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# To ban or not to ban? Spatial and temporal effects of banning long-term supplementary feeding on red deer space use, forest browsing damage and the performance and nitrogen content of bilberry plants

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# Abstract

Supplementary feeding (i.e. diversionary feeding) of red deer (*Cervus elaphus*) and other cervids is a widespread tool in wildlife management in Europe and North America. In 2016 supplementary feeding was banned in Norway to prevent the lethal Chronic Wasting Disease (CWD) from spreading. The main objective of this study was to assess the effects the ban on long-term supplementary feeding has on the forest ecosystem. I predicted that: H1) the spatial distribution of the red deer was more spread after the ban than before; H2) browsing damage on young trees would be more evenly spread after the ban. H3) bilberry (*Vaccinium myrtillus*) cover and height was lower at the feeding site centres because of high deer densities and the long-term supplementary feeding activity; and lastly H4) forage remains and deer feces at the feeding sites have caused higher N levels in bilberry plants. The predictions were tested by investigating five previously active supplementary feeding sites in the county of Vestland.

Although, as expected (H1), my results showed that deer density at the centre of the feeding sites was 35 % lower after the feeding had stopped, a lagging effect from the long ongoing feeding activity was still present. Contrary to what I expected (H2), browsing damage did not significantly differ as the average percentage of browsed trees was 42 % before and 47 %, after the ban respectively. Further, there was 15 % less browsing damage at 350 – 400 m from the feeding site compared to the centre. At 750 m, browsing damage had increased and was 20 % higher than at 350 – 400 m again. In accordance with what I predicted (H3), the average bilberry cover increased from 79 % to 93 % with increased distance to the feeding site, whilst average ramet height increased from 13 cm to 17 cm in the same distance interval (0 – 750 m). In contrast to what I expected (H4), the decomposing forage and deer feces at the feeding sites had no significant effect on N levels in bilberry plants as the only factors affecting N concentration were canopy openness (i.e. available light), fruit production (i.e. berries per $m^2$) and bilberry cover. These factors explained 41 % of the variation in bilberry leaf N. Nevertheless, the centres of the feeding sites were dominated by N demanding graminoids and stinging nettles (*Urtica dioica*), indicating a clear fertilizing effect on the overall field layer vegetation, and that bilberry gets outcompeted under N rich conditions.

My results suggest that the ban on supplementary feeding and the long-term feeding activity have affected the forest ecosystem surrounding the feeding sites, both spatially and temporally, and that the effects are still present even after feeding stopped. These effects could be seen both in case of changed in space use by the red deer and the forest vegetation surrounding the previously active feeding sites.

# Sammendrag

Tilleggsfôring (avledningsfôring) av hjort (*Cervus elaphus)* og andre hjortedyr er et utbredt verktøy i viltforvaltning i Europa og Nord-Amerika. I 2016 ble tilleggsfôring forbudt i Norge for å hindre spredningen av den dødelige skrantesjuken (CWD). Hensikten med denne studien var å vurdere effektene forbudet mot tilleggsfôring har på skogøkosystemet. Jeg predikerte at: H1) den romlige fordelingen av hjorten var mer spredt etter forbudet enn før; H2) beiteskader på unge trær ville være jevnere spredt etter forbudet. H3) dekning og høyde av blåbærplanter (*Vaccinium myrtillus*) var lavere ved fôringsplassenes sentre på grunn av høye hjortetettheter og den langvarige fôringsaktiviteten; og til slutt H4) fôrrester og avføring på fôringsplassene har forårsaket høyere N-nivåer i blåbærplanter. Prediksjonene ble testet ved å undersøke fem tidligere aktive fôringsplasser i Vestland fylke.

Selv om resultatene mine, som forventet (H1), viste at hjortetettheten ved sentrum av fôringsplassene var 35% lavere etter at fôringen hadde stoppet, var det fortsatt en etterslepende effekt fra den langvarige fôringsaktiviteten. I motsetning til hva jeg forventet (H2), var ikke beiteskadene signifikant forskjellige før og etter forbudet, ettersom den gjennomsnittlige prosentandelen av beita trær var henholdsvis 42% før og 47% etter forbudet. Videre var det 15% mindre beiteskader 350 – 400 m fra fôringsplassen sammenlignet med sentrum av stasjonen. Ved 750 m var beiteskadene 20% høyere enn ved 350 – 400 m igjen. I samsvar med hva jeg predikerte (H3), økte gjennomsnittlig blåbærdekke fra 79% til 93% med økt avstand til fôringsplassen, mens gjennomsnittlig plantehøyde økte fra 13 cm til 17 cm i samme avstandsintervall (0 – 750 m). I motsetning til hva jeg forventet (H4), hadde fôrrestene og avføringen på fôringsplassene ingen signifikant effekt på N-nivåene i blåbærplantene, da de eneste faktorene som påvirket N-konsentrasjonen var kronetetthet (dvs. tilgjengelig lys), fruktproduksjon (dvs. bær per $m^2$) og blåbærdekke. Disse faktorene forklarte 41% av variasjonen i N-innhold i blåbærblad. Til tross for dette var fôringsplassene dominert av N krevende graminoider og brennesle (*Urtica dioica*), noe som indikerer en klar gjødslingseffekt på den generelle feltvegetasjonen, og at blåbær blir utkonkurrert under N-rike forhold.

Resultatene mine tyder på at forbudet mot tilleggsfôring og den langvarige fôringsaktiviteten har påvirket skogøkosystemet rundt fôringsplassene, både i rom og tid, og at effektene fortsatt er til stede selv etter at fôringen har opphørt. Disse effektene kunne sees både i form av endringer i områdebruken av hjort og skogsvegetasjon rundt de tidligere fôringsplassene.

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# 1 Introduction

Forest ecosystems are complex and show big structural diversity in both spatial and temporal context. These large variations may be due to both direct (e.g. habitat change) and indirect (e.g. climate change) effects of environmental changes as well as different silvicultural approaches and forest management strategies (D'Amato et al., 2011; McElhinny et al., 2005). Ungulates are an important part of forest ecosystems, and can shape the complexity in forest ecosystems by directly affecting the species composition or by indirectly affecting nutrient cycling and net primary production (Hobbs, 1996; Rooney & Waller, 2003; Weisberg & Bugmann, 2003).

Changes in both climate and land use have caused red deer (*Cervus elaphus*) populations to increase rapidly throughout Europe the last decades (Milner et al., 2006; Mysterud et al., 2002; Mysterud et al., 2003). This is concerning for forest management and conservation as dense cervid populations can have negative effects on economically important tree species and biodiversity (Mysterud, 2006; Thorvaldsen et al., 2010). Red deer is an intermediate feeder which shows a clear selectivity of forage type throughout the year (Hofmann, 1989). During the growing season, red deer show a clear preference for nutrient rich forage such as graminoids (e.g. timothy grass (*Phleum pratense*)) (Langvatn & Hanley, 1993). Whereas during winter, when nutrient rich forage is not as accessible, the diet mainly consists of twigs and shoots from woody species (e.g. young trees and shrubs) (Schröder, 1977). Red deer have also been shown to be among the main drivers of tree species composition and forest recruitment in European mixed forests (Klopcic et al., 2010). Thus, red deer can have a large impact on the forest vegetation (Hegland & Rydgren, 2016).

Supplementary feeding is a commonly used wildlife management practice in Europe and North America (Milner et al., 2014; Putman & Staines, 2004). Often the purpose of laying out additional winter forage is to maintain or increase animal densities, body weight and overwinter survival (Peterson & Messmer, 2007). Supplementary feeding can also be used to lure animals away from undesired places (i.e. diversionary feeding), for example to reduce traffic accidents with wildlife or to reduce damage on agriculture fields or economically important forest stands (Arnold et al., 2018; Putman & Staines, 2004). Irrespective of the purpose, supplementary feeding will alter space use of red deer and aggregate many animals on a relatively small space (reviewed by Putman & Staines, 2004). Supplementary feeding sites can have a large impact on the habitat selection and space use of red deer between summer and winter, as deer strongly select for areas around feeding sites during winter (Arnold et al., 2018). Gathering large amounts of animals in one area may lead to elevated stress and increased browsing impact on the forest vegetation (reviewed by Putman & Staines, 2004). A study on moose (*Alces alces*) from southern Norway showed that the forest vegetation was affected by supplementary feeding, as the animals severely foraged on the vegetation surrounding feeding sites (van Beest et al., 2010). This effect has also been shown for other members of the cervid-family (e.g. red deer, roe deer (*Capreolus capreolus*) and elk (*Cervus e. canadensis*)) across Europe and North America (Jerina et al., 2008; Putman & Staines, 2004; Schmidt, 1991; Ueckermann, 1983). High browsing pressure by moose around supplementary feeding sites might be related to nutrient balancing (e.g. high quality silage vs. fibrous tree browse) of the animals' diet as they try to achieve a specific nutritional target (Felton et al., 2017). Also red deer strive to balance their diet by foraging on woody plants around supplementary feeding sites (Miranda et al., 2015). Furthermore, supplementary feeding in an area can be contra productive as it can increase the animals carrying capacity, resulting in unsustainably high animal populations and high levels of browsing damage at landscape scale (1-10 km) (Mathisen et al., 2014).

The space use of deer typically differs between foraging and resting areas (Ager et al., 2003), by feeding in one area and resting in another, they can act as vectors for nutrient distribution in the landscape (Abbas et al., 2012). Thus, nutrients will not be evenly spatial distributed (Harrison et al., 2004). Nitrogen (hereafter N) provided by cervid feces can have a fertilizing effect in forest ecosystems (Kamler et al., 2003). A study from Louisiana showed that feces from American white-tailed deer (*Odocoileus virginianus*) that visited feeding sites contained higher levels of N than feces from naturally foraging deer (Johnson et al., 1987). Thus, supplementary feeding sites may present nutrient hotspots as feces and remaining forage aggregate and decompose at the feeding sites, resulting in nutrient leaching to the surrounding area. Increased levels of N input can affect the forest ground vegetation by changing the competitive interactions between species, thus altering species composition and lead to biodiversity changes (Nordin et al., 2005).

Bilberry (*Vaccinium myrtillus*) is an ecological keystone species in boreal forest ecosystems as it is considered to play an important role as food source for many animal species in the forest (Nilsson & Wardle, 2005; Nybakken et al., 2013; Selås et al., 2011). Increased amounts of nutrients, as presumably can be found around feeding sites, can increase N levels in shoots of bilberry plants (Selås et al., 2011). Herbivores seem to prefer bilberry plants with high nutrient content (Fernández-Calvo & Obeso, 2004), as the amount of amino acids increases and the concentration of condensed tannins decreases with higher levels of nutrient content (Ohlson et al., 1995; Strengbom et al., 2003). Although bilberry may not be a dominant food plant, it is shown that bilberry plants play an important role in the winter forage composition of red deer (Hegland et al., 2005). Both, Mathisen et al. (2010) and Hegland et al. (2005) found that cervid browsing negatively affected the reproduction and ramet size (e.g. ramet height) in the field layer vegetation. Despite this, bilberry is also shown to be quite resilient to browsing as it shows greater ability of regrowth than other dwarf-shrubs, depending on multiple factors (e.g. light availability) (Hegland et al., 2010; Hegland & Rydgren, 2016). Furthermore, forest structure (i.e. stand density and age) is shown to be of great importance for the cover of bilberry in the field layer vegetation (Hedwall et al., 2013). Bilberry prefers semi-light conditions as found in older development classes, and has been shown to be sensible to changes in light irradiation due to for example forestry activities (Atlegrim & Sjöberg, 1996; Parlane et al., 2006).

In 2016 the first cases of the prion disease Chronic Wasting Disease (CWD) were confirmed in wild reindeer (*Rangifer tarandus*) and moose (*Alces alces*) in Norway (Benestad et al., 2016). This highly mortal disease has been known to affect captive and wild living cervids in North America during the last decades (Williams & Young, 1980; Williams et al., 2002). CWD can be directly transmitted between individuals by body fluids and animal droppings (i.e. blood, saliva, urine and feces) or indirectly through contaminated environments (Mathiason et al., 2006). Hence, supplementary feeding sites may present hotspots for CWD spreading (Sorensen et al., 2014). To prevent the spreading of CWD in Norway, supplementary feeding became banned in July 2016 (*Forskrift om tiltak for å begrense spredning av CWD*, 2016).

The effects of supplementary feeding of red deer and other cervids on forest ecosystems whilst feeding sites are in use is relatively well documented (Arnold et al., 2018; Mathisen et al., 2014; Putman & Staines, 2004). Whereas to my knowledge, the effects after feeding is stopped are relatively unknown. The latter is highly relevant as banning supplementary feeding can play a vital role in preventing CWD from spreading, and thus may be more implicated in future wildlife management practices.

The main objective of this study was to assess the plant – herbivore interactions in a semi-natural setting by identifying the effects the ban on supplementary feeding and the long-term feeding activity has had on the surrounding forest vegetation. This was done by comparing data on red deer space use, browsing damage to young trees and bilberry performance (i.e. ramet height and cover) two years before (2014) (Sjöblom, 2015) and two years after (2018) the ban on supplementary feeding. In addition, I investigated if supplementary feeding (i.e. decomposing of remaining forage and aggregated red deer feces) has had a fertilizing effect on the bilberry plants in the studied forest ecosystem.

I hypothesized that the forest ecosystem surrounding the feeding sites was affected, spatially and temporally, by both the ban on supplementary feeding and the long-term feeding activity in the area. Based on this general hypothesis I predicted that: H1) red deer would change their use of the areas around the feeding sites compared with the time before the ban, i.e. be more evenly distributed along the distance gradient from feeding sites; H2) the proportion of young trees browsed would be more evenly distributed across the landscape after feeding was prohibited. H3) bilberry cover and ramet height would be lower close to previously active feeding sites as a result of high deer density and high browsing pressure over long time; and lastly that H4) the long-term feeding has led to increased N levels in bilberry plants as a result of a fertilizing effect of decomposing forage remains and aggregation of feces close to the previous feeding sites.

# 2 Materials and methods

## 2.1 Study area

The study was conducted over a period of two weeks in July 2018 in Kaupanger in the western Norwegian county of Vestland (UTM32 6784713N 405257E) (Figure 1). Kaupanger is located in the inner part of the Sognefjord. The study area is situated in the border area between the southern boreal- and the boreonemoral zone and the local climate can be characterized as slightly continental (Moen & Lillethun, 1999). Climate data from weather stations in and around my study area (Lærdal IV and Sogndal Lufthavn) report that the mean temperature in the period 2003 – 2019 for December ranged between -6.2 °C and 1.7 °C, whereas the mean temperature in June ranged from 12.4 °C to 15.6 °C. The annual mean precipitation in the area for the period 2003 – 2019 ranged from 541 mm to 939 mm (KSS, 2020). As in 2014, also the summer of 2018 showed a higher average temperature than normal, the average temperature in June was about 2 °C to 3 °C above normal for both 2014 and 2018 in the study area (KSS, 2020).

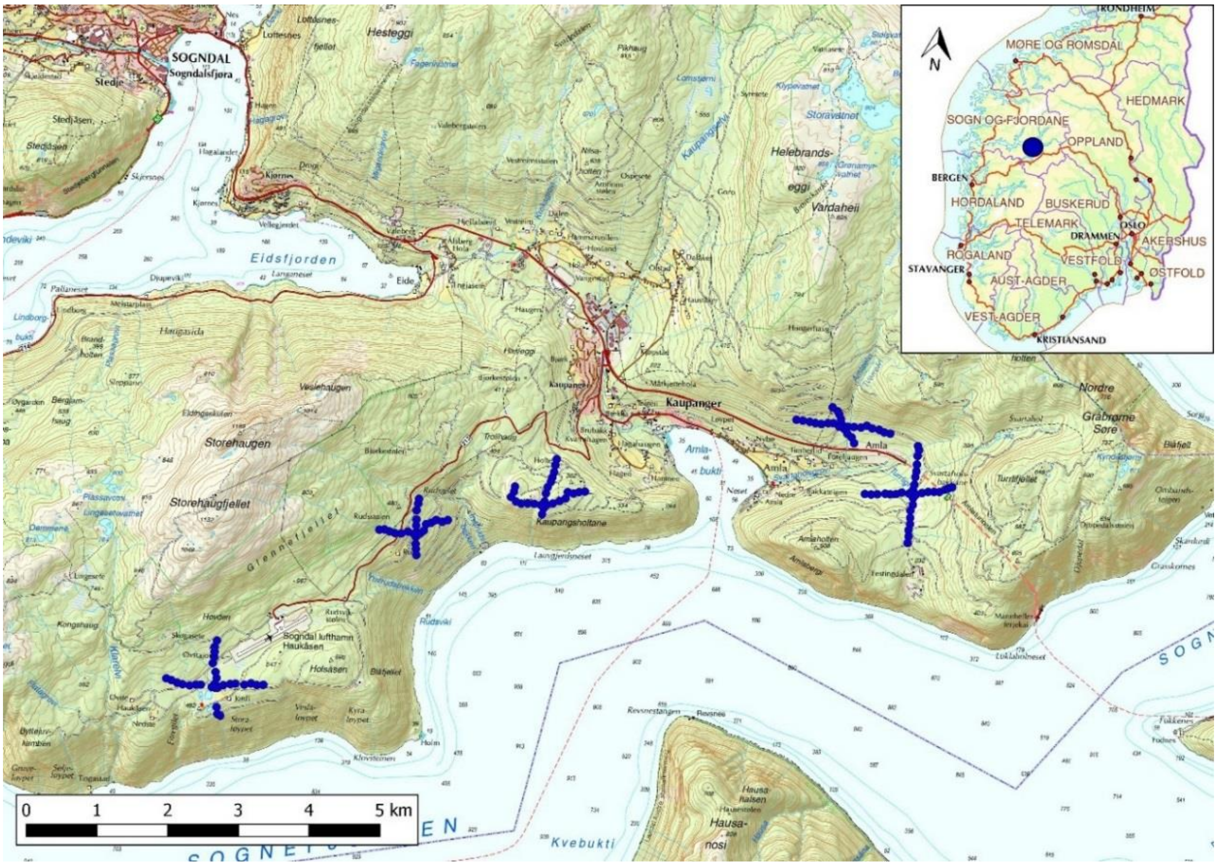

**Figure 1:** Overview over the study sites in Kaupanger with the individual sampling plots marked in blue showsing the transects in the cardinal directions (N,S,E and W) and feeding sites in the centre of the crosses.

The landscape in the study area is typical for the fjord-landscape of western Norway and is characterized by steep slopes which lead from the mountainous alpine region's trough the south boreal and boreonemoral forests and down into the fjords. This type of topography lead to great climatic gradients from the fjord to the highest mountains (1500 m.a.s.l.). My study plots ranged from 150 – 540 m.a.s.l, thus only covering a relatively narrow spectre of the altitudinal gradient in the area. Due to the natural variations in topography and small-scale climate, the forest vegetation is complex (Jones, 2008). The forest stands in the study area mainly consist of conifers such as scots pine (*Pinus sylvestris*) and some Norway spruce (*Picea abies*) (Figure 2). Mixed conifer – deciduous stands with tree species such as birch (*Betula spp*), rowan (*Sorbus aucuparia*), and alder (*Alnus spp*) within the dominating scots pine are represented. The understorey vegetation mainly consists of young coniferous and deciduous trees, whereas the field-layer vegetation is dominated by bilberry, crowberry (*Empetrum nigrum*), cowberry (*Vaccinium vitis-idaea*) and bryophytes (e.g. *Pleurozium schreberi*). In the centre of the old supplementary feeding sites and on open areas such as old clearcuts, graminoids (e.g. *Avenella flexuosa*) dominate the field layer (Figure 2).

Red deer are very abundant in the area, and the yearly red deer harvest is about 1.1 animals/km$^2$ in Sogndal[1] municipality for the last years (Hjorteviltregisteret, 2019; Sogndal Kommune, 2017). Furthermore, the Kaupanger peninsula is one of the most important winter areas for the deer in the area (Hegland pers. comm., 2020). Supplementary feeding in Kaupanger started in the middle of the 1990's with the purpose to concentrate deer on a smaller space, and thus limit the amount of deer induced damage to forest stands, and to divert deer away from the crossing highway to reduce deer-vehicle collisions (Hegland pers. comm., 2018). Later feeding ended with the ban in 2016 (Hegland pers. comm., 2018).

**Figure 2:** Pictures from the study area in Kaupanger, showing a typical clear-cut area on the left and the centre from one of the previous feeding sites on the right. (Photo: Maximilian Zimmermann)

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[1] It is here referred to the old Sogndal municipality (before 1st Jan 2020).

## 2.2 Study design

This study is a resampling of the same plots investigated by a master thesis in natural resource management at the Norwegian University of Life Sciences (NMBU) completed in 2015 (Sjöblom, 2015), and the dataset from this thesis was provided for further analyses (Sjöblom pers. comm., 2018). All plots had decimal degree coordinates obtained in 2014 (Sjöblom pers. comm., 2018). In order to find the position of the plots in the field, a hand-held GPS unit (GARMIN ASTRO 320) was used. To correct for possible GPS error, the last 10 m were walked up using a compass for guidance. The data collection was based on five different supplementary feeding sites, where the deer had been fed with round bale silage throughout the winter months (November – March) from ca 1995 to 2016 (Figure 1; Figure 2). Transects of up to 750 m length were placed in all cardinal directions (North, South, East and West) with sampling plots every 100 m along the transects. The feeding site itself had one plot in the centre and additionally one plot 50 m from the centre in each cardinal direction. This is because the forage was spread out in an approximately 50 m radius to prevent the deer from competing too much over the forage at the feeding site. The plots were 4 m in radius giving a total area of 50 $m^2$ per plot. Furthermore, each plot consisted of three subplots with an area of 0.25 $m^2$ (Figure 2). The location of the subplots was established by randomly throwing a stick within the perimeter of the plot. In case the position of the subplots interfered with an obstacle (e.g. trees or stones etc.), the location was adjusted by 0.5 m away from the obstacle.

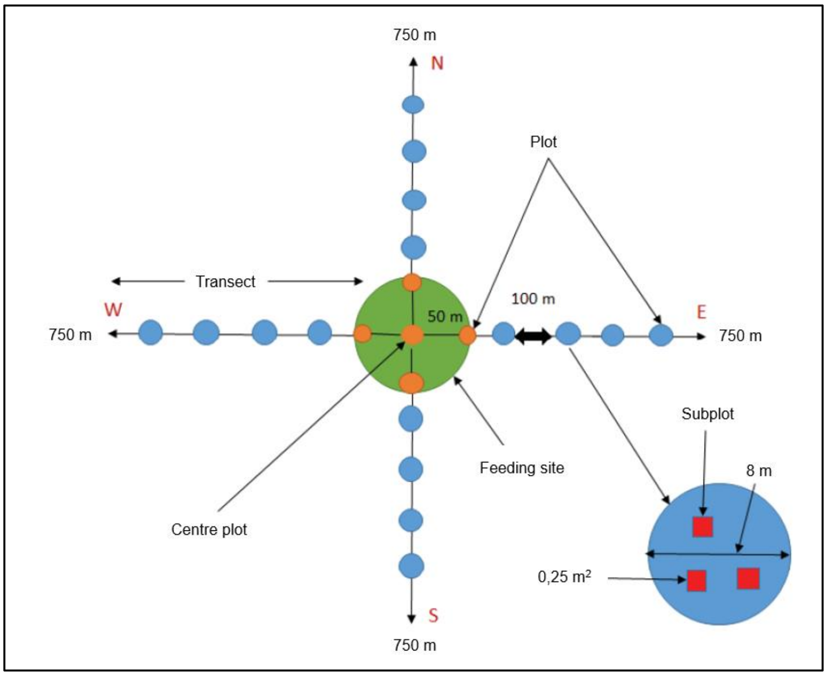

**Figure 3:** Sketch of the transects, plots and subplots used at each of the five studied feeding sites (adapted from Sjöblom, 2015).

## 2.3 Data collection

### 2.3.1 General forest variables

At each plot location, several general habitat and forest characteristics that were thought to be proxies for red deer space use (H1), browsing damage (H2), bilberry performance (H3) and/or N levels in bilberry leaves (H4) were registered. Distance from feeding site and altitude at each plot were obtained from the 2014 dataset (Sjöblom pers. comm., 2018). Slope (in °) and aspect (N, S, E and W) were registered by using a clinometer (Suunto PM-5/360 PC Clinometer) and the handheld GPS-unit, respectively. Forest stand characteristics such as site-index (H40-system) (Tveite & Braastad, 1981), development class (Table 1), basal area (in $m^2$/ha) and canopy openness (in %) were registered. Site-index and development classes were obtained from forestry management plans for the properties (Foran Norge, 2012). Basal area was registered using a relascope (Järvis, 2013), and canopy openness was measured as a proxy for available light for the understorey vegetation using a densiometer (Lemmon, 1956).

**Table 1:** Definition of development classes in forest, according to Norwegian forestry practice.

| Development class | Definition |
|---|---|
| I | Clear-cut |
| II | Young forest |
| III | Younger production forest |
| IV | Older production forest |
| V | Mature forest |

### 2.3.2 Deer density and space use

Counting fecal pellet groups is commonly used practice to obtain an index of deer density in an area when direct counting of individual animals is difficult (Bennett et al., 1940; Forsyth et al., 2007; Marques et al., 2001). In order to obtain an estimate of red deer density and space use around the previously active feeding sites (H1), I counted pellet groups within each plot along the transects. Pellet groups were defined as clearly distinguishable “piles” containing more than 15 individual pellets.

### 2.3.3 Browsing damage and species composition of young trees

To investigate whether the browsing damage had changed after the feeding became banned or not (H2), the total number of small trees (5 – 300 cm) where counted and assessed for browsing damage at each plot. Each tree was categorized into one of six species categories (Scots pine, Norway spruce, Alder spp., Birch spp., Rowen and "Others"). These were then further classified into four different browsing categories (Table 2). In 2014, the browsing impact upon young trees was only measured as a total number of browsed and un-browsed trees for each species at each plot without any further classification. In order to compare the data sampled in 2018 with the 2014-data, the total number of browsed and un-browsed trees per plot in 2018 was established by summing all trees categorized as B2-B4 and B1 respectively.

**Table 2:** Categories for browsing damage on young trees (5-300 cm)

| Browsing index | Category description | % of shoots browsed |
|---|---|---|
| B1 | Undamaged | 0 % |
| B2 | Lightly browsed | 1-33 % |
| B3 | Medium to heavily browsed | 34 -100 % |
| B4 | Dead due to browsing | |

### 2.3.4 Bilberry performance

To assess whether bilberry cover and ramet height were affected by the deer density and the long-term feeding activity (H3), I quantified bilberry cover (i.e. ground covered by bilberry ramets) (as a binary proportion between 0 and 1) and height of bilberry ramets (in cm) were measured at subplot level. In order to estimate bilberry cover, each subplot was divided into a 4 x 4 grid and the frequency (0-16) of bilberry ramet presence was counted. If bilberry ramets were present in half of the grid the frequency was noted as eight (proportional cover = 0.5), and if they were present in all grids the frequency was noted as sixteen (proportional cover = 1). The results at subplot level were then averaged to obtain an average bilberry cover at plot level. At each subplot the height from ground level to the highest point of four ramets (one in each of the four corner squares of the measuring grid) was measured using a folding ruler. All height measurements were averaged to obtain a mean value for ramet height at plot level.

Additionally, I counted the total number of berries, both ripe and unripe, at subplot level. To avoid zeroes in the dataset all berries from all three subplots were added together and then multiplied by a factor of 1.33 in order to get an estimate of the total berry production per $m^2$ (i.e. fruit production per $m^2$).

### 2.3.5 Bilberry leaf analysis

To assess if the supplementary feeding sites have had any fertilizing effects on the bilberry plants (H4), the carbon (hereafter C) and N concentrations as well as the C/N-ratio in bilberry leaves were analyzed. Samples were taken at the center plot of each feeding site as well as the two extremes (closest and furthest plot in relation to the feeding site) at each transect. At each plot, three bilberry samples were taken, one from each subplot. The sample ramets were chosen randomly within each subplot. The leaves were stripped of and put into a paper envelope prepared with silica granulate to prevent the samples from decaying. After each day in the field the closed envelopes were laid out individually on a dry and airy place for further drying. When the field work period was done, the samples were packed and stored until December 2018 when they were analyzed. Although the samples were dry, they were dried at 30 °C for 24 hours to ensure a homogenous moisture content before analyzing. The final analyses were done by milling the plant samples to fine powder using a Retsch MM400 ball mill (Retsch, Haag, Germany). About 5-6 mg of the powder was then transferred into a small tin foil container and analyzed using a Micro Cube (Elementar Analysen, Hanau, Germany), C and N concentrations were then reported as % of dry matter.

## 2.4 Data analysis

All data analyses were done with the statistical software R (R Development Core Team, 2020). Mixed-effect regression models were fitted to investigate red deer space use (pellet counts) (H1), browsing damage (proportion of browsed trees per plot) (H2) and bilberry performance (H3) using the glmer and lmer functions in the lme4-package (Bates et al., 2008). Bilberry leaf N concentration (H4) was analyzed by using linear regression. Data exploration was performed as described in Zuur et al. (2010). I visually checked for outliers in the dataset using Cleveland dot plots (Zuur et al., 2010), and clear outliers, when detected, were removed from the data. In accordance to Zuur et al. (2010), outliers were defined as observations with a relatively small or large values compared to the rest of the dataset. Correlation matrixes were made for comparing continuous explanatory variables in order to check for collinearity. When correlation values between variables exceeded 0.6 or -0.6, I considered them to be collinear. Boxplots where used to visually assess collinearity between continuous variables and categorical variables.

During data exploration, I found that sampling method of bilberry fruit production differed between sampling years. I counted the total number of berries at each subplot, whereas in 2014 berries were counted on only four ramets at each subplot. Hence, these data were not comparable and fruit production was only used as an explanatory variable when analyzing 2018-data only. Furthermore, variables such as aspect, side index, basal area and development class were only sampled in 2018, hence these were only considered as candidate explanatory variables for analyses when using only 2018 data. The C/N ratio was depending mainly on variations in N concentration. Therefore, only analyses on N levels were performed.

To account for data dependency and pseudoreplication, the different feeding sites were fitted as random effects on the intercept in the mixed models for browsing damage (H2). The ratio between browsed and un-browsed trees was used as response variable, possible explanatory variables were ‘distance to feeding site’, ‘year (2018 vs. 2014)’, ‘canopy openness’, ‘deer density’, ‘bilberry cover’, ‘altitude’ and ‘slope’ and the model family was set to binomial. Also, for analyses on bilberry performance (H3), feeding sites were fitted as random effects on the intercept for both bilberry cover and ramet height models. Response variables were ramet height and bilberry cover, whereas potential explanatory variables were ‘distance to feeding site’, ‘year (2018 vs. 2014)’, ‘canopy openness’, ‘deer density’, ‘bilberry cover’ (only for ramet height models), ‘ramet height’ (only for bilberry cover models), ‘altitude’ and ‘slope’. The model families were set to binomial and gaussian for bilberry cover and ramet height models respectively. Whereas, for the analyses of red deer’s space use around the feeding sites (H1), the transects were used as random effects on the intercept by nesting them within feeding sites. This was done as the variance between the feeding sites was very close to zero ($s^2 = 1.0 \times 10^{-14}$) when using only feeding sites as random effects (Supplementary figure 1). Thus, giving problems with singularity. Number of pellet groups per plot as a proxy for deer density was used as response variable for the space use models and possible explanatory variables were ‘distance to feeding site’, ‘year (2018 vs. 2014)’, ‘canopy openness’ and ‘slope’ and model family was set to poisson.

For the linear regression analysis of N concentration in bilberry leaves (H4) the concentration of N in bilberry leaves (in % of dry matter) was used as response variable, whereas possible explanatory variables were ‘distance to feeding site’, ‘year (2018 vs. 2014)’, ‘deer density’, ‘bilberry cover’, ‘canopy openness’, ‘fruit production’, ‘basal area’, ‘development class’, ‘altitude’ and ‘slope’.

Continuous explanatory variables such as ‘distance to feeding site’, ‘canopy openness’, ‘slope’ and ‘altitude’ were scaled to improve model fitting and to prevent misinterpretations of the numerical results. By centering explanatory variables at their mean (i.e. scaling) it allows for direct comparison on effects imposed by continuous variables, especially when the models include interaction terms (Aiken et al., 1991).

To assess if the number of deciduous vs. coniferous trees differed along the distance gradient to the feeding sites in 2018, a negative binomial regression model was fitted using the glm.nb function in the MASS package in R (Ripley et al., 2019). Total count of trees, both browsed and un-browsed, was used as response variable, whereas ‘species type (coniferous vs. deciduous)’ and ‘distance to feeding site’ (as a factor) were fitted as explanatory variables in an interaction term.  Furthermore, to assess if there was a significant dependence between species types and browsing index (B1 – B4), a chi-squared test of independence was used ($H_{0:}$ Browsing index and species type are independent, $H_a$: Browsing index and species type are not independent). Although not the main focus of my thesis, these tests provided important information for a better understanding of the main results.

For all regression analyses, except the negative binomial regression model, a range of candidate models were fitted using different explanatory variables and combinations of these. Choosing explanatory variables for the models was done by comparing scatterplots showing the relationship of different explanatory variables and response variables. Further variable selection was based on logical and biological sense. Model selection was performed by using the model.sel function in the MuMIn-package (Barton, 2019). Selecting the most parsimonious models with the lowest corrected Akaike’s Information Criteria ($AIC_C$) to prevents overfitting when having small sample sizes (Hurvich & Tsai, 1989). When having multiple models with delta values close to the top model the simplest models with the least degrees of freedom (i.e. the most parsimonious model) where chosen. A significance level of $p = 0.05$ was chosen for all analyses.

For visualization of the regression models, I used graphic plotting functions in the Predictor Effects Graphics Gallery in the effects-package, sjPlot-package and ggplot2-package (Fox et al., 2019; Lüdecke, 2018; Wickham, 2020).

# 3 Results

## 3.1 Red deer space use around previous feeding sites (H1)

The space use of red deer decreased with increasing distance from the feeding sites during both years, although this effect was weaker after the ban on supplementary feeding compared to before. On average, the centres of the feeding sites were used 35 % less after the ban (Figure 4; Supplementary table 1). This was shown by the most parsimonious model to explain the variation in red deer space use around ously active feeding sites. The model included 'deer density' (number of pellet groups per plot) as response variable and 'distance to feeding site' ($\beta = -0.45349$, se = 0.0781, p-value = <0.001) and 'year (2018 vs. 2014)' ($\beta = 0.07086$, se = 0.10258, p-value = 0.490) together as an interaction term ($\beta = 0.26536$, se = 0.10531, p-value = 0.012; $\Delta$AICc = 0.00, df = 6) as explanatory variables. The second-ranked model ($\Delta$AICc = 0.72, df = 7) also had $\Delta$AICc < 2, but was discarded as the model formulation was more complicated.

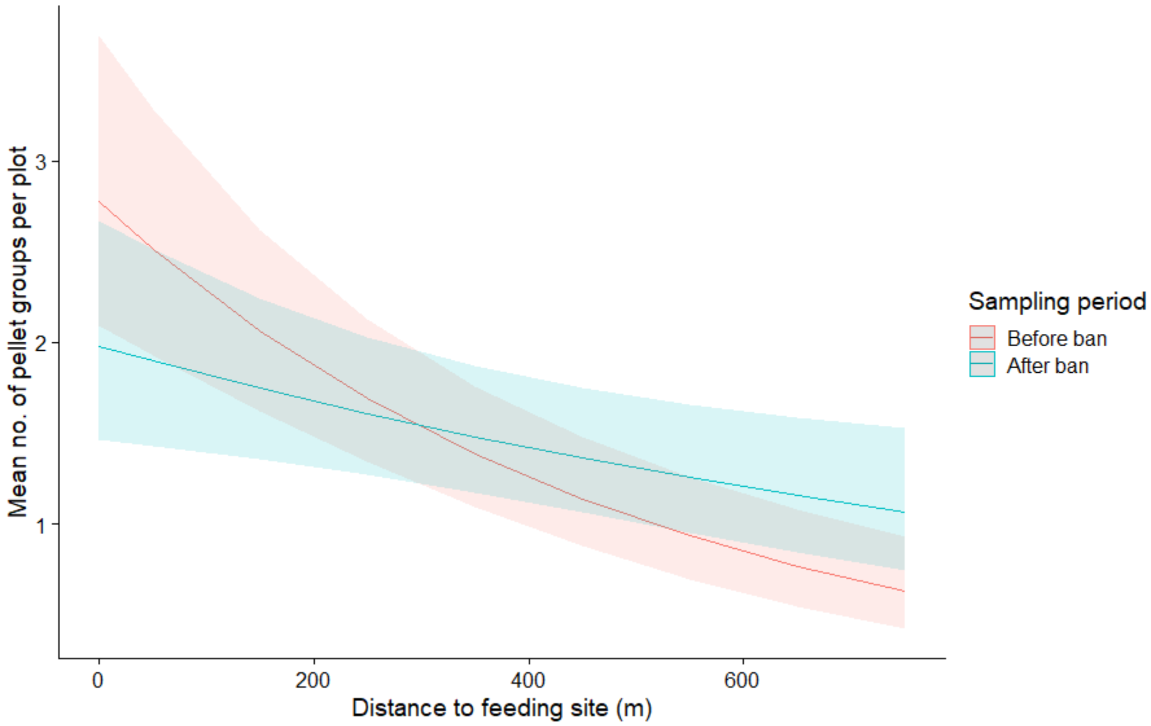

**Figure 4:** Predicted space use of red deer based on pellet counts around the supplementary feeding sites before (2014) and after (2018) the ban on supplementary feeding. The shaded area indicates 95 % confidence interval.

## 3.2 Browsing damage (H2)

The average percentage of trees that showed signs of browsing damage was relatively high, 42 % and 47 %, before and after the ban respectively. Despite the difference, 'year (2018 vs. 2014)' had no effect on browsing damage as it was discarded during the model selection process. The best model to assess red deer browsing damage around feeding sites included the ratio between browsed and un-browsed trees as response variable and 'distance to feeding site', 'canopy openness', 'deer density' and 'altitude' as explanatory variables ($\Delta$AICc = 0.00, df = 8). The second-ranked model ($\Delta$AICc = 0.34, df = 9) also had $\Delta$AICc < 2, but was discarded as the model formulation was more complicated. 'Distance to feeding site' ($\beta$ = 0.06008, se = 0.07400, p-value = 0.417) had a significant positive effect on browsing damage as a square term ($\beta$ = 0.24606, se = 0.07500, p-value = 0.001) (Supplementary table 2): Browsing damage at the centre (0-50 m) and at the point furthest away (750 m) from the feeding site was higher, 15 % and 20 % respectively, than at medium distances (350-400 m) (Figure 5). Although browsing damage was lowest at 350 – 400 m from the feeding site, still about 40 % of the trees showed signs of browsing (Figure 5).

Although not so relevant for answering H2, but still interesting, 'canopy openness' showed a highly significant negative effect on the browsing damage ($\beta$ = -0.48641, se = 0.06512, p-value = <0.001), indicating less browsing in open areas (Supplementary table 2). Furthermore, 'deer density' ($\beta$ = 0.05330, se = 0.03780, p-value = 0.159) and 'altitude' ($\beta$ = -0.19168, se = 0.14903, p-value = 0.198) showed a significant negative effect as an interaction term ($\beta$ = -0.14218, se = 0.04860, p-value = 0.003). Showing that browsing damage was generally higher at lower altitudes, especially when red deer densities were high (Figure 6; Supplementary table 2).

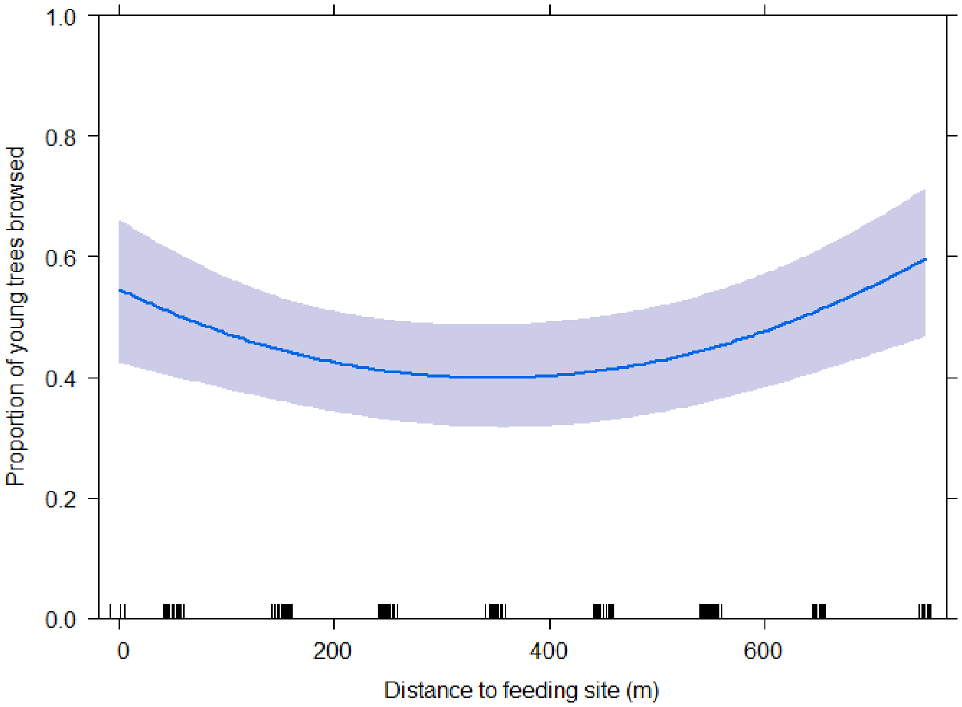

**Figure 5:** Predicted proportion of young trees (5 – 300 cm) browsed in relation to the distance to the closest supplementary feeding site (m). The shaded area indicates 95 % confidence interval.

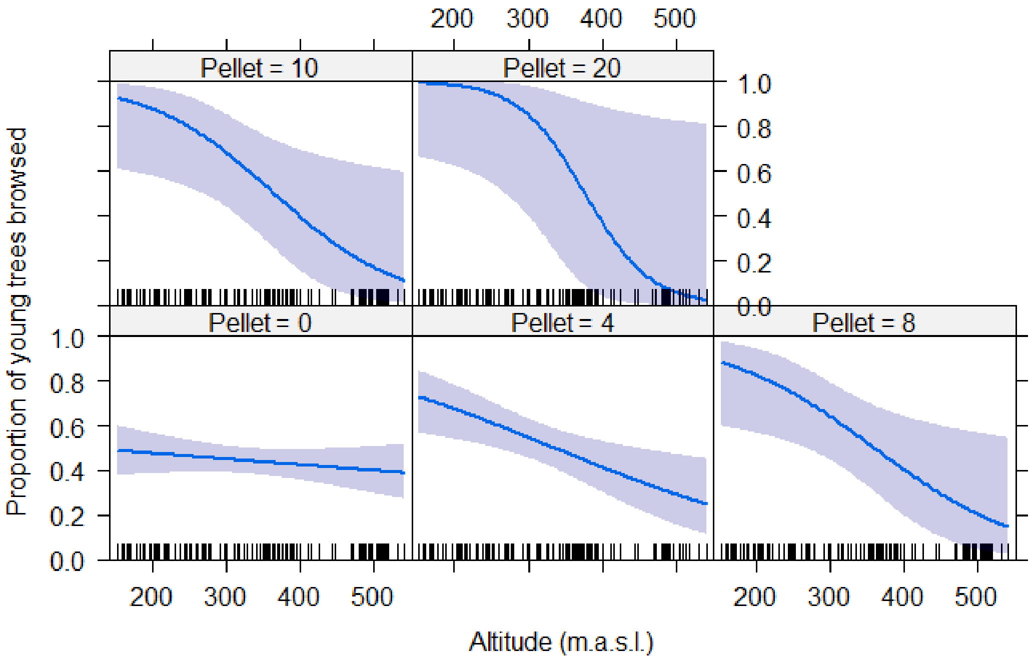

**Figure 6:** Predicted likelihood of proportional browsing damage on young trees at different deer densities (pellet densities) in relation to altitude (m.a.s.l.). The shaded area indicates 95 % confidence interval. For easier visualization of the effects of the interaction term, the mixed effects model from supplementary table 2 was refitted as a normal generalized linear regression model without random effects.

In 2018 the total number of trees at each distance away from the feeding site increased rapidly from 0 m to 150 m and decreased slowly after that out to 750 m (Figure 7). The ratio between coniferous and deciduous trees was relatively even in the interval from 50 m to 350 m away from the feeding site, whereas deciduous species dominated from 450 m to 750m (Figure 7; supplementary figure 2). The number of deciduous species peaked at 150 m and 450 m to the feeding site, whereas conifers only peaked at 150 m (supplementary figure 2). For estimates, standard errors and p-values see supplementary table 6 in Appendix I

Browsing index (B1-B4; see Table 2) and species types were not independent, meaning that there is a relationship between species type and browsing index. This was also shown by the chi-squared test ($\chi^2$ = 33.909, df = 3, p-value = <0.001). In total, deciduous trees were browsed three to four times as often as conifers for browsing indexes B2 and B3 (Supplementary figure 3). For browsing index B4, twice as many conifers were dead due to browsing compared to deciduous trees (Supplementary figure 3).

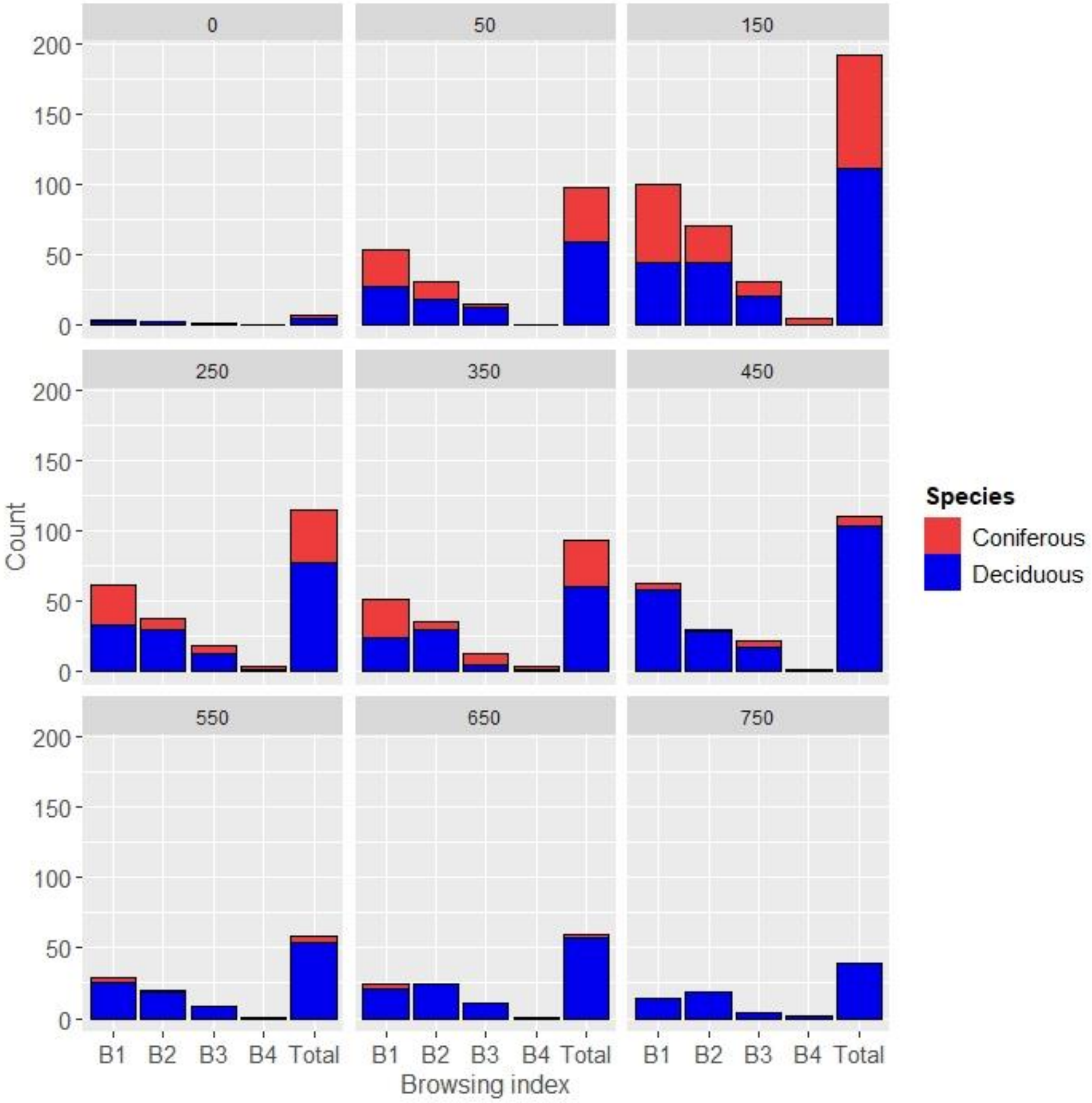

**Figure 7:** Number of coniferous (red) and deciduous (blue) trees for each browsing index B1 (not browsed), B2 (lightly browsed), B3 (medium to heavily browsed) and B4 (death by browsing) at each distance point away from the feeding site (0-750 m) in 2018.

## 3.3 Bilberry performance (H3)

### 3.3.1 Bilberry cover

The best model to explain bilberry cover in plots included bilberry cover as response variable and ‘distance to feeding site’, ‘year’, ‘deer density’, ‘altitude’, ‘canopy openness’ and ‘slope’ as explanatory variables (ΔAICc = 0.00, df = 9). The second-ranked model (ΔAICc = 45.06, df = 9) was not further evaluated as ΔAICc > 2. The average overall bilberry cover was significantly higher after the ban on feeding compared to before (β = 0.51906, se = 0.09471, p-value = <0.001; Supplementary table 3). It also increased significantly with increased distance to the feeding site (β = 0.38091, se = 0.05187, p-value = <0.001), from 79 % cover close to the feeding site to 93 % at 750 m from the site (Figure 8; Supplementary table 3). Furthermore, areas with high deer density had a highly significant positive effect on bilberry cover (β = 0.20472, se = 0.02722, p-value = <0.001) (Figure 8; Supplementary table 3).

Not relevant for H3, but still interesting. ‘Canopy openness’ (β = -0.09956, se = 0.05889, p-value = 0.091) and ‘slope’ (β = -0.12973, se = 0.05765, p-value = 0.024) had a highly significant positive effect on bilberry cover as an interaction term (β = 0.48745, se = 0.04802, p-value = <0.001): On steep slopes bilberry cover was highest under open canopies, in contrast to areas with gentle slopes where bilberry cover was highest under denser canopies (Supplementary figure 4). On average, the highest bilberry cover appeared to be present at approximately 37 % canopy openness (Supplementary figure 4).

### 3.3.2 Ramet height

Average ramet height did not differ before and after the ban as ‘year (2018 vs. 2014)’ was discarded in the model selection process. Instead, the most parsimonious model to explain bilberry ramet height included ramet height as response variable and ‘distance to feeding site’, ‘canopy openness’, ‘deer density’, ‘bilberry cover’ and ‘altitude’ as explanatory variables (ΔAICc = 0.00, df = 8). The second-ranked model (ΔAICc = 4.21, df = 8) was not considered as an alternative as ΔAICc > 2. In contrast to bilberry cover, ramet height was significantly negative affected of increased deer density (β = -0.4022, se = 0.1105, p-value = <0.001) (Figure 8; Supplementary table 4) as ramet height was 25 % lower in areas with high deer density compared to areas with low deer density. Average ramet height increased significantly from 13 cm at the feeding site to 17 cm at 750 m away from the feeding site (β = 1.2120, se = 0.2107, p-value = <0.001).

Furthermore, ‘bilberry cover’ (β = 6.7030, se = 0.8343, p-value = <0.001) and ‘altitude’ (β = 1.3332, se = 0.3341, p-value = 0.004) also effected bilberry ramet height positively (Figure 8; Supplementary table 4). ‘Canopy penness’ only showed a strong tendency of having a positive effect on bilberry ramet height (β = 0.4001, se = 0.2086, p-value = 0.056; Supplementary table 4).

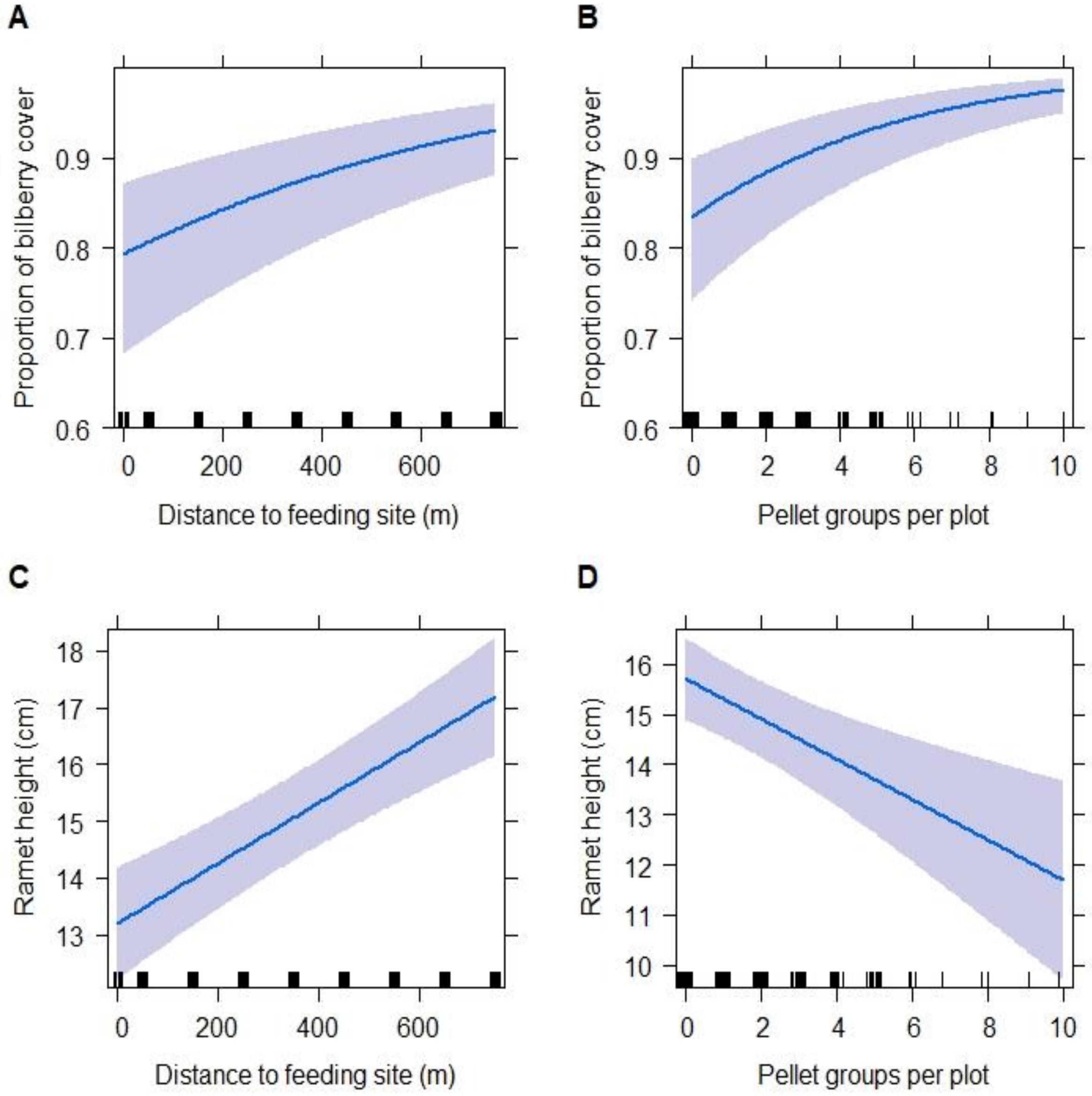

**Figure 8:** Predicted effects of distance to feeding site (m) and deer density on bilberry cover (A and B), and ramet height (C and D). The shaded area indicates 95 % confidence interval.

## 3.4 Bilberry leaf nitrogen (H4)

Both ‘deer density’ and ‘distance to feeding site’ had no effect on N concentration in bilberry leaves as these were discarded during the model selection process. Indicating that leaf N concentration in bilberry was not affected by the feeding sites. The chosen model explained about 41 % of the variation in N concentration in bilberry leaves by including ‘berries per $m^2$’, ‘bilberry cover’ and ‘canopy openness’ as explanatory variables. N concentration in bilberry leaves was significantly negative affected by fruit production ($\beta$ = -0.00887, se = 0.00369, p-value = 0.022), ‘bilberry cover’ ($\beta$ = -0.50799, se = 0.20713, p-value = 0.019) and ‘canopy openness’ ($\beta$ = -0.00229, se = 0.00103, p-value = 0.033) (Figure 9; Supplementary table 5).

The top three ranked models all had ΔAICc < 2. The second-ranked model (ΔAICc = 0.08, df = 5) was chosen over the first- (ΔAICc = 0.00, df = 7) and third- (ΔAICc = 1.16, df = 8) ranked models because it had the simplest model formulation (i.e. the most parsimonious model).

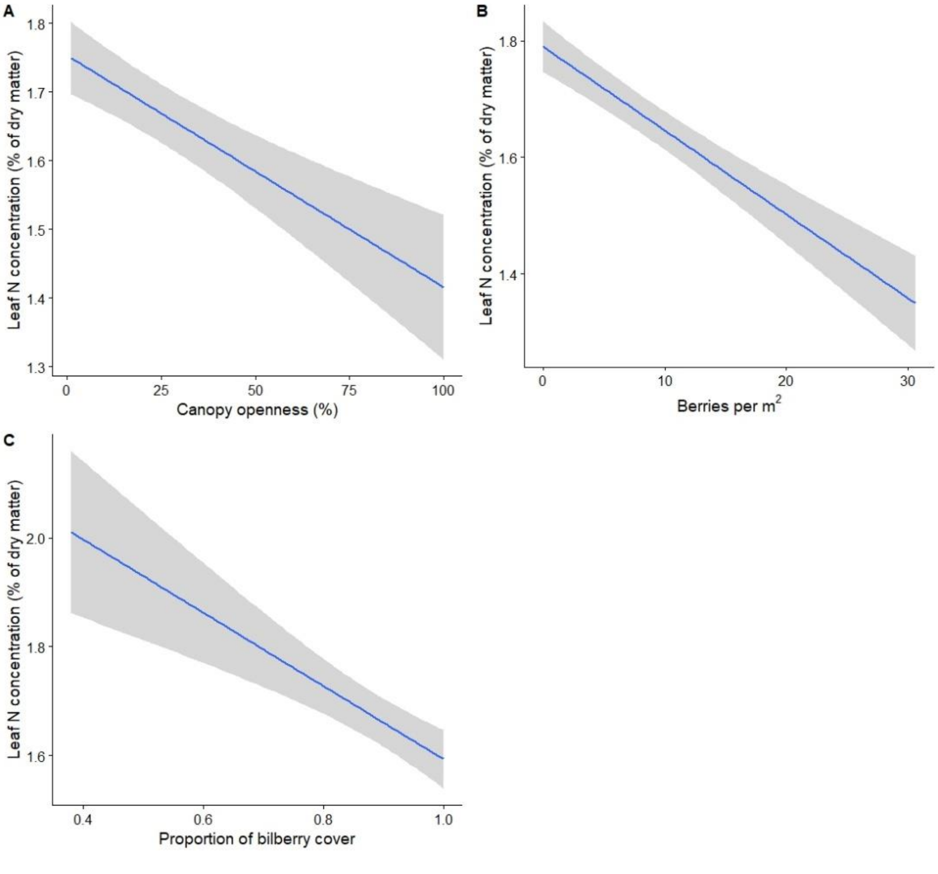

**Figure 9:** Predicted effects of bilberry abundance (A), fruit production (B) and canopy openness (C) on N concentration in bilberry leaves. The shaded area indicates 95 % confidence interval.

# 4 Discussion

## 4.1 Space use of red deer and the ban on supplementary feeding (H1)

Supporting my assumptions in H1, space use of red deer surrounding supplementary feeding was affected both spatially and temporally by the ban on supplementary feeding (Figure 4). The animals were more uniformly spread across the landscape now compared to when the feeding sites were still in use. Although they used the area more evenly, the deer still used the area close to previous feeding sites proportionally more than areas further away. This may be explained in a behavioural context, as it is assumable that due to the long-term feeding activities in the area, deer have adapted to use the area around the feeding sites during winter season. This is shown to be normal for a range of ungulates when supplementary feeding is still ongoing (Arnold et al., 2018; Milner et al., 2014). Also, Reinecke et al. (2014) showed that the home range sizes of red deer are proportional with the intensity of supplementary feeding activity in an area, indicating that the animals stay in close vicinity to feeding sites where forage is supplied frequently. In accordance with my results, a study on American white-tailed deer showed that the deer were less concentrated around feeding sites when supplementary feeding stopped (Hurst & Porter, 2008). Furthermore, a review by Putman and Staines (2004) showed that deer that are used to being fed during wintertime will continue to revisit the same locations even if feeding has ceased (i.e. lagging effect). Altogether this shows that deer react, by altering their space use, to changes in supplementary feeding strategies. It is likely that this effect will reduce over time when the deer learn that the feeding sites no longer represent a reliable food source. As data was gathered only two years after feeding had ended, the lagging effect of the supplementary feeding sites is probably still present.

## 4.2 Browsing damage (H2)

Interestingly, browsing damage on young trees was only affected spatially as it did not differ before and after the feeding had stopped. Thus, giving no direct support for H2. This may also be attributed to the fact that the data was sampled only two years after feeding ended and results from H1 indicate that albeit reduced, red deer densities were still higher close to feeding sites compared to areas further away. Repeated browsing of the same trees even after feeding had ended may be a possible explanation for why there was no significant difference in browsing damage between sampling periods. Rebrowsing occurs on both deciduous and coniferous tree species (Bergqvist et al., 2003; Miller et al., 1998). Plants can respond to browsing by increased biomass (e.g. branches and twigs) production (Aldous, 1952; Bryant et al., 1983), thus compensating for lost plant tissue (Edenius et al., 1993; Guillet & Bergström, 2006). Increased biomass production can also allow for faster growth past herbivores reaching distance to escape future browsing (Danell et al., 1985). These fresh shoots may also have a greater palatability and digestive value for the animals and therefore be more attractive to the herbivores (Bergvall et al., 2006). Furthermore, Miller et al. (1998) showed that young scots pine trees were more susceptible to being killed by browsing, whereas deciduous species showed a higher tolerance. The latter supports my findings that most trees that were dead due to browsing were coniferous species (Supplementary figure 3).

Browsing damage was reduced in the interval 0 – 350 m from the feeding sites and reached a minimum at 350 – 400 m, whereas it increased again in the interval 400 – 750 m (Figure 5; supplementary table 2). In accordance with my findings, Gundersen et al. (2004) (moose) and Garrido et al. (2014) (fallow deer (*Dama dama*)) showed that supplementary feeding led to severe browsing damage on the forest vegetation surrounding feeding sites at local scale (< 200 m). Contrary to this, Jerina et al. (2008) found no clear evidence that supplementary feeding can reduce red deer induced damage to forests. Furthermore, van Beest et al. (2010) showed that, within 1000 m to feeding sites, 40 – 100 % of the trees showed signs of browsing when moose densities were high during wintertime. Thus, the relatively high average browsing impact (42 % and 47 %, before and after the ban respectively) might be due to the high red deer density in my study area.

The increase in browsing damage at distances greater than 350 – 400 m may be related to the availability of deciduous trees. The total number of deciduous trees was very high at 450 m and decreased slightly thereafter (Supplementary figure 2), whereas conifers were almost completely absent. Browsing impact on deciduous species was high regardless of the distance to the feeding site (Figure 7). This is in accordance with van Beest et al. (2010), they showed that browsing by moose on highly preferred deciduous tree species was high even when distances to supplementary feeding sites exceeded 500 m. As shown by Dumont et al. (2005) and Månsson et al. (2007), large herbivores such as moose and red deer tend to select for deciduous tree species. Thus, an explanation for the high browsing pressure on the deciduous species might be that the red deer in my study area selected specifically for them regardless of distance. Furthermore, I think that browsing pressure might not be proportional with the availability of deciduous species, but that the proportion of browsed trees is lower when the availability is high (i.e. dilution effect). This effect has also previously been shown in young scots pine stands (Lyly & Saksa, 1992). Thus, leading to an increase in browsing damage when distances exceed 400 m in my study.

Canopy openness had a negative effect on browsing damage, meaning that browsing decreased when the canopy got more open. Less dense canopies allow more light to go through, which may alter the understorey structure in forests (Hedwall et al., 2013). Many of the preferred forage species such as rowan and aspen are light preferring pioneer species (Myking et al., 2013). Pioneer species are known for quick post-disturbance establishment and can often occur in larger numbers, as often can be seen shortly after clearcutting or in young development forest classes (Widenfalk & Weslien, 2009). According to the forestry management plans, my study area mainly consisted of pine stands with medium productivity on relatively nutrient poor soils (Foran Norge, 2012). Even on clear-cut areas the rejuvenation of deciduous tree species was largely absent (Figure 2), leading to less available forage trees for the deer. Furthermore, Lone et al. (2014) showed that the available forage biomass is of greater importance than canopy structure for determining moose's browsing habitat choice. In my study, high browsing impact in areas with dense canopies could therefore be explained by red deer preferring habitats with denser vegetation where light availability was low. Areas with denser forest were probably more attractive as the available forage biomass potentially was higher than in more open areas.

The interaction between altitude and deer density had a negative effect on browsing damage. Browsing damage was highest at lower altitudes (Figure 6), especially under higher deer densities. Seasonal differences in habitat use of the animals is a possible explanation for these results. Red deer show large potential in movement between areas and along altitudinal gradients (Bischof et al., 2012; Luccarini et al., 2006; Pépin et al., 2008). Furthermore, Luccarini et al. (2006) also showed that snow depth is of great importance for regulating the animals altitudinal movement, indicating a clear trend in habitat use between winter and summer. In my study area, snow depth at higher altitudes can become as deep as two meters, whereas lower areas closer to the fjord (i.e. lower altitudes) typically have less snow (KSS, 2020). As woody species make up most of the winter forage for red deer (Schröder, 1977), browsing damage on young trees is most likely to occur at lower altitudes. Altogether, these findings suggest that higher browsing damage at lower altitudes and increased deer densities can be allocated to seasonal patterns in habitat use by the red deer.

## 4.3 Bilberry performance (H3)

Both bilberry cover and ramet height were significantly positively affected by distance to the supplementary feeding sites (Figure 8). Thus, showing a spatial relationship between distance to feeding site and bilberry cover and height. Meaning that bilberry cover and ramet height were increasing as distance to the feeding sites increased, thereby supporting my assumptions in H3. This is also in accordance with a master thesis from Hedmark which showed that bilberry cover was clearly reduced close to supplementary feeding sites (Torgersen, 2008). Supporting my assumptions that bilberry cover was reduced at the feeding sites due to heavy browsing over a long period of time, Melis et al. (2006) showed that bilberry cover was higher in medium and un-browsed areas, 40 % and 60 % respectively, than in heavy browsed areas. Furthermore, Strengbom et al. (2003) give support to my assumption that also ramet height is low at the feeding sites due to repeated browsing as they showed that repeated damaging of bilberry plants led to a reduction in height growth. Thus, limiting ramet height. At the feeding sites in my study area browsing intensity on bilberry plants was most likely very high for many years (~15-20 years). Hence, both spatial and temporal effects of concentrated high browsing pressure over a long period of time close to the feeding sites has led to a significant reduction of bilberry cover and ramet height.

My results suggest that bilberry cover was higher in terrain with high deer densities, whereas, as expected in H3, ramet height was negatively affected by deer density (Figure 8; Supplementary table 3; Supplementary table 4). This has also been shown earlier as bilberry cover remained largely unaffected by red deer grazing, whereas ramet height was significantly reduced (Baines et al., 1994). In a survey on the isle of Svanøy, Hegland et al. (2005) found that both bilberry cover and ramet height were reduced when red deer grazing intensity increased. Supporting my results, Hegland & Rydgren (2016) showed that bilberry can withstand browsing to some degree before the cover is reduced due to overbrowsing. A possible explanation for my results may therefore be that the animals stay in areas with dense bilberry cover and feed on the bilberry plants. Thus, reducing the height of bilberry ramets, but browsing is not severe enough to reduce their cover.

The general bilberry cover was significantly higher across the landscape after the ban on supplementary feeding (Supplementary table 3). It is likely that this effect is due to climatic conditions rather than the change in animals spatial use and browsing behaviour. In the case of the latter, a more distinct recovery of bilberry cover close to the feeding sites would be expected. Instead, relatively low average snow depth in 2013 coincided with low average temperature for the first quarter-year (i.e. January through to March) (KSS, 2020). A study by Wheeler et al. (2014) demonstrated that earlier snowmelt and accompanying spring frost can harm bilberry plants, and that repeated spring frost episodes could increase their lethality. According to this, relatively low snow depth coinciding with low temperatures in 2013 may have led to severe spring frost damage on bilberry plants. Thus, bilberry cover was lower in 2014 due to temporal between-year variations in climatic conditions.

Bilberry cover was highest under dense canopies (i.e. potential light availability is low) in flat terrain, whereas it was highest under open canopies in steep terrain (Canopy openness interacting with slope for bilberry cover; Supplementary figure 4). Studies have shown that bilberry prefer intermediate light conditions (Atlegrim & Sjöberg, 1996; Eldegard et al., 2019; Parlane et al., 2006). In the study by Eldegard et al. (2019) the authors found that solar irradiation may vary greatly, depending on the terrain position. A possible explanation for my findings may be that the amount of light irradiance in steep topography shows a greater variation during the day, compared to when its flat. Thus, possibly giving favourable conditions for high bilberry cover even when light availability is high. On average, the highest bilberry cover occurred at approximately 37 % canopy openness (Supplementary figure 4). This result is in accordance with the findings in Parlane et al. (2006), who found that bilberry cover reached an optimum at around 40 % light irradiance.

Further, canopy openness tended to positively affect ramet height (Supplementary table 4). Tolvanen (1995) showed that bilberry ramets grew straighter and more vertically in open areas where light was no limiting factor. Ramets growing in forest habitats showed more horizontal growth in order to intercept more diffuse light (Tolvanen, 1995). Contrasting this, a master thesis from a study area close to mine found that bilberry ramet size (i.e. ramet height, stem diameter and number of shoots) was negatively affected by elevated light levels (Berge, 2018). Altogether, the results presented in this and earlier studies show that bilberry cover has an optimum at intermediate light levels, and that the effects of light availability on bilberry ramet height remain unclear.

Ramet height increased with increasing altitude, whereas bilberry cover decreased (Supplementary table 3; Supplementary table 4). Higher elevations are associated with contesting climatic conditions, e.g. lower temperatures and longer snow cover, leading to shorter growing seasons (Jones, 2001). Rixen et al. (2010) showed that bilberry cover is higher in areas with early natural snowmelt. These areas are often associated with lower altitudes (Jones, 2001). In contrast, Miina et al. (2009) found that bilberry cover was higher at higher elevations. The comparability of my results to these studies is questionable, as my results and the results from the presented studies come from a wide range of different geographical locations with different climatic conditions. Rixen et al. (2010) represent a more continental climate as their study area was situated in the central alps of Switzerland. Although my own study area is characterized as slightly continental (Moen & Lillethun, 1999), a decisive influence by oceanic climate characteristics may be present. Thus, it is difficult to give an exact explanation for my results from a climatic point of view.

Furthermore, bilberry plant size, with ramet height being the most important variable, may have an altitudinal optimum in my study area as plant size has been shown to increase to around 500 – 600 meter above sea level and decrease after that (Berge, 2018). Bilberry have a very wide niche and can be found at heights up to around 2200 m.a.s.l. in the boreal zone (Timoshok, 2000). The surveyed plots in my study ranged from 150 – 540 meters above sea level, only covering a small part of that altitude spectrum. These results could possibly also be linked to my results which showed that browsing damage was highest on young trees at low altitudes. It is possible that bilberry plants in areas with high browsing pressure on young trees also were browsed by red deer, thus giving a reasonable explanation to why bilberry plants were shorter at low altitudes.

Bilberry cover also had a highly positive effect on ramet height (Supplementary table 4). Meaning that bilberry ramets grew taller when there was a high coverage of bilberry. The results by Woziwoda et al. (2019) show that bilberry plant height is clearly positive correlated to bilberry aboveground biomass. As done by Nybakken et al. (2013), biomass calculations usually consist of measurements at ramet level and then multiplied by the number of ramets (i.e. cover). Hence, bilberry aboveground biomass also is strongly correlated to cover, which indirectly support my results. The exact relationship between bilberry cover and plant height might still be unclear, but my results present evidence that bilberry plants tend grow taller in areas with dense bilberry cover.

The exact ecological explanation for my results for both bilberry cover and ramet height may be uncertain. Large-scale variations in bilberry cover and ramet height might be determined by a complex combination of environmental and climatic factors. Whereas, browsing by red deer probably is one of the most important factors in my study area to explain small-scale variations in bilberry cover and ramet height.

## 4.4 Bilberry leaf nitrogen (H4)

Surprisingly, the long-term feeding showed neither spatial nor temporal effects on bilberry leaf N, as N concentrations did not significantly differ with distance to the feeding sites. Thus, not giving direct support to H4. Instead, environmental factors and factors affecting plant physiology such as available light, fruit production and bilberry cover appeared to be of greater importance (Supplementary table 5). N concentration in bilberry leaves was reduced with increased bilberry cover (Figure 9). Higher levels of N input can lead to a reordering of species abundance and composition along a nutrient gradient (Cleland & Harpole, 2010). Both Strengbom et al. (2001) and Strengbom and Nordin (2008) showed that low bilberry cover was coinciding with increased N levels. They also found that the abundance of graminoids and nitrophilous herbs increased significantly under nutrient rich conditions (Strengbom et al., 2001; Strengbom & Nordin, 2008). This can also be seen in my study area where graminoids dominated the centres of the previous feeding sites (Figure 2). Furthermore, in the remaining silage from earlier feeding, dense communities of stinging nettles (*Urtica dioica*) were observed (Figure 2). The latter is a highly nitrophilous herb indicating nutrient rich conditions (Hofstra et al., 1985). In originally N-limited systems, as in my study area, the long-term effects of increased N input may be considerable (Strengbom et al., 2001; Strengbom & Nordin, 2008). Supporting this, a master thesis showed that species composition in the field layer vegetation changed towards more nutrient demanding species close to long-term feeding sites (Torgersen, 2008). Supplementary feeding has clearly had a fertilizing effect from the long-term aggregation (i.e. temporal effect) of remaining forage and animal droppings close to the centre of the feeding sites (i.e. spatial effect) in my study area. Thus, indirectly giving support to H4. Bilberry leaf N concentration seem not applicable as a proxy for studying fertilizing effects of supplementary feeding or other sources of nutrient input, as bilberry get outcompeted under nutrient rich conditions.

As the number of berries per $m^2$ increased, N concentration in bilberry leaf tissue decreased (Figure 9). This is in accordance with several earlier studies (Fernández-Calvo & Obeso, 2004; Granath & Strengbom, 2017; Lähdesmäki et al., 1990; Selås et al., 2011). It is likely that N levels are reduced due to a trade-off in nutrient allocation to reproduction rather than growth. It has also been shown by Pakonen (1988) that N concentration in certain bilberry plant tissues may be lower due to allocation of proteins for flowering and fruit production (i.e. reproductive allocation). Whereas, Selås et al. (2011) concluded that between-year differences in environmental factors such as weather and solar irradiance play a major role in determining

N concentration and berry production. Among other things, they showed that N-levels were negatively affected by high spring temperatures and that bilberry production increased in years with high summer precipitation (Selås et al., 2011). Altogether, these results corroborate that N concentration in bilberry leaves is reduced with increased fruit production.

Lastly, canopy openness negatively affected bilberry leaf N concentration (Figure 9). N-concentrations are related to chlorophyll content in photosynthetic active plants, as N is an important component of the chlorophyll molecule (Evans, 1989). Björkman (1981) showed that chlorophyll concentrations in shade tolerant plants tend to decrease when light availability increases. Furthermore, Pato and Obeso (2012) showed that bilberry plants have higher photosynthetic efficiency (i.e. higher chlorophyll content) under shady conditions than plants living in habitats not limited by light availability. Thus, giving the assumptions that bilberry plants in open areas have lower leaf N concentration than plants standing under dense canopies.

With support from all the presented studies and my results, I suggest that the level of N concentration in bilberry leaves is determined by complex mechanisms, with variations in environmental factors (e.g. weather and light availability) and nutrient allocation in the plants being the most important.

# 5 Conclusion

The Norwegian ban on supplementary feeding might be an appropriate measure to avoid spreading of CWD, but other factors must also be considered. Disregarding effects a ban has on the frequency of traffic accidents with wildlife or damage to agricultural fields, this study shows that the effects on forest ecosystems can be considerable.

In accordance with what I predicted (H1); space use of the red deer was lower at the centres of the feeding sites after the ban compared to before. Despite this, a clear lagging effect of the long-term feeding program was present, as the animals still were attracted towards the centres of the feeding sites. Furthermore, high deer densities in the study area might have contributed to the lagging effect and the generally high browsing pressure on young trees. Browsing damage surrounding the supplementary feeding sites was not affected by the ban. Therefore, not giving support to my prediction (H2). It is likely that differences in browsing damage will become clearer over time when the lagging effect has faded out.

Supporting my prediction (H3), high deer densities and high browsing pressure at the feeding sites over a long period led to a reduction in both bilberry cover and bilberry ramet height close to the feeding sites. This effect was still present after the ban on supplementary feeding. As a result of increased N input at the feeding site centres due to decomposing forage and red deer feces, bilberry was mostly outcompeted by graminoids and other nitrophilous species. Thus, indirectly supporting my last prediction (H4), that the feeding sites have had a fertilizing effect on the surrounding vegetation.

Altogether my study present important knowledge about the long-term effects of supplementary feeding and what happens after feeding is ended. I can conclude that both the ban on supplementary feeding and the long-term feeding sites themselves have led to significant spatial and temporal effects on animal space use and the forest vegetation surrounding the feeding sites. Furthermore, it is in this study shown that these effects persist even after the supplementary feeding is ceased. The effects could mainly be seen in an altered species composition towards more nitrophilous species due to increased N availability at the feeding site centres, reduced bilberry cover and ramet height close to the sites and high browsing pressure as deer revisited the feeding sites also after the ban. Thus, resulting in a slow recovery of the ecosystem around the feeding sites. This study could give valuable information for forest and wildlife managers when considering supplementary feeding as a tool for their management strategy.

It would be interesting to follow up the development of the forest vegetation surrounding the previously active feeding sites with two – five-year intervals. This could give important knowledge for better understanding of restauration ecology and “rewilding”. Future studies could include a more detailed evaluation of the field layer vegetation, including species composition and relative cover of the respective species. Furthermore, browsing damage could be investigated in more detail at species level.

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# Appendix I – Supplementary tables

**Supplementary table 1:** The best GLMM model using distance from supplementary feeding site and sampling year as explanatory variables to explain red deer spatial use around the feeding sites in Kaupanger before (2014) and after (2018) the ban on supplementary feeding.

| **Variable** | **Estimate** | **SE** | **z** | **p** | |
|---|---|---|---|---|---|
| (Intercept) | 0.31830 | 0.12147 | 2.620 | **0.009** | ** |
| Distance to feeding site | -0.45349 | 0.07810 | -5.807 | **<0.001** | *** |
| Year (2018 vs. 2014) | 0.07086 | 0.10258 | 0.691 | 0.490 | |
| Distance to feeding site x Year (2018 vs. 2014) | 0.26536 | 0.10531 | 2.520 | **0.012** | * |

Significance levels: * P<0.05, ** P<0.01, *** P<0.001

**Supplementary table 2:** The best GLMM model for browsing damage using distance from supplementary feeding site, sampling year, canopy openness, pellet groups, bilberry abundance and altitude as explanatory variables.

| **Variable** | **Estimate** | **SE** | **z** | **p** | |
|---|---|---|---|---|---|
| (Intercept) | -0.49068 | 0.18735 | -2.619 | **0.009** | ** |
| Distance to feeding site | 0.06008 | 0.07400 | 0.812 | **0.417** | |
| Distance to feeding site$^2$ | 0.24606 | 0.07500 | 3.281 | **0.001** | ** |
| Canopy openness | -0.48641 | 0.06512 | -7.469 | **<0.001** | *** |
| Deer density | 0.05330 | 0.03780 | 1.410 | 0.156 | |
| Altitude | -0.19168 | 0.14903 | -1.286 | 0.198 | |
| Deer density x Altitude | -0.14218 | 0.04860 | -2.926 | **0.003** | ** |

Significance levels: * P<0.05, ** P<0.01, *** P<0.001

**Supplementary table 3:** The best GLMM to explain bilberry abundance, using canopy openness, slope, distance to feeding site, sampling year, pellet groups and altitude as explanatory variables.

| Variable | Estimate | SE | z | p | |
|---|---|---|---|---|---|
| (Intercept) | 1.3604 | 0.29119 | 4.672 | **<0.001** | *** |
| Canopy openness | -0.09956 | 0.05889 | -1.691 | 0.091 | |
| Slope | -0.12973 | 0.05765 | -2.250 | **0.024** | * |
| Distance to feeding site | 0.38091 | 0.05187 | 7.343 | **<0.001** | *** |
| Year (2018 vs. 2014) | 0.51906 | 0.09471 | 5.481 | **<0.001** | *** |
| Deer density | 0.20472 | 0.02722 | 7.521 | **<0.001** | *** |
| Altitude | -0.31691 | 0.12891 | -2.458 | **0.014** | * |
| Canopy openness x Slope | 0.48745 | 0.04802 | 10.151 | **<0.001** | *** |

Significance levels: * P<0.05, ** P<0.01, *** P<0.001

**Supplementary table 4:** The best LME model for explaining bilberry ramet height using distance to feeding site, canopy openness, pellet groups, bilberry abundance and altitude as explanatory variables.

| Variable | Estimate | SE | t | p | |
|---|---|---|---|---|---|
| (Intercept) | 10.0141 | 0.7985 | 12.541 | **<0.001** | *** |
| Distance to feeding site | 1.2120 | 0.2107 | 5.752 | **<0.001** | *** |
| Canopy openness | 0.4001 | 0.2086 | 1.918 | 0.056 | |
| Deer density | -0.4022 | 0.1105 | -3.639 | **<0.001** | *** |
| Bilberry cover | 6.7030 | 0.8343 | 8.035 | **<0.001** | *** |
| Altitude | 1.3332 | 0.3341 | 3.990 | **0.004** | ** |

Significance levels: * P<0.05, ** P<0.01, *** P<0.001

**Supplementary table 5:** The best linear model for explaining N concentration in bilberry leaves (% of dry matter), using fruit production (berries per $m^2$), bilberry abundance and canopy openness explanatory variables.

| Variable | Estimate | SE | t | p | |
|---|---|---|---|---|---|
| (Intercept) | 2.252281 | 0.182618 | 12.333 | **<0.001** | *** |
| Berries per $m^2$ | -0.008872 | 0.003689 | -2.405 | **0.022** | * |
| Bilberry cover | -0.507993 | 0.207131 | -2.453 | **0.019** | * |
| Canopy openness | -0.002288 | 0.001033 | -2.215 | **0.033** | * |
| $R^2/R^2$ adjusted: 0.460 / 0.414 | | | | | |

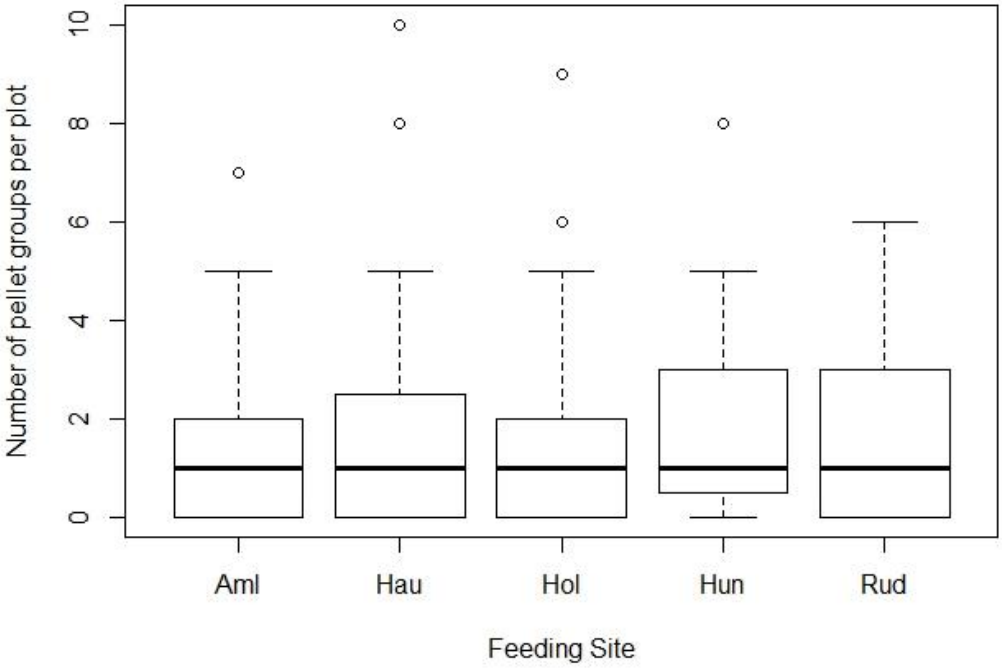
Significance levels: * P<0.05, ** P<0.01, *** P<0.001

**Supplementary table 6:** Results from the negative binomial regression model that describes the occurrence of young trees by using distance to feeding site (0-650 m) and species type (deciduous vs. coniferous) as explanatory variables).

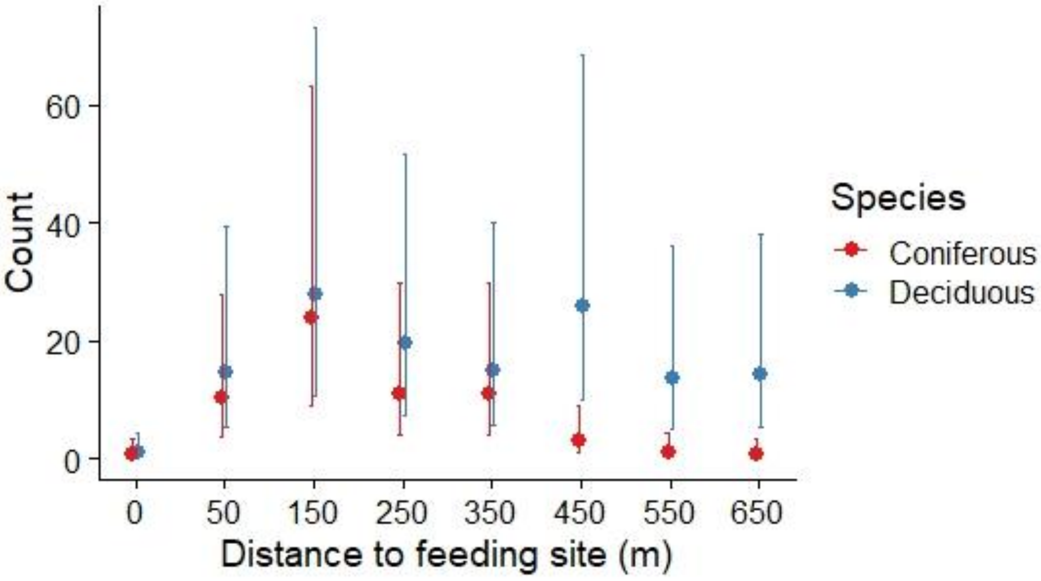
| **Variable** | **Estimate** | **SE** | **z** | **p** | |
|---|---|---|---|---|---|
| (Intercept) | -2.877e-01 | 7.537e-01 | -0.382 | 0.703 | |
| Distance50 | 2.615e+00 | 9.094e-01 | 2.875 | **0.004** | ** |
| Distance150 | 3.466e+00 | 9.017e-01 | 3.843 | **<0.001** | *** |
| Distance250 | 2.686e+00 | 9.085e-01 | 2.956 | **0.003** | ** |
| Distance350 | 2.686e+00 | 9.085e-01 | 2.956 | **0.003** | ** |
| Distance450 | 1.386e+00 | 9.413e-01 | 1.473 | 0.141 | |
| Distance550 | 5.108e-01 | 1.001e+00 | 0.510 | 0.610 | |
| Distance650 | -4.070e-15 | 1.066e+00 | 0.000 | 1.000 | |
| Species – deciduous vs. coniferous | 5.108e-01 | 1.001e+00 | 0.510 | 0.610 | |
| Distance50 x Species – deciduous vs. coniferous | -1.469e-01 | 1.230e+00 | -0.119 | 0.905 | |
| Distance150 x Species – deciduous vs. coniferous | -3.656e-01 | 1.221e+00 | -0.299 | 0.765 | |
| Distance250 x Species – deciduous vs. coniferous | 6.169e-02 | 1.228e+00 | 0.050 | 0.960 | |
| Distance350 x Species – deciduous vs. coniferous | -2.007e-01 | 1.229e+00 | -0.163 | 0.870 | |
| Distance450 x Species – deciduous vs. coniferous | 1.649e+00 | 1.251e+00 | 1.318 | 0.188 | |
| Distance550 x Species – deciduous vs. coniferous | 1.869e+00 | 1.300e+00 | 1.437 | 0.151 | |
| Distance650 x Species – deciduous vs. coniferous | 2.434e+00 | 1.350e+00 | 1.802 | 0.071 | |

Significance levels: * P<0.05, ** P<0.01, *** P<0.001

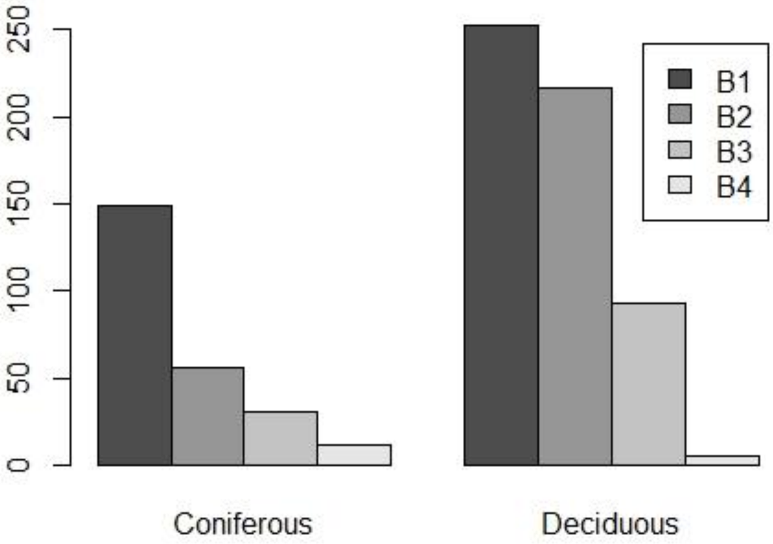
# Appendix II – Supplementary figures



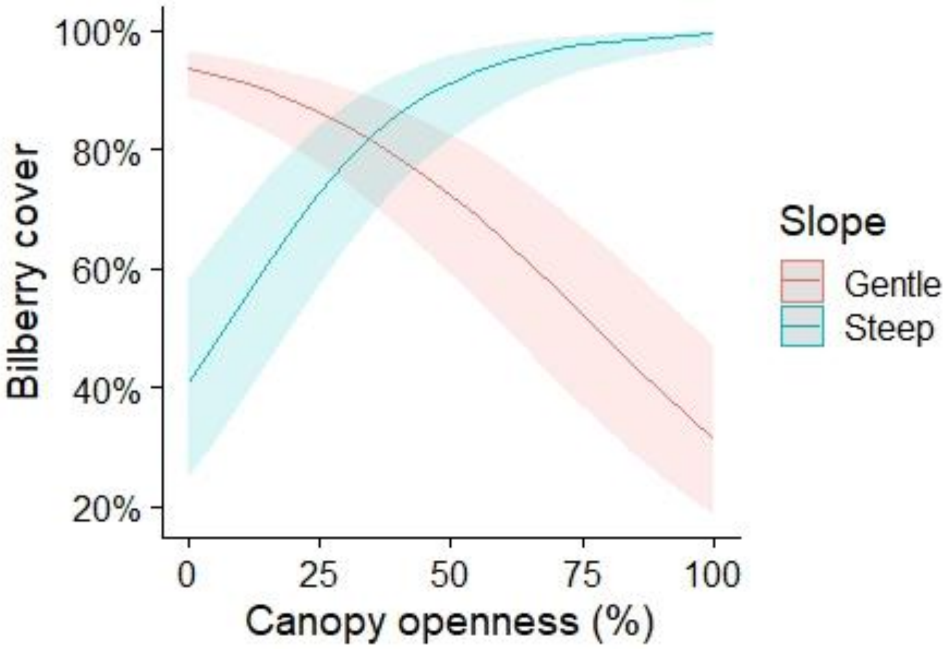
**Supplementary figure 1:** Boxplot of the number of pellet groups per plot according to the five different feeding sites (Aml = Amla, Hau = Haukåsen, Hol = Holten, Hun = Hungerhaugen, Rud = Rud). The 25 and 75 percentiles are marked by the lower and upper box boundaries respectively. The median is shown by the black line inside the box. 10 and 90 percentiles are maked by the lower and upper error bars respectively. Circles show individual observations falling outside the 10 and 90 percentiles



**Supplementary figure 2:** Predicted count of young trees, conifers and deciduous, at each distance from the feeding site (0 – 650 m). Standard error is shown by the error lines. The error bars indicate 95 % confidence intervals.



**Supplementary figure 3:** Number of trees in browsing indexes B1 (not browsed), B2 (lightly browsed), B3 (medium to heavily browsed) and B4 (dead due to browsing).



**Supplementary figure 4:** Predicted effects of canopy openness on bilberry abundance at different slopes, exemplified by gentle (1%) and steep (49%) slope respectively. The shaded area indicates 95 % confidence interval.

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