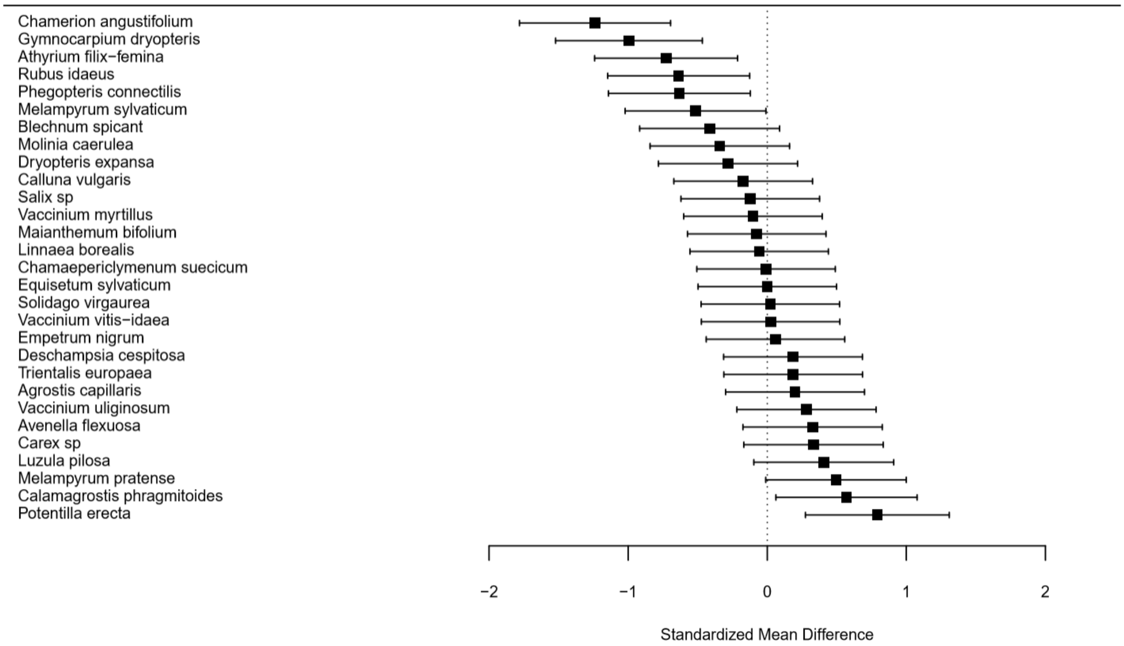


Figure 4: Effect size (SMD) and corresponding confidence intervals for plant species in 2019 using all sites in Trøndelag and Telemark (Open – exclosed).

Three graminoids were included in the analysis for Telemark, with none of them significantly affected by herbivores (Figure 5). *Avenella flexuosa* tended towards a negative herbivore effect in 2011, but in general it was close to zero most years. Both *Agrostis capillaris* and *Luzula pilosa* were only included in three years. *A. capillaris* showed tendency towards a negative herbivore effect in 2017, but this was not significant.

The only fern present was *Gymnocarpium dryopteris* which was only abundant enough to be included in the analysis of the final three years of recording (Figure 5). After showing no response in 2015 and 2017 it showed a negative effect of herbivory in 2019.

There were some temporal trends for multiple species in Telemark. *Rubus idaeus* showed a U-shaped response over time. There was a negative herbivore effect four (2013) and six (2015) years into the study, but this effect was absent in the final two years of recording (2017 and 2019) (Figure 5).

Temporal trends among forbs varied between species. *Linnea borealis* showed a tendency towards a negative effect of herbivory multiple years, while being significantly negatively affected by herbivory in 2017 (Figure 5). However, in 2019, although not significant it tended towards positive herbivore effect and showed a strong temporal shift from 2017. Neither *Mainathemum bifolium, Melampyrum pratense* or *Trientalis europea* showed a significant effect in any of the years.

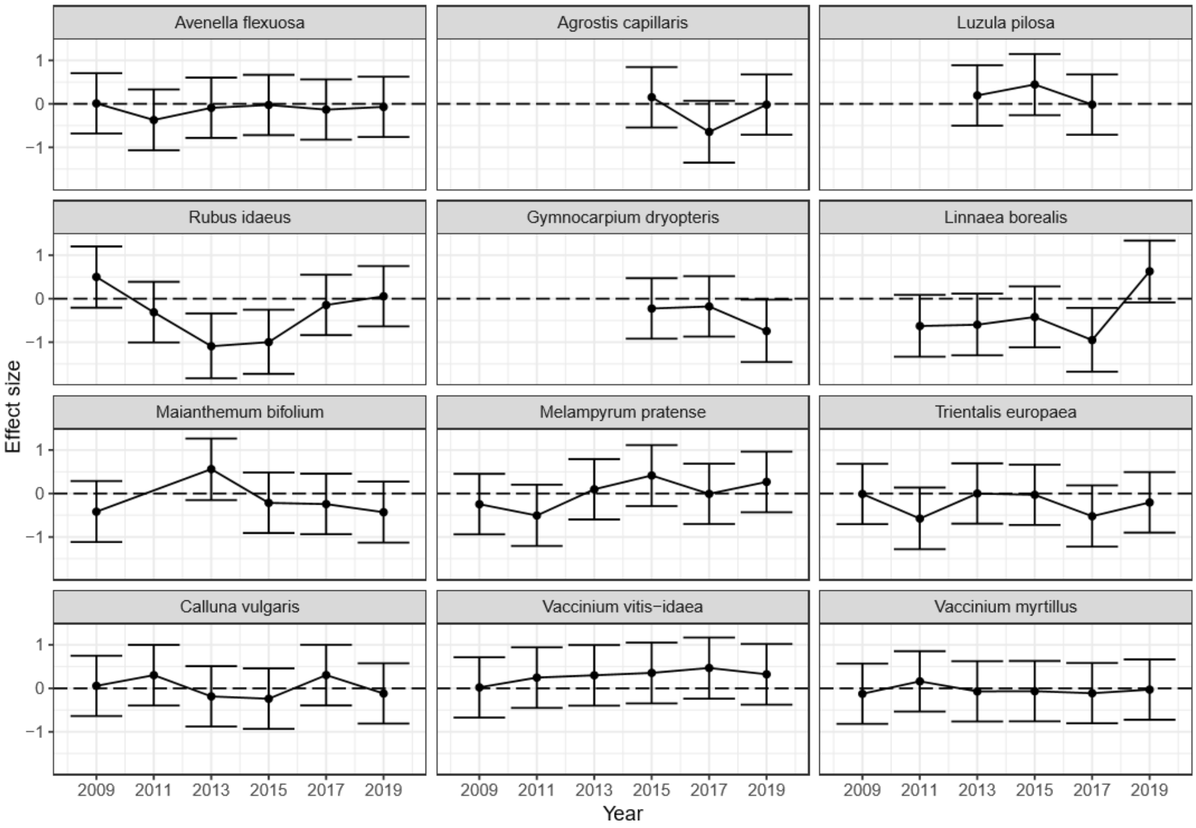


Figure 5: Effect size calculated per year in Telemark region (Open – exclosed) and corresponding confidence intervals, excluding rare species (present in fewer than five sites)

Four graminoid species were present in Trøndelag; *Avenella flexuosa, Agrostis capillaris, Dechampsia cespitosa* and *Luzula pilosa*. *A. flexuosa* was close to zero in the first four recordings between 2008 and 2016, but in 2019 it tended towards being relatively more abundant outside exclosures, although not statistically significant (Figure 6). *A.capillaris* was only present in 2010, 2016 and 2019 and did not show any strong temporal trends. Neither *D. cespitosa* nor *L. pilosa* did showed any particular temporal trends. *L. pilosa* showed a weak tendency shifting from a negative effect of herbivory in 2008, 2010 and 2012 to positive in 2014, 2016 and 2019 (Figure 6).

The three ferns species *Gymnocarpium dryopteris, Phegopteris connectilis* and *Aythureum felix-femina* all had periods during the study where they were more abundant inside exclosures, with *Gymnocarpium dryopteris* showing a “hump-shaped” pattern over time where it was more abundant inside exclosures in the first year of the study and again in the final year (Figure 6).

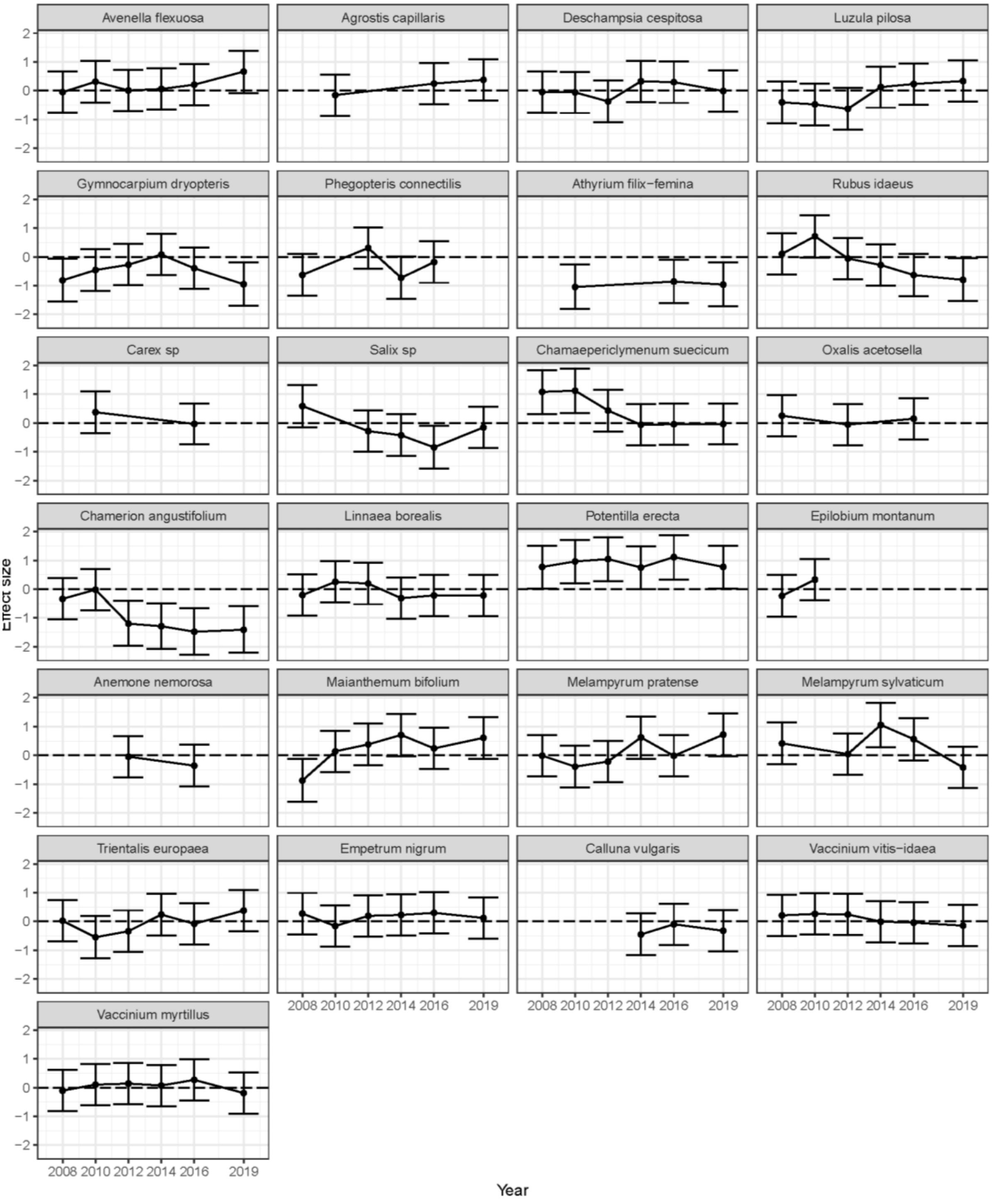
Gymnocarpium dryopteris was initially more abundant inside exclosures in 2008. This effect was absent until 2019, when it again showed to be more abundant inside exclosures than outside. *Phegopteris connectilis* tended towards a negative response in 2008 and did show a negative response to herbivory in 2014. *Aythureum felix-femina* was sufficiently abundant to be included in the analysis only in three years (2010, 2016 and 2019) but did in all these three years show a negative effect of herbivory.

Rubus ideaus showed indications of a temporal trend, where it tended towards a positive herbivore effect in 2010 while in 2019 it was significantly more abundant inside exclosures, indicating a negative effect of herbivory. *Salix* sp showed a negative response to herbivory only in 2016.

The forbs recorded in Trøndelag show varying temporal responses to herbivory. *Chamaepericlymenum suecicum* showed a noticeable temporal trend where it was positively affected by herbivore presence in 2008 and 2010. This effect did however not persist, and it stabilized at no significant effect since 2012. *Epilobium angustifolium* showed no effect in the first two years of recording (2008 and 2010), but a strong negative effect in the following years. *Potentilla erecta* show a consistent positive herbivore effect in all years of recording. *Melampyrum sylvaticum* did not differ significantly from zero apart from in 2014, when the effect of herbivory was positive. *Epilobium montanum* and *Anemone nemrosa* were only present in two years, neither of these were different from zero.

Maianthemum bifolium was significantly more abundant inside exclosures in 2008. This effect is not present in any following years, and it tends toward being more abundant outside exclosures. Particularly in 2014 and 2019, although not statistically significant there seem to be a temporal shift from being relatively more abundant in the absence of herbivores to being relatively more abundant in the presence of herbivores. *Linnea borealis, Melampyrum pratense* and *Trientalis europea* are among the most common forbs, but none of them showed a significant response in any of the years. Both *M. pratense* and *T. europea* seem to fluctuate close to zero. Both species actually seem to vary similarly between years, and *M. pratense* tends toward a positive herbivore effect in 2014 and 2019.

None of the shrubs seem to show any temporal trends apart from some variations between years. *Calluna vulgaris* was only present in the final three years, in all of which it tended towards a negative effect of herbivory, but not statistically significant.



Red deer ratio had an impact on the effect size of three species; *Trientalis europaea*, *Vaccinium uliginosum* and *Dryopteris expansa* (Figure 7). *D. expansa* was present in only 5 of the 31 sites from which effect sizes were calculated, while *V. uliginosum* was present in 7 sites.

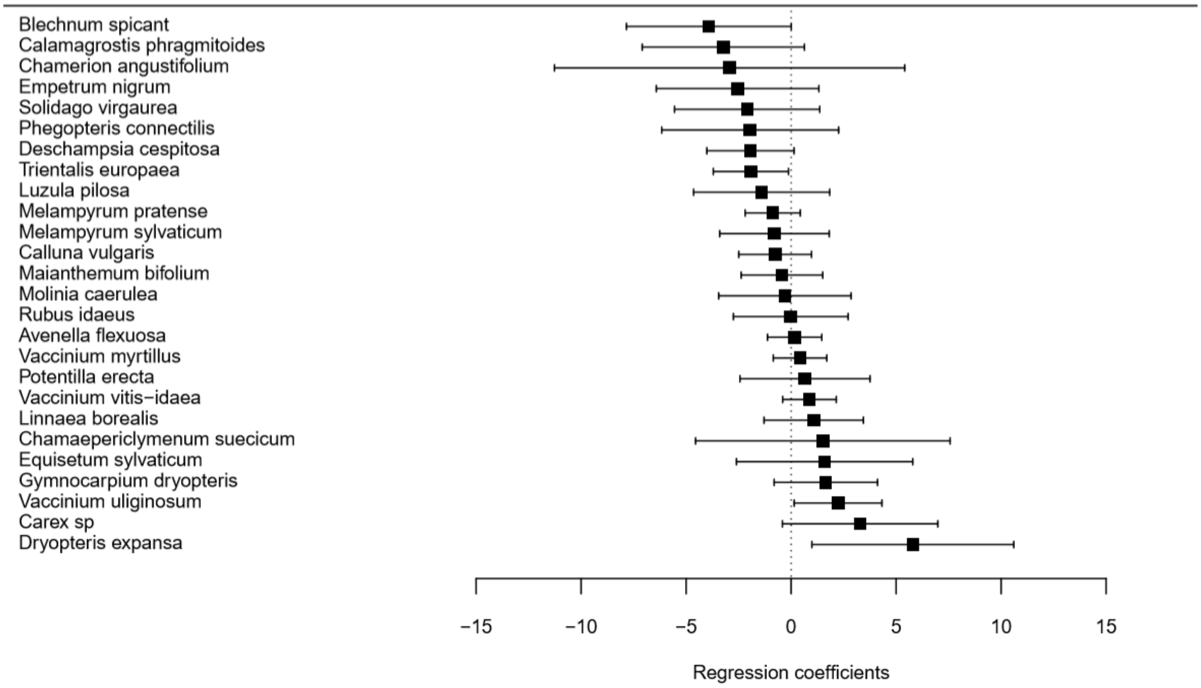


Figure 7: Model coefficients for all species present in five or more sites and their corresponding confidence intervals. All models were linear meta-regression models with effect size (Open – exclosed) as response variable and red deer ratio as explanatory variable

Both *Vaccinium uliginosum* (β=2.2348) and *Dryopteris expansa* (β=5.7965) showed a positive effect of red deer ratio on effect size (Table A5, Figure 8). This means that with an increasing red deer ratio in the herbivore community, the effect of herbivory becomes increasingly positive. Thus, indicating that these species suffer more from herbivore presence in moose dominated communities, but benefit in red deer dominated communities. *Trientalis europaea* had a negative effect of red deer ratio (β=-1.9151) (Table A5). Its relative abundance decreased with increasing red deer ratio in the herbivore community.

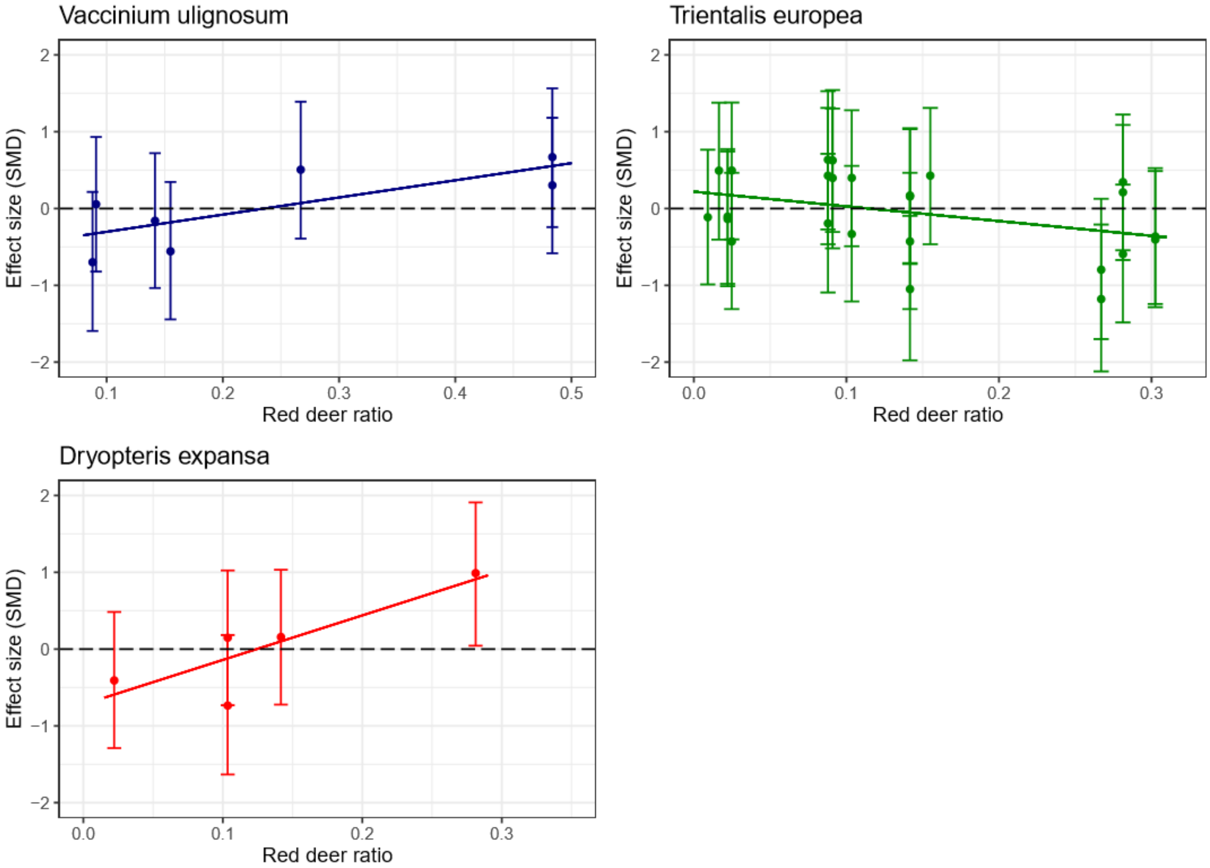


Figure 8: Species with a significant effect of red deer ratio on effect size. X-axis is the effect size from each site. Y-axis is the red deer ratio (red deer density divided by the sum of moose density and red deer density). Dots represents effect size for a single site with corresponding confidence interval. The line represents the regression line from the linear (fixed effect) meta-regression.

4 Discussion

4.1 Herbivore community

The temporal changes in the cervid community has been quite substantial in most of the focal municipalities. The difference between the municipalities in Trøndelag and the ones in Telemark is most noticeable in the change in moose densities. All five Telemark municipalities had moose densities which increased drastically between 1960 and 1999 where it peaked at around 60 kg km^{-2} unenclosed land. The recent decline is moose density in Telemark has been described by Solberg et al. (2017) and the trend represented here illustrates this.

In Trøndelag the changes in moose density has been less pronounced. In Tydal, Verdal and Midtre-Gauldal there has been a modest increase while Malvik, Namdalseid, Selbu, Steinkjer and Trondheim have experienced steady and higher growth. Solberg et al. (2017) documented a moose population which has stabilized in the county formerly known as "Nord-Trøndelag" which covers the municipalities Namdalseid, Steinkjer and Verdal.

Although not as eye-catching there has also been a change in red deer densities mainly in the Telemark municipalities, but also a slight increase in Midtre Gauldal. The changes in Telemark seem to illustrate a shift from an herbivore community previously dominated by moose to one which consists of a mix of moose and red deer. The changes in cervid densities presented here also illustrate part of the functional shift from livestock to cervids that has occurred since 1949 (Speed et al., 2019).

Comparing the two regions it appears that the herbivore community in Trøndelag has remained quite stable compared to Telemark. The moose is the most dominant herbivore in all focal municipalities in Trøndelag and while this is also true for the ones in Telemark the red deer has a stronger presence here. This shift that is occurring in Telemark is interesting from an ecological perspective. As covered earlier the moose and red deer occupy different feeding types and the shift in herbivore community is likely to affect the plant community. Particularly the fact that having an herbivore community with an increasing proportion of red deer and thus more grazing is interesting to investigate. However, the fact that the changes in herbivore composition is relatively recent and still ongoing might mean that potential change in plant composition will only be visible after some time. As covered by Nuttle et al. (2014) herbivores can have long lasting legacy effects, even after changes in density.

4.2 Herbivore exclusion

Browsing was shown to have a significant effect for multiple species in this study (Figure 4). Exclusion of large herbivores over a 10- (Telemark) and 11-year (Trøndelag) period has affected the relative abundances of multiple species, illustrating that large herbivores are a strong force in shaping the composition of species in the community.

In total six species showed a significant negative effect of herbivory. These included *Chamerion angustifolium*, which followed the expectation (Table 1), and *Rubus ideaus*. This response is in accordance with existing literature that has demonstrated an increased red deer density has a negative impact on both aboveground biomass and cover of *C. angustifolium* and *Rubus* spp (Tremblay et al., 2006, Rooney, 2009). Although there are also studies documenting no such relationship between *Rubus ideaus* relative densities and presence of either red deer or moose in both spruce and pine forests (Speed et al., 2014). *C. angustifolium* has also been shown to associate with temporal divergence of understory plant communities between exclosed and unexclosed plots in the same system (Kolstad et al., 2018). The fact that *C. angustifolium* shows the strongest effect of herbivory (Table 1A, Figure 4) is largely supported in the literature. This would then indicate that herbivory is an important factor in limiting *C. angustifolium* abundance.

Three of the five ferns showed a negative effect of herbivory in 2019. These three were *Gymnocarpium dryopteris*, *Athyrium filix-femina* and *Phegopteris connectilis*. The remaining two species *Blechnum spicant* and *Drypoteris expansa* tended towards a negative effect without it being statistically significant. This is consistent with the findings of Kolstad et al. (2018) who also documented increased fern biomass inside exclosures compared to outside. Rooney (2009) found similar effects, where cover of ferns was nearly twenty times greater in exclosures, although the fern species present in his study differed from the ones in present in this study.

The negative effect of herbivores on ferns here is interesting, considering multiple studies have documented a positive effect of herbivores on ferns (Nuttle et al., 2014). Ferns are generally not thought to be preferred by herbivores; however, they may be more vulnerable to defoliation and trampling and thus might be inhibited by herbivores despite not being popular forage (Kolstad et al., 2018, Mysterud, 2000). The discrepancy in effect on ferns among studies could also suggest that functional differences between fern species play a role in determining their response to presence of herbivores. Furthermore, it is possible that variations among studies and study systems cause the results to differ. Species of both ferns and herbivores differ between studies from Europe (Kolstad et al., 2018, Speed et al., 2014) and North-America (Rooney, 2009, Nuttle et al., 2014). Type of vegetation measurement also vary between biomass and cover percentage. It is therefore possible that variations in methodology is why the literature appears ambiguous.

Only one of the seven species (including *Carex* sp) of graminoids was significantly more abundant outside exclosures and thus showed a positive response to herbivory. The remaining six showed no effect. Contrary to expectations, the most common graminoid in the study system; *Avenella flexuosa* did not show any effect of herbivory. This was surprising, as multiple studies have reported positive effects of herbivores on graminoids (Tremblay et al., 2006, Rooney, 2009, Mathisen et al., 2010). However, Kolstad et al. (2018) only found weak indications of this when doing similar analysis for graminoids as a group. Hegland and Rydgren (2016) were also not able to document a positive relationship between red deer densities and graminoid abundance probability, contrary to their hypothesis. They note that this could be due to red deer being a mixed feeder that potentially forage on graminoids. The sites in this study system consist of both moose and red deer and how this might affect species responses will be discussed further down. *Calamagrostis phragmitoides* was the only graminoid which was more abundant outside of exclosures and thus benefitted from the presence of herbivores.

The nine forb species included in the analysis with the most recent data (Figure 4) ranged from negative effect of herbivores on *Chamerion angustifolium* to positive effect on *Potentilla erecta*. Forbs are a functionally diverse group and I did not have any predictions regarding their response apart from *C. angustifolium*. However, it is interesting to note that species such as *Maiantehmum bifolium* and *Trientalis europea* have related species within the same genera in North-America that has shown higher percentage cover in exclosure plots than in controls (Rooney, 2009). It is reasonable to expect these species to be functionally similar and that their response to herbivory would reflect this, yet this is not the case. Speed et al. (2014) however, found no effect of herbivore exclusion on either *M. bifolium* or *T. europea*, which suggest a functional difference between the species or an interplay with other ecological factors which moderate their response.

It is also interesting that species most positively associated with herbivore presence was *Potentilla erecta*, while in Speed et al. (2014) although no effect was observed in red deer dominated pine forests, there was a negative effect in red deer dominated deciduous forests. It is noteworthy that the effect appears opposite between mature red deer dominated deciduous forests and younger pine and spruce forests dominated by moose, but with presence of red deer in some sites. The lack of effect in red deer dominated pine forests would suggest that *P. erecta* suffer more under herbivory in deciduous forests. Furthermore, the positive effect observed here could indicate that moose facilitate *P. erecta* abundance indirectly by improving light conditions or reducing competition.

None of the five shrub species (*Vaccinium myrtillus*, *Vaccinium vitis-idaea*, *Calluna vulgaris*, *Vaccinium ulignosum* and *Empetrum nigrum*) in the study showed any response to herbivore exclusion in 2019. The expected negative impact of herbivory on *C. vulgaris* was not observed. This was unexpected considering multiple studies have documented a negative effect of herbivores on *C. vulgaris* (Bernes et al., 2018, Hegland and Rydgren, 2016). Speed et al. (2014) also documented a negative effect of herbivores in moose dominated pine forests in an earlier analysis of data from the study system used in this analysis. It is hard to know the reason for this discrepancy with the literature. The study site Hegland and Rydgren (2016) used was a mature forest, as opposed to a young forest which was the case in this study. It is possible that *C. vulgaris* response is dependent on the successional stage of the forest. A negative response has been found in both moose and red deer dominated forests, so it would seem unlikely that differing herbivore species is the cause for this. Climatic conditions, experimental design and forest age and type often vary among studies and it is possible that *C. vulgaris* response to herbivory is regulated by variations in these factors.

4.3 Temporal trends

Analysis per regions and years to allowed further examination of how the effect of herbivores might change temporally, possibly through mechanisms relating to succession stages of the ecosystems. These results can be hard to interpret, yet there seem to be some indications of temporal patterns for certain species. The pattern for *Rubus ideaus* in Telemark suggests a U-shaped response over time (Figure 6). It is possible that this relates to *R. ideaus* being an early successional and herbivore preferred species, and as more preferential species such as rowan emerge, the impact of herbivores on *R. ideaus* is reduced. In Trøndelag however, the pattern appears to be different with a significant negative effect of herbivores not occurring before 2019.

Herbivory has the potential to alter successional trajectories for species and ecosystems (Hidding et al., 2013). It is interesting to note the difference in temporal trend of *Rubus ideaus* in Trøndelag and Telemark. In Telemark *R. ideaus* has had differing trajectories in the exclosed and open plots but appear to have stabilized at similar states after 11 years of exclusion. Whether the trajectory in Trøndelag will result in the same stable state remains to be seen, although it is likely that climax species eventually will lead to similar states for *R. ideaus* in both exclosed and open plots.

Chamerion angustifolium in Trøndelag did not show a negative effect of herbivory until 2012, four years since exclusion. Since then there has been significantly higher abundance of *C. angustifolium* inside exclosures. This suggests that despite *C. angustifolium* being vulnerable to herbivory, it does not significantly affect abundance until a few years have passed. In Hidding et al. (2013) *C. angustifloium* remained at low densities in delayed exclosures, and thus it might seem that despite it being browsing sensitive it might still avoid extirpation for some time while in the presence of herbivores. In Trøndelag it is possible that continued moose presence can cause legacy effects for *C. angustifolium* and thus drive succession to an alternate state.

Potentilla erecta in Trøndelag remained more abundant in open plots than inside exclosures throughout the duration of the study. This could indicate that *P. erecta* benefit from either the improved light conditions driven by moose herbivory, or reduction in competition, perhaps from *Chamerion angustifolium*. *Maianthemum bifolium*, *Chamaepericlymenum suecicum* and *Melampyrum sylvaticum* show tendencies and periods of higher abundance in the open plots in Trøndelag. *M. bifolium* shifted from an initial negative effect of herbivores towards a positive effect. The positive effect has not been consistent for all years, and particularly for *M. sylcaticum* it was closer to a negative effect than positive in 2019. *C. suecicum* is more abundant in the open plots initially, but after 2010 there is no significant difference in abundance. It is possible that there is a temporal shift in the limiting factor for these species.

There appear to be a trend in Trøndelag with smaller forbs periodically being more abundant in open plots. For *P. erecta* this effect seems to be more consistent. Trøndelag is dominated by moose. It is possible that moose preference for woody browse create better conditions for certain field layer forbs, at least periodically.

4.4 Effects of variations in herbivore community

A point that has been mentioned above is how plant responses might be affected by what type of herbivore is present in the system. It is quite possible that variations in responses to herbivory among studies relate to which herbivore species are present in the system. This could be particularly relevant if the herbivores are functionally differing through different feeding types.

Of all species analyzed, only three showed a significant effect of red deer ratio on change in abundance. These were *Trientalis europea*, *Vaccinium ulignosum* and *Dryopteris expansa* (Figure 8 and 9). *V. ulignosum* was present in five sites and *D. expansa* in seven and thus the relationship between red deer ratio and their effect size must be interpreted with caution. However, both appear to be positively affected by an increased red deer ratio. This suggests that the relative abundance of these species increases when red deer ratio increases. Kolstad et al. (2018) suggested that *D. expansa* is trampling intolerant, but whether this intolerance is the reason for the effect of red deer ratio on relative abundance seems unlikely. The effect of the red deer ratio on *T. europea* however, seem more robust and does indicate that as the proportion of red deer increases, *T. europea* relative abundance decreases. It is possible that this effect is driven by red deer herbivory. *T. europea* was classified as an intermediate-impact benefiter of red deer exclusion by Hegland and Rydgren (2016), while showing no response in moose dominated spruce forest (Speed et al., 2014). Red deer as a mixed feeder was expected to have a stronger direct influence on species in the field layer. With this in mind it would seem that indeed, the composition of herbivore communities is an important driver in determining the response of *T. europea* to herbivores.

Vaccinium myrtillus was expected to be negatively affected by red deer ratio, based on positive response of *V. myrtillus* in moose dominated pine forest and the negative impact red deer have on *V. myrtillus* performance (Table 1) (Speed et al., 2014, Hegland et al., 2005). However, no such effect was observed (Figure 7). It is possible that the lack of an observable effect is because the density of the red deer in the system is not high enough to cause a reduction in abundance of *V. myrtillus*. Furthermore, it could be that the response is non-linear and that a certain threshold of red deer is required for the effect to be noticeable, and that variation of red deer to moose alone does not reveal potential effects on *V. myrtillus*. It is also possible that the effect of moose on *V. myrtillus* is not that different from the one of red deer and herbivory by moose may counteract any potential facilitation through improved light conditions (Wam and Hjeljord, 2010, Mathisen et al., 2010). Furthermore, there could be local variations in herbivore composition that are not captured sufficiently with herbivore data on municipality level.

There was no expected response of red deer ratio on either *Avenella flexuosa*, *Calluna vulgaris* or *Chamerion angustifolium* (Table 1). Although it is possible that *A. flexuosa* does benefit from red deer herbivory through improved light conditions and possibly grazing lawn dynamics, it showed no effect of red deer ratio (Figure 7). Hegland and Rydgren (2016) found no effect of red deer herbivory on graminoids, contrary to their expectations. They suggest that the positive effect from herbivores on graminoids is stronger in communities with browsers such as moose as opposed to red deer, given that red deer also forage on graminoids. Then again, graminoids are grazing tolerant and can benefit from grazing through positive feedback. It is possible that these effects contribute to the lack of observable effect for *A. flexuosa*. Similarly, *C. vulgaris* has been shown to be negatively affected by herbivory in systems of both browsers and mixed feeders, and thus the lack of effect of red deer ratio is unsurprising (Speed et al., 2014, Hegland and Rydgren, 2016, Bernes et al., 2018). No effect was expected for *C. angustifolium* either, but it is worth mentioning that it was only present in sites with low ratio of red deer. Hence, any potential effect might have gone unnoticed because of this lack of variation in red deer ratio.

As was demonstrated by Nuttle et al. (2014), effects of herbivores can be long lasting and past densities of herbivores can leave legacy effects that persist for decades. This is important to have in mind, particularly when investigating responses in regions of different herbivore densities. Herbivore data used for the regression analysis (Figure 8) was collected in 2015 and although I believe that this is sufficient to illustrate potential effects it is important to remember that particularly the herbivore community in Telemark has been highly dynamic. Densities of moose have plummeted, and densities of red deer have increased the last 20 years (Figure 3). It is possible that this is reflected in the results and that the effects of red deer will become more apparent after time, especially if their densities continue to increase.

4.5 Conclusions

In this study it has been shown how the cervid densities in focal municipalities in Trøndelag and Telemark have changed through time. Most noticeably moose densities in Telemark have dropped since 1999 and red deer densities have increased, while in Trøndelag moose densities have remained stable and red deer densities have remained low. Furthermore, it has demonstrated the substantial impacts that large herbivores can have on relative abundances of field layer species. Both *Chamerion angustifolium* and *Gymnocarpium dryopteris* were negatively impacted through herbivory and trampling, while *Potentilla erecta* became more abundant in the presence of herbivores, likely through improved light conditions or reduction in competition. There are both temporal trends and spatial variations in plant responses to herbivory. Moreover, an effect of the proportion of red deer vs moose in the herbivore community on species responses to herbivory has also been demonstrated for *Vaccinium ulignosum*, *Dryopteris expansa* and *Trientalis europea*. The effect on *T. europea* is likely caused by increased grazing from red deer. Therefore, with increasing red deer densities and higher grazing pressure, it's abundance will become increasingly impaired. The strong effects of herbivory and the varying effects depending on herbivore composition means that if the red deer continues to expand, the herbivore pressure is likely to shift even more. *T. europea* and possibly functionally similar species are likely to experience reduced abundances, while the opposite might happen for *V. ulignosum* and *D. expansa*.

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Appendix

Table A1: Densities (kg/km2 utmark) of moose, red deer and roe deer in focal municipalities for all recorded years

Moose density	**Red deer density**	**Roe deer density**	**Municiaplity**	**Year**
1.64098	0.25171	0.23463	Trondheim	1949
29.16061	0.48735	11.3231	Trondheim	2015
32.62406	0.17099	11.48258	Trondheim	2009
2.54797	0	8.27055	Trondheim	1969
2.20461	0	2.46357	Trondheim	1959
15.06913	0	4.08286	Trondheim	1989
21.62947	0	4.45789	Trondheim	1979
22.04617	0	3.15771	Trondheim	1999
7.48825	0.26481	0.64983	Midtre Gauldal	1979
13.23468	2.42668	0.98993	Midtre Gauldal	2015
1.49463	0	0.92834	Midtre Gauldal	1959
5.4747	0.50439	0.93928	Midtre Gauldal	1989
1.56068	0.10859	0.59413	Midtre Gauldal	1969
1.27711	0.0362	0	Midtre Gauldal	1949
5.91625	0.6258	0.36404	Midtre Gauldal	1999
6.79669	1.04919	0.5748	Midtre Gauldal	2009
7.48825	0.26481	0.64983	Støren	1979
13.23468	2.42668	0.98993	Støren	2015
1.49463	0	0.92834	Støren	1959
5.4747	0.50439	0.93928	Støren	1989
1.56068	0.10859	0.59413	Støren	1969
1.27711	0.0362	0	Støren	1949
5.91625	0.6258	0.36404	Støren	1999
6.79669	1.04919	0.5748	Støren	2009
10.77419	0	4.14169	Malvik	1979
17.067	0	3.33532	Malvik	1989
1.90382	0	3.74724	Malvik	1969
4.76529	0	0.69028	Malvik	1959
35.08096	0	7.77531	Malvik	2009
2.27193	0	0	Malvik	1949
33.43231	0.30724	7.5072	Malvik	2015
36.07068	0	1.34057	Malvik	1999
16.92435	0.87011	0.98109	Selbu	2009
20.60281	1.98483	1.59882	Selbu	2015
2.13337	0	0	Selbu	1949
1.84914	0.1147	0.40094	Selbu	1969
2.58331	0	0.12028	Selbu	1959
14.27582	0.3381	1.22506	Selbu	1989
11.92989	0.39935	0.66133	Selbu	1999
8.16798	0.12237	0.36084	Selbu	1979

3.35523	0	0.29104	Tydal	1989
0.83008	0	0.18927	Tydal	1969
2.93601	0	0.10816	Tydal	1979
4.256	0.08356	0	Tydal	2009
2.74141	0	0.24182	Tydal	1999
6.0137	0.1531	0	Tydal	2015
0.46496	0	0	Tydal	1949
1.34116	0	0	Tydal	1959
3.87882	0	2.22189	Steinkjer	1969
7.81414	0	0	Steinkjer	1949
39.26124	0.88744	6.52053	Steinkjer	2015
14.26356	0	0.30566	Steinkjer	1959
31.25763	0.33964	8.43833	Steinkjer	2009
34.46636	0.20593	2.22465	Steinkjer	1999
19.77965	0	5.9368	Steinkjer	1979
16.33306	0.06759	4.03385	Steinkjer	1989
8.61972	0.80377	2.80814	Verdal	2009
6.71806	0.04178	1.99111	Verdal	1979
6.10871	0	0.71339	Verdal	1959
8.28202	0.27428	0.57321	Verdal	1999
2.402	0	1.07541	Verdal	1969
10.31847	1.032	2.54759	Verdal	2015
6.10595	0.06122	1.76936	Verdal	1989
1.88022	0	0	Verdal	1949
5.42465	0	0.46038	Namdalseid	1969
15.5555	0	0.18415	Namdalseid	1959
21.12691	2.08574	3.16729	Namdalseid	2009
5.99323	0	0	Namdalseid	1949
31.70412	0.47415	0.20587	Namdalseid	1999
27.69913	3.19684	2.6922	Namdalseid	2015
20.75174	0.2736	4.41968	Namdalseid	1979
16.00988	0.24052	2.3786	Namdalseid	1989
20.36156	0.10994	1.84202	Notodden	1989
5.27673	0	1.48852	Notodden	1969
33.14042	1.8538	2.89058	Notodden	2009
5.69198	0	4.04429	Notodden	1959
16.69902	2.75565	1.29867	Notodden	2015
60.06983	0.47641	5.23656	Notodden	1999
12.14294	0	4.08642	Notodden	1979
4.64421	0	0.14043	Notodden	1949

58.84914	8.21845	2.64297	Siljan	2009
16.27821	7.05944	4.22875	Siljan	2015
63.16136	0	3.46511	Siljan	1989
64.21145	2.46618	4.22875	Siljan	1999
16.80565	0	3.07127	Siljan	1969
30.78165	0	3.83909	Siljan	1979
17.33602	0	5.55191	Siljan	1959
5.45785	0	0	Siljan	1949
24.40441	3.65386	3.53193	Drangedal	2009
23.79854	0.12359	3.88576	Drangedal	1989
12.58951	0	5.52895	Drangedal	1979
9.85746	3.5905	1.8366	Drangedal	2015
3.71397	0	0	Drangedal	1949
62.15748	1.32857	4.16767	Drangedal	1999
6.35172	0	0.87611	Drangedal	1969
6.68532	0	2.49809	Drangedal	1959
22.53599	9.50748	8.86493	Nome	2009
38.5234	0.92722	4.79106	Nome	1989
11.01869	10.31418	5.4924	Nome	2015
13.96512	0.34045	3.68219	Nome	1979
72.96607	3.11883	6.68724	Nome	1999
2.74911	0	0.1938	Nome	1949
6.1738	0	2.03489	Nome	1969
3.88253	0	4.74808	Nome	1959
20.52719	0.24676	1.32926	Kviteseid	1989
8.30885	0	1.49396	Kviteseid	1979
4.4772	0	0.73752	Kviteseid	1969
4.01763	0	1.09683	Kviteseid	1959
2.85119	0	0	Kviteseid	1949
12.50146	4.8917	1.07189	Kviteseid	2015
30.46265	3.77841	2.14378	Kviteseid	2009
44.37298	1.97406	1.20729	Kviteseid	1999

Table A2: Standardized mean difference for each species in 2019 with corresponding sampling variances

Species	**SMD**	**Sampling variance**

Epilobium angustifolium (Geitrams)	-1.23857	0.07689
Gymnocarpium dryopteris (Fugletelg)	-0.99423	0.07249
Athyrium filix-femina (Skogburkne)	-0.72741	0.06878
Rubus idaeus (Bringebær)	-0.63688	0.06779
Phegopteris connectilis (Hengeving)	-0.63165	0.06773
Melampyrum sylvaticum (Småmarimjelle)	-0.51605	0.06666
Blechnum spicant (Bjønnkam)	-0.41453	0.0659
Molinia caerulea (Blåtopp)	-0.34106	0.06545
Dryopteris expansa (Sauetelg)	-0.28206	0.06516
Calluna vulgaris (Røsslyng)	-0.17302	0.06476
Salix sp (Vier)	-0.12228	0.06464
Vaccinium myrtillus (Blåbær)	-0.10256	0.0646
Maianthemum bifolium (Maiblom)	-0.07587	0.06456
Linnaea borealis (Linnea)	-0.0582	0.06454
Chamaepericlymenum suecicum (Skrubbær)	-0.00874	0.06452
Equisetum sylvaticum (Skogsnelle)	0.00032	0.06452
Solidago virgaurea (Gullris)	0.02189	0.06452
Vaccinium vitis-idaea (Tyttebær)	0.02409	0.06452
Empetrum nigrum (Krekling)	0.05918	0.06454
Deschampsia cespitosa (Sølvbunke)	0.18528	0.06479
Trientalis europaea (Skogstjerne)	0.18643	0.0648
Agrostis capillaris (Engkvein)	0.1999	0.06484
Vaccinium uliginosum (Blokkebær)	0.28206	0.06516
Avenella flexuosa (Smyle)	0.32589	0.06537

Carex sp (Starr)	0.33278	0.06541
Luzula pilosa (Hårfrytle)	0.40621	0.06585
Melampyrum pratense (Stormarimjelle)	0.4943	0.06649
Calamagrostis phragmitoides (Skogrøyrkvein)	0.56972	0.06713
Potentilla erecta (Tepperot)	0.79152	0.06957

Table A3: SMD and corresponding sampling variance and confidence intervals for all species per year in Telemark

Year	**Species**	**SMD**	**Sampling variance**	**CI Lower**	**CI Upper**
2009	*Avenella flexuosa* (Smyle)	0.01039	0.125	-0.68265	0.70326
2009	*Calluna vulgaris* (Røsslyng)	0.05721	0.12505	-0.63637	0.74983
2009	*Maianthemum bifolium* (Maiblom)	-0.41802	0.12773	-1.11554	0.28628
2009	*Melampyrum pratense* (Stormarimjelle)	-0.24598	0.12595	-0.93967	0.45176
2009	*Rubus idaeus* (Bringebær)	0.50089	0.12892	-0.20749	1.20121
2009	*Trientalis europaea* (Skogstjerne)	-0.01028	0.125	-0.70315	0.68276
2009	*Vaccinium myrtillus* (Blåbær)	-0.12528	0.12525	-0.81791	0.56943
2009	*Vaccinium vitis-idaea* (Tyttebær)	0.02122	0.12501	-0.67192	0.71402
2011	*Avenella flexuosa* (Smyle)	-0.37094	0.12715	-1.06714	0.33132
2011	*Calluna vulgaris* (Røsslyng)	0.30368	0.12644	-0.39597	0.99835
2011	*Linnaea borealis* (Linnea)	-0.62792	0.13116	-1.33374	0.08782
2011	*Melampyrum pratense* (Stormarimjelle)	-0.50529	0.12899	-1.20578	0.20332
2011	*Rubus idaeus* (Bringebær)	-0.31246	0.12653	-1.00731	0.38751
2011	*Trientalis europaea* (Skogstjerne)	-0.57589	0.13018	-1.27929	0.13667
2011	*Vaccinium myrtillus* (Blåbær)	0.16076	0.1254	-0.5347	0.85357
2011	*Vaccinium vitis-idaea* (Tyttebær)	0.24749	0.12596	-0.4503	0.94121

2013	*Avenella flexuosa* (Smyle)	-0.09049	0.12513	-0.78307	0.60358
2013	*Calluna vulgaris* (Røsslyng)	-0.18603	0.12554	-0.87903	0.51004
2013	*Linnaea borealis* (Linnea)	-0.59836	0.13059	-1.30278	0.11555
2013	*Luzula pilosa* (Hårfrytle)	0.1945	0.12559	-0.50179	0.88758
2013	*Maianthemum bifolium* (Maiblom)	0.56104	0.12992	-0.15065	1.26379
2013	*Melampyrum pratense* (Stormarimjelle)	0.09719	0.12515	-0.597	0.78977
2013	*Rubus idaeus* (Bringebær)	-1.09281	0.14366	-1.83058	-0.33929
2013	*Trientalis europaea* (Skogstjerne)	0	0.125	-0.69295	0.69295
2013	*Vaccinium myrtillus* (Blåbær)	-0.0705	0.12508	-0.76309	0.62327
2013	*Vaccinium vitis-idaea* (Tyttebær)	0.30023	0.12641	-0.3993	0.99483
2015	*Agrostis capillaris* (Engkvein)	0.15262	0.12536	-0.54266	0.84538
2015	*Avenella flexuosa* (Smyle)	-0.02576	0.12501	-0.71853	0.66743
2015	*Calluna vulgaris* (Røsslyng)	-0.23911	0.12589	-0.9327	0.45843
2015	*Gymnocarpium dryopteris* (Fugletelg)	-0.22627	0.1258	-0.9197	0.47089
2015	*Linnaea borealis* (Linnea)	-0.42052	0.12776	-1.11812	0.28389
2015	*Luzula pilosa* (Hårfrytle)	0.44595	0.12811	-0.25966	1.14435
2015	*Maianthemum bifolium* (Maiblom)	-0.2154	0.12572	-0.9087	0.48145
2015	*Melampyrum pratense* (Stormarimjelle)	0.4151	0.12769	-0.28907	1.11253
2015	*Rubus idaeus* (Bringebær)	-0.99875	0.14059	-1.72862	-0.25417
2015	*Trientalis europaea* (Skogstjerne)	-0.03007	0.12501	-0.72281	0.66317
2015	*Vaccinium myrtillus* (Blåbær)	-0.06555	0.12507	-0.75816	0.62814
2015	*Vaccinium vitis-idaea* (Tyttebær)	0.3549	0.12697	-0.34669	1.0507
2017	*Agrostis capillaris* (Engkvein)	-0.64519	0.1315	-1.35187	0.07166
2017	*Avenella flexuosa* (Smyle)	-0.13127	0.12527	-0.82392	0.56356

2017	*Calluna vulgaris* (Røsslyng)	0.30508	0.12645	-0.39463	0.99978
2017	*Gymnocarpium dryopteris* (Fugletelg)	-0.1787	0.1255	-0.87163	0.51719
2017	*Linnaea borealis* (Linnea)	-0.95167	0.13915	-1.67786	-0.21133
2017	*Luzula pilosa* (Hårfrytle)	-0.01669	0.125	-0.70952	0.67641
2017	*Maianthemum bifolium* (Maiblom)	-0.24264	0.12592	-0.93629	0.455
2017	*Melampyrum pratense* (Stormarimjelle)	-0.00792	0.125	-0.70081	0.6851
2017	*Rubus idaeus* (Bringebær)	-0.14522	0.12533	-0.83794	0.5499
2017	*Trientalis europaea* (Skogstjerne)	-0.52214	0.12926	-1.22328	0.18738
2017	*Vaccinium myrtillus* (Blåbær)	-0.11251	0.1252	-0.80511	0.58195
2017	*Vaccinium vitis-idaea* (Tyttebær)	0.46823	0.12843	-0.23847	1.16737
2019	*Agrostis capillaris* (Engkvein)	-0.01686	0.125	-0.70968	0.67625
2019	*Avenella flexuosa* (Smyle)	-0.0701	0.12508	-0.76269	0.62366
2019	*Calluna vulgaris* (Røsslyng)	-0.11816	0.12522	-0.81078	0.57641
2019	*Gymnocarpium dryopteris* (Fugletelg)	-0.74511	0.13367	-1.45727	-0.02141
2019	*Linnaea borealis* (Linnea)	0.62991	0.1312	-0.08596	1.33583
2019	*Maianthemum bifolium* (Maiblom)	-0.43048	0.1279	-1.12838	0.2744
2019	*Melampyrum pratense* (Stormarimjelle)	0.26777	0.12612	-0.43066	0.96179
2019	*Rubus idaeus* (Bringebær)	0.05584	0.12505	-0.63772	0.74847
2019	*Trientalis europaea* (Skogstjerne)	-0.20551	0.12566	-0.89869	0.49107
2019	*Vaccinium myrtillus* (Blåbær)	-0.02924	0.12501	-0.72198	0.664
2019	*Vaccinium vitis-idaea* (Tyttebær)	0.32325	0.12663	-0.37712	1.01832

Table A4: SMD and corresponding sampling variance and confidence intervals for all species per year in Trøndelag

Year	**Species**	**SMD**	**Sampling variance**	**CI Lower**	**CI Upper**

2008	*Avenella flexuosa* (Smyle)	-0.05281	0.13338	-0.76815	0.66347
2008	*Chamaepericlymenum suecicum* (Skrubbær)	1.08192	0.15284	0.30429	1.84281
2008	*Deschampsia cespitosa* (Sølvbunke)	-0.04675	0.13337	-0.76211	0.66945
2008	*Empetrum nigrum* (Krekling)	0.27557	0.1346	-0.44613	0.99242
2008	*Epilobium angustifolium* (Geitrams)	-0.33796	0.13524	-1.05608	0.38608
2008	*Epilobium montanum* (Krattmjølke)	-0.23186	0.13423	-0.94804	0.48842
2008	*Gymnocarpium dryopteris* (Fugletelg)	-0.81785	0.14448	-1.55792	-0.06438
2008	*Linnaea borealis* (Linnea)	-0.20618	0.13404	-0.92205	0.51334
2008	*Luzula pilosa* (Hårfrytle)	-0.40733	0.1361	-1.1273	0.31973
2008	*Maianthemum bifolium* (Maiblom)	-0.87793	0.14618	-1.62222	-0.11944
2008	*Melampyrum pratense* (Stormarimjelle)	-0.01163	0.13334	-0.72721	0.70415
2008	*Melampyrum sylvaticum* (Småmarimjelle)	0.41513	0.13621	-0.3123	1.13533
2008	*Oxalis acetosella* (Gauksyre)	0.25241	0.1344	-0.46851	0.96889
2008	*Phegopteris connectilis* (Hengeving)	-0.62924	0.13993	-1.35816	0.11032
2008	*Potentilla erecta* (Tepperot)	0.77284	0.14329	0.02296	1.50997
2008	*Rubus idaeus* (Bringebær)	0.1033	0.13351	-0.61381	0.81856
2008	*Salix sp_* (Vier)	0.58943	0.13912	-0.14758	1.31641
2008	*Trientalis europaea* (Skogstjerne)	0.02396	0.13334	-0.69196	0.73945
2008	*Vaccinium myrtillus* (Blåbær)	-0.10367	0.13351	-0.81894	0.61344
2008	*Vaccinium vitis-idaea* (Tyttebær)	0.21214	0.13408	-0.50755	0.92807
2010	*Agrostis capillaris* (Engkvein)	-0.1543	0.13373	-0.86974	0.56387
2010	*Athyrium filix-femina* (Skogburkne)	-1.04977	0.1517	-1.80782	-0.27537
2010	*Avenella flexuosa* (Smyle)	0.31163	0.13495	-0.41138	1.02917
2010	*Carex sp_* (Starr)	0.37385	0.13566	-0.35169	1.09287

2010	*Chamaepericlymenum suecicum* (Skrubbær)	1.12439	0.1544	0.3424	1.88917
2010	*Deschampsia cespitosa* (Sølvbunke)	-0.06069	0.13339	-0.776	0.6557
2010	*Empetrum nigrum* (Krekling)	-0.15736	0.13375	-0.87282	0.56089
2010	*Epilobium angustifolium* (Geitrams)	-0.0179	0.13334	-0.73344	0.69795
2010	*Epilobium montanum* (Krattmjølke)	0.32915	0.13514	-0.39454	1.04707
2010	*Gymnocarpium dryopteris* (Fugletelg)	-0.45994	0.13686	-1.18161	0.2697
2010	*Linnaea borealis* (Linnea)	0.25414	0.13441	-0.46684	0.97063
2010	*Luzula pilosa* (Hårfrytle)	-0.47784	0.13714	-1.20016	0.25272
2010	*Maianthemum bifolium* (Maiblom)	0.1383	0.13365	-0.57951	0.85366
2010	*Melampyrum pratense* (Stormarimjelle)	-0.39453	0.13593	-1.11413	0.33194
2010	*Potentilla erecta* (Tepperot)	0.96351	0.14881	0.19737	1.71434
2010	*Rubus idaeus* (Bringebær)	0.71481	0.14185	-0.0307	1.44839
2010	*Trientalis europaea* (Skogstjerne)	-0.54854	0.13835	-1.27367	0.18598
2010	*Vaccinium myrtillus* (Blåbær)	0.10471	0.13352	-0.61241	0.81998
2010	*Vaccinium vitis-idaea* (Tyttebær)	0.26362	0.13449	-0.45767	0.98027
2012	*Anemone nemorosa* (Kvitveis)	-0.04752	0.13337	-0.76289	0.66868
2012	*Avenella flexuosa* (Smyle)	0.0076	0.13333	-0.70815	0.72321
2012	*Chamaepericlymenum suecicum* (Skrubbær)	0.43318	0.13646	-0.29511	1.15396
2012	*Deschampsia cespitosa* (Sølvbunke)	-0.37556	0.13568	-1.09462	0.35007
2012	*Empetrum nigrum* (Krekling)	0.19553	0.13397	-0.52369	0.91129
2012	*Epilobium angustifolium* (Geitrams)	-1.20056	0.15736	-1.97268	-0.41042
2012	*Gymnocarpium dryopteris* (Fugletelg)	-0.27515	0.1346	-0.99199	0.44654
2012	*Linnaea borealis* (Linnea)	0.19462	0.13396	-0.52458	0.91037
2012	*Luzula pilosa* (Hårfrytle)	-0.63392	0.14003	-1.36307	0.10595

2012	*Maianthemum bifolium* (Maiblom)	0.37919	0.13573	-0.34659	1.09836
2012	*Melampyrum pratense* (Stormarimjelle)	-0.21706	0.13412	-0.93306	0.50277
2012	*Melampyrum sylvaticum* (Småmarimjelle)	0.0436	0.13337	-0.67255	0.75898
2012	*Oxalis acetosella* (Gauksyre)	-0.0546	0.13338	-0.76994	0.6617
2012	*Phegopteris connectilis* (Hengeving)	0.30848	0.13492	-0.41441	1.02595
2012	*Potentilla erecta* (Tepperot)	1.04666	0.15159	0.27257	1.80444
2012	*Rubus idaeus* (Bringebær)	-0.05704	0.13339	-0.77237	0.6593
2012	*Salix sp_* (Vier)	-0.2821	0.13466	-0.99906	0.43983
2012	*Trientalis europaea* (Skogstjerne)	-0.33854	0.13524	-1.05668	0.38552
2012	*Vaccinium myrtillus* (Blåbær)	0.14142	0.13367	-0.57646	0.85679
2012	*Vaccinium vitis-idaea* (Tyttebær)	0.24392	0.13432	-0.47673	0.96027
2014	*Avenella flexuosa* (Smyle)	0.0587	0.13339	-0.65767	0.77401
2014	*Calluna vulgaris* (Røsslyng)	-0.45179	0.13674	-1.17319	0.27743
2014	*Chamaepericlymenum suecicum* (Skrubbær)	-0.06304	0.1334	-0.77835	0.65338
2014	*Deschampsia cespitosa* (Sølvbunke)	0.32583	0.1351	-0.39773	1.04368
2014	*Empetrum nigrum* (Krekling)	0.22751	0.1342	-0.49263	0.94363
2014	*Epilobium angustifolium* (Geitrams)	-1.28965	0.16105	-2.07092	-0.48947
2014	*Gymnocarpium dryopteris* (Fugletelg)	0.07719	0.13343	-0.63946	0.79246
2014	*Linnaea borealis* (Linnea)	-0.31513	0.13499	-1.03274	0.40802
2014	*Luzula pilosa* (Hårfrytle)	0.12481	0.13359	-0.59271	0.84012
2014	*Maianthemum bifolium* (Maiblom)	0.70942	0.14172	-0.03569	1.44269
2014	*Melampyrum pratense* (Stormarimjelle)	0.62304	0.1398	-0.11612	1.35164
2014	*Melampyrum sylvaticum* (Småmarimjelle)	1.05786	0.15198	0.28266	1.81662
2014	*Phegopteris connectilis* (Hengeving)	-0.73103	0.14224	-1.46557	0.01567

2014	*Potentilla erecta* (Tepperot)	0.75183	0.14275	0.00356	1.48763
2014	*Rubus idaeus* (Bringebær)	-0.28608	0.1347	-1.00312	0.43599
2014	*Salix sp_* (Vier)	-0.42887	0.1364	-1.14951	0.29921
2014	*Trientalis europaea* (Skogstjerne)	0.23981	0.13429	-0.48071	0.9561
2014	*Vaccinium myrtillus* (Blåbær)	0.07427	0.13343	-0.64233	0.78955
2014	*Vaccinium vitis-idaea* (Tyttebær)	-0.00444	0.13333	-0.72008	0.71127
2016	*Agrostis capillaris* (Engkvein)	0.24556	0.13434	-0.47514	0.96193
2016	*Anemone nemorosa* (Kvitveis)	-0.3605	0.1355	-1.07917	0.36448
2016	*Athyrium filix-femina* (Skogburkne)	-0.85948	0.14565	-1.60244	-0.10257
2016	*Avenella flexuosa* (Smyle)	0.20713	0.13405	-0.51241	0.92301
2016	*Calluna vulgaris* (Røsslyng)	-0.09649	0.13349	-0.81175	0.62049
2016	*Carex sp_* (Starr)	-0.03207	0.13335	-0.74751	0.68394
2016	*Chamaepericlymenum suecicum* (Skrubbær)	-0.04506	0.13337	-0.76044	0.67111
2016	*Deschampsia cespitosa* (Sølvbunke)	0.29549	0.13479	-0.42692	1.01271
2016	*Empetrum nigrum* (Krekling)	0.30132	0.13485	-0.4213	1.01865
2016	*Epilobium angustifolium* (Geitrams)	-1.48104	0.16989	-2.28395	-0.65757
2016	*Gymnocarpium dryopteris* (Fugletelg)	-0.39817	0.13598	-1.11787	0.32847
2016	*Linnaea borealis* (Linnea)	-0.21666	0.13412	-0.93265	0.50316
2016	*Luzula pilosa* (Hårfrytle)	0.23141	0.13423	-0.48885	0.94759
2016	*Maianthemum bifolium* (Maiblom)	0.24031	0.1343	-0.48022	0.95661
2016	*Melampyrum pratense* (Stormarimjelle)	-0.01747	0.13334	-0.73301	0.69837
2016	*Melampyrum sylvaticum* (Småmarimjelle)	0.56217	0.1386	-0.17316	1.2879
2016	*Oxalis acetosella* (Gauksyre)	0.14866	0.1337	-0.56938	0.86407
2016	*Phegopteris connectilis* (Hengeving)	-0.1849	0.1339	-0.90056	0.53403

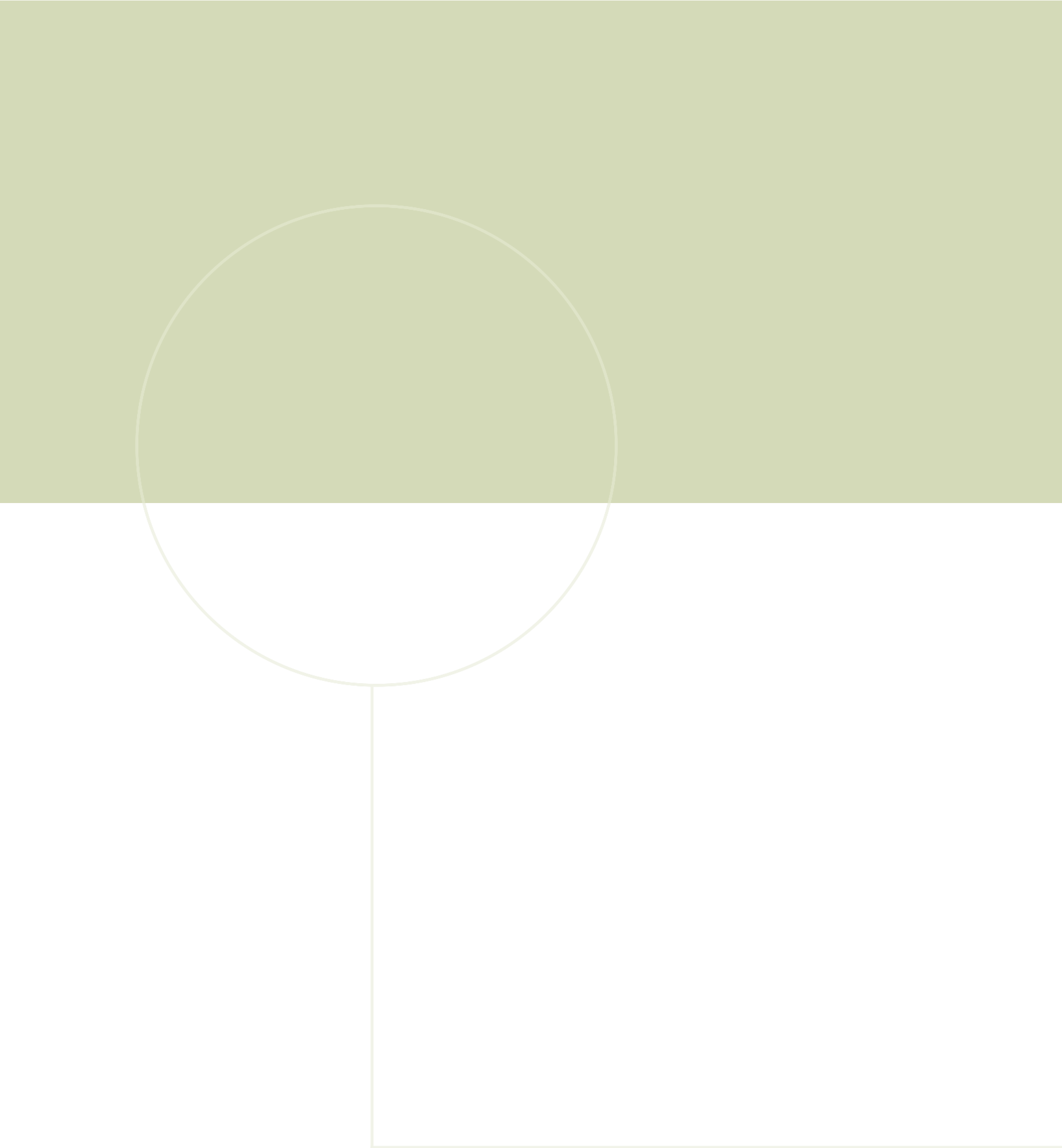
2016	*Potentilla erecta* (Tepperot)	1.1155	0.15407	0.33443	1.87946
2016	*Rubus idaeus* (Bringebær)	-0.63288	0.14001	-1.36198	0.10692
2016	*Salix sp_* (Vier)	-0.84748	0.1453	-1.5896	-0.09158
2016	*Trientalis europaea* (Skogstjerne)	-0.08034	0.13344	-0.79561	0.63636
2016	*Vaccinium myrtillus* (Blåbær)	0.26962	0.13454	-0.45188	0.98637
2016	*Vaccinium vitis-idaea* (Tyttebær)	-0.04107	0.13336	-0.75646	0.67505
2019	*Agrostis capillaris* (Engkvein)	0.37485	0.13568	-0.35074	1.0939
2019	*Athyrium filix-femina* (Skogburkne)	-0.96556	0.14887	-1.71655	-0.19923
2019	*Avenella flexuosa* (Smyle)	0.66155	0.14063	-0.08019	1.39215
2019	*Calluna vulgaris* (Røsslyng)	-0.3228	0.13507	-1.04058	0.40064
2019	*Chamaepericlymenum suecicum* (Skrubbær)	-0.03342	0.13335	-0.74885	0.68261
2019	*Deschampsia cespitosa* (Sølvbunke)	-0.01197	0.13334	-0.72755	0.70382
2019	*Empetrum nigrum* (Krekling)	0.12257	0.13358	-0.5949	0.83788
2019	*Epilobium angustifolium* (Geitrams)	-1.41167	0.16655	-2.20643	-0.59691
2019	*Gymnocarpium dryopteris* (Fugletelg)	-0.95415	0.14851	-1.70423	-0.18888
2019	*Linnaea borealis* (Linnea)	-0.2185	0.13413	-0.93451	0.50138
2019	*Luzula pilosa* (Hårfrytle)	0.33562	0.13521	-0.38832	1.05369
2019	*Maianthemum bifolium* (Maiblom)	0.60901	0.13951	-0.12924	1.33692
2019	*Melampyrum pratense* (Stormarimjelle)	0.71946	0.14196	-0.02638	1.45332
2019	*Melampyrum sylvaticum* (Småmarimjelle)	-0.4209	0.13629	-1.14129	0.3068
2019	*Potentilla erecta* (Tepperot)	0.77395	0.14332	0.02398	1.51114
2019	*Rubus idaeus* (Bringebær)	-0.80245	0.14407	-1.5415	-0.05023
2019	*Salix sp_* (Vier)	-0.15385	0.13373	-0.86929	0.56431
2019	*Trientalis europaea* (Skogstjerne)	0.38074	0.13575	-0.34511	1.09995

2019	*Vaccinium myrtillus* (Blåbær)	-0.18703	0.13392	-0.90271	0.53196
2019	*Vaccinium vitis-idaea* (Tyttebær)	-0.14536	0.13369	-0.86075	0.57261

Table A5: Model coefficients and corresponding p value and confidence interval per species

Species	**estimate**	**pval**	**ci.lb**	**ci.ub**
Blechnum spicant (Bjønnkam)	-3.9164	0.0504	-7.8404	0.0075
Calamagrostis phragmitoides (Skogrøyrkvein)	-3.2294	0.1011	-7.0901	0.6313
Epilobium angustifolium (Geitrams)	-2.9296	0.491	-11.267	5.4078
Empetrum nigrum (Krekling)	-2.5484	0.1969	-6.4192	1.3223
Solidago virgaurea (Gullris)	-2.0931	0.2355	-5.5511	1.3649
Phegopteris connectilis (Hengeving)	-1.9501	0.3641	-6.1618	2.2616
Deschampsia cespitosa (Sølvbunke)	-1.9379	0.0672	-4.0133	0.1374
Trientalis europaea (Skogstjerne)	-1.9151	0.0361	-3.7056	-0.1245
Luzula pilosa (Hårfrytle)	-1.4032	0.3958	-4.6421	1.8357
Melampyrum pratense (Stormarimjelle)	-0.8758	0.1903	-2.1863	0.4347
Melampyrum sylvaticum (Småmarimjelle)	-0.7945	0.5504	-3.4018	1.8128
Calluna vulgaris (Røsslyng)	-0.7608	0.3891	-2.4921	0.9705
Maianthemum bifolium (Maiblom)	-0.4356	0.6602	-2.3777	1.5065
Molinia caerulea (Blåtopp)	-0.2982	0.8529	-3.4496	2.8532
Rubus idaeus (Bringebær)	-0.0159	0.9909	-2.7483	2.7165
Avenella flexuosa (Smyle)	0.1669	0.8001	-1.125	1.4589
Vaccinium myrtillus (Blåbær)	0.425	0.5134	-0.8495	1.6995
Potentilla erecta (Tepperot)	0.6597	0.6762	-2.4361	3.7556

Vaccinium vitis-idaea (Tyttebær)	0.8729	0.1801	-0.4035	2.1494
Linnaea borealis (Linnea)	1.0769	0.3723	-1.2888	3.4427
Chamaepericlymenum suecicum (Skrubbær)	1.5096	0.6254	-4.5507	7.5699
Equisetum sylvaticum (Skogsnelle)	1.5951	0.4562	-2.6005	5.7907
Gymnocarpium dryopteris (Fugletelg)	1.6513	0.1885	-0.8099	4.1125
Vaccinium uliginosum (Blokkebær)	2.2348	0.036	0.1455	4.3242
Carex sp (Starr)	3.2859	0.0817	-0.4141	6.9859
Dryopteris expansa (Sauetelg)	5.7965	0.0181	0.9902	10.6028



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