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## ABSTRACT

Herbivory and forestry activities are two drivers that affect forest vegetation structure. Increased cervid populations is a cause of concern as they have a substantial impact on vegetation structure. In addition, forestry activities alter tree species and understory vegetation composition. In this study, I used supplementary feeding sites to evaluate effects from red deer (*Cervus elaphus*) herbivory and forestry activities on bilberry (*Vaccinium myrtillus*) and on regeneration of young understory trees (deciduous tree species and juniper). I estimated bilberry performance (i.e. bilberry biomass, bilberry abundance and berry production) and occurrences of young understory trees, with a nested, hierarchical sampling design with transect surveys at five supplementary feeding sites. Distance from feeding sites was a proxy for browsing intensity, whereas light availability was an estimate proxy on forestry activity and altitude as a habitat variable. Berry production increased significantly with decreased browsing intensity and was positively affected by light availability. The interaction between browsing intensity and light levels had a positively significant effect on bilberry biomass. This indicates that the positive effect from reduced browsing intensity increased with higher light levels. Enhanced light levels had a significant negative impact on bilberry abundance, which indicates that abundance were low in areas with higher light levels. Browsing intensity had no significant effect upon abundance, which indicate that bilberry handles a certain browsing impact. Enhanced light levels had a significant negative influence on young understory trees, while browsing intensity had no significant effect. An explanation for this is that deciduous understory trees and juniper were not present in clear-cut areas, which have higher light levels. Distance from supplementary feeding site appear to be a suitable proxy for browsing intensity on bilberry biomass and berry sampling, but not suitable for estimating browsing intensity on bilberry abundance and understory trees. This indicates that specific estimates for browsing impact, like evaluating the extent of the browsing impact is a better option.



## SAMMENDRAG

Beiting og skogbruk er to drivere som påvirker strukturen til skogsvegetasjonen. Økning av hjortebestander er en grunn til bekymring ettersom de har en betydelig påvirkning på vegetasjonssammensetningen. På sin side endrer skogbruk sammensetningen til treslag, noe som igjen påvirker sammensetningen til undersjiktvegetasjonen. I denne oppgaven brukte jeg fôringsstasjoner for å evaluere effekter av hjortebeiting og skogbruk på blåbær og regenerering av unge trær (hovedsakelig løvtrær og einer (*Juniperus communis*)). På fem fôringsstasjoner brukte jeg et nøstet, hierarkisk design med transekter for å samle inn målinger på blåbær (e.g. biomasse, tetthet og bærproduksjon) og antall ungrær. Avstand fra fôringsstasjonen ble brukt som et mål på beiteintensitet, lystilgang var et generelt mål på skogbruk og høyde over havet ble brukt som en habitat variabel. Bærproduksjon økte tydelig med avtakende beiteintensitet og var positivt påvirket av lystilgang. Interaksjonen mellom beiteintensitet og lystilgang var positivt signifikant for blåbærmassen, noe som indikerer at den positive effekten av redusert beiteintensitet økte med bedre lystilgang. Høy lystilgang hadde en betydelig negativ effekt på blåbærtetthet, noe som betyr at tettheten var lav i områder med høy lystilgang. Beiteintensitet hadde ikke en stor påvirkning på blåbærtetthet, noe som viser til at blåbærplanten i seg selv tåler et visst beitetrykk. Ungtrær var også signifikant negativt påvirket av økt lystilgang, mens beiteintensitet hadde ikke en signifikant effekt. En forklaring på dette er at unge løvtrær og einer var ikke tilstede i hogstflateområder, som har høy lystilgang. Avstand fra fôringsstasjon virker å være et bra mål på beiteintensitet på biomassen til blåbær og bærproduksjon, men mindre velegnet for å måle beiteintensitet på blåbærtetthet og ungrær. Dette viser til at man bør ha et mer spesifikt mål for beitetrykk, som for eksempel skadeomfang, for å få et mer presist estimat på beiteintensitet for ungrær.



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## 1. INTRODUCTION

Forest ecosystems are complex as both natural and anthropogenic drivers directly and indirectly affect forest dynamics (Hein & Ierland 2006; Schumacher et al. 2004).

Cervid populations have increased rapidly in both Europe and North America (Gill 1990). As cervid herbivores in general have a substantial impact on forest vegetation and dynamics, such population increases are cause of concern (Côté et al. 2004; Milner et al. 2006). Through selective browsing and grazing, herbivores both directly and indirectly affect vegetation communities and structure (Côté et al. 2004; Hulme 1996). Direct effects on vegetation includes feeding, trampling and creating gaps on the ground (Tremblay et al. 2007). Because of these direct effects, herbivores indirectly influences conditions for the remaining vegetation. For example, by browsing taller growing plant species, light conditions improves for the understory vegetation (Hegland et al. 2013; Pedersen et al. 2014), and nutrient cycling are affected by adding nitrogen in form of dung and urine (Hobbs 1996).

Forestry activities alter stand structures and tree species composition, in addition to understory species composition (Hart & Chen 2006; Hedwall et al. 2013). Light is important for photosynthetic processes and when forestry increases tree density within an area, increased tree canopy diminishes light interception toward the understory vegetation (Ricard et al. 2003). In Sweden, fertilizing practices and tree stumps increases nitrogen levels and improves conditions for nutrient demanding species like grasses (Hedwall et al. 2010; Strengbom & Nordin 2008).

It can be challenging to distinguish between effects of browsing and grazing, forestry and climate on vegetation (Pickup et al. 1994). Supplementary feeding sites provides an opportunity to study herbivory impact upon the surrounding vegetation (Gundersen et al. 2004; Mathisen et al. 2014; van Beest et al. 2010). Supplementary winter-feeding of ungulates is common in North America and Europe (Mathisen et al. 2014; Putman & Staines 2004). Aims include improved winter condition and survival, diverting animals away from agricultural fields or valuable forestry areas and mitigating traffic accidents (Putman & Staines 2004). Supplementary feeding sites can be regarded as piospheres (Andrew 1988; Lange 1969). Lange (1969) defined piospheres as “*ecological systems which are defined by interactions between a water-point and the grazing animals*”, and thereby reflects how herbivores utilize and interact within an area. The browsing impact is most pronounced at the

centre of a supplementary feeding site and attenuates gradually along a browsing gradient away from the centre (Andrew 1988; Washington-Allen et al. 2004). Studies have shown that supplementary feeding sites indirectly affect vegetation structure as animals severely forage adjacent vegetation (Gundersen et al. 2004; van Beest et al. 2010).

Bilberry (*Vaccinium myrtillus*) is an important and dominant species in Nordic boreal forest ecosystems (Hegland et al. 2005). Bilberry is an intermediate preferred browsing plant and tolerate high browsing pressure due to its ability for clonal growth (Mysterud et al. 2008; Tolvanen et al. 1994), making it an ideal plant for browsing studies. Studies from Sweden indicates that bilberry biomass have been reduced over time due to forestry activities (Hedwall et al. 2010; Hedwall et al. 2013). Parlane et al. (2006) found that bilberry cannot survive in completely dense and shaded forest areas, whereas Tonteri et al. (2013) found that bilberry does not tolerate enhanced light levels and dry soil in clear-cut areas.

Young understory tree species like rowan (*Sorbus aucuparia*), aspen (*Populus tremula*) and goat willow (*Salix caprea*) are highly preferred browsing plants for cervids (Mysterud et al. 2010; van Beest et al. 2010). Intense browsing pressure by cervids delays tree growth, in addition to suppressing young tree regeneration (Didion et al. 2009; Persson et al. 2005). Yet, low browsing intensities can also reduce young tree growth (Speed et al. 2013), suggesting that intermediate browsing levels are optimal. Studies from Sweden have shown that fertilizing practices in forestry might increase the palatability of young understory trees for browsers, and in addition reduce the growth rates of trees because of the decreased light availability in the denser fertilised forests (Hedwall et al. 2010; Månsson et al. 2009).

Previous studies have commonly focused on how either herbivory or forestry activities affect understory vegetation, while the combined effects of browsers and forest utilization have often been overlooked (but see Parlane et al. (2006), Tremblay et al. (2007)). In this study, I used supplementary feeding sites utilized by red deer (*Cervus elaphus*) in forests with different management practices to explore effects of both herbivory and forestry on bilberry (*Vaccinium myrtillus*) and on young understory trees.

The main aim of this study was to identify how red deer herbivory, forestry affect bilberry performance (i.e. bilberry biomass, abundance and berry production) and the occurrences of young understory trees within a local scale up to 750 m from the supplementary feeding sites. Specifically, I predicted 1) an improved performance of bilberry plants and an increased abundance of young understory trees along a reducing browsing gradient from the centre of

the supplementary feeding site, showing an approximately linear response (Manthey & Peper 2010; Rosenberg & McKelvey 1999), and 2) that bilberry plants and occurrences of young trees first increases with decreasing browsing intensity, and then opposite factors, like light availability, interacts and evens out the effects from the reducing browsing intensity. Showing an approximately sigmoid response (Andrew 1988).

## 2. MATERIALS AND METHODS

### 2.1 Study area

The fieldwork was conducted from 17 June – 4 July 2014 in Kaupanger (61°11N, 7°14E), Norway. Kaupanger is located within Sogndal municipality, in Sogn og Fjordane county, and is situated along Sognefjorden in western Norway. The inner part of Sognefjorden has a slightly continental climate with cold and dry winters and warm summers with little precipitation (Moen 1999). Data from weather stations nearby (Fresvik, Hafslo, Lærdal IV and Sogndal Lufthavn), showed that the mean 1961-1990 temperatures in January ranged between -2.9 °C in the lowland and -5.2 °C at higher elevations, and for July the mean temperatures ranged between 14.9 °C in the lowland and 12.9 °C at higher elevations. The mean 1961-1990 annual precipitation varied between 508 mm in the lowland and 1048 mm at higher elevations (NMI 2015). However, in 2014, when this study was conducted, Norway had overall higher average temperatures (NOAA National Climatic Data Center 2014). In January 2014, the overall temperature was 0.8 °C above the mean 1961-1990, and approximately 3 – 4 °C above the average temperature in Kaupanger (NMI 2014c). In July 2014, the overall temperature for Norway was 4.3 °C above the mean 1961-1990, and approximately 4 – 5 °C above the average temperature in Kaupanger (NMI 2014a).

Steep slopes, hills, valleys and elevations up to 1100 m.a.s.l. characterize the local topography (Fig. 1). Forestry activities have been ongoing in the area for centuries. Old-growth forest occur at higher elevations, whereas forestry activities are performed in less steep areas at low- and mid-elevations.



**Figure 1:** Pictures from fieldwork area in Kaupanger, illustrating the landscape variation.

The boreal forest vegetation in the study area mainly consists of mixed stands of natural regenerated and planted Scots pine (*Pinus sylvestris*) and patches of planted Norwegian spruce (*Picea abies*). Deciduous tree species as grey alder (*Alnus incana*), birch (*Betula spp.*), rowan, aspen and goat willow were patchy interspersed throughout the study area (Pers.obs.). Common understory species are juniper (*Juniperus communis*), bryophytes (e.g. *Hylocomium splendens*) and dwarf-shrubs such as bilberry, cowberry (*Vaccinium vitis-idaea*) and crowberry (*Empetrum nigrum*).

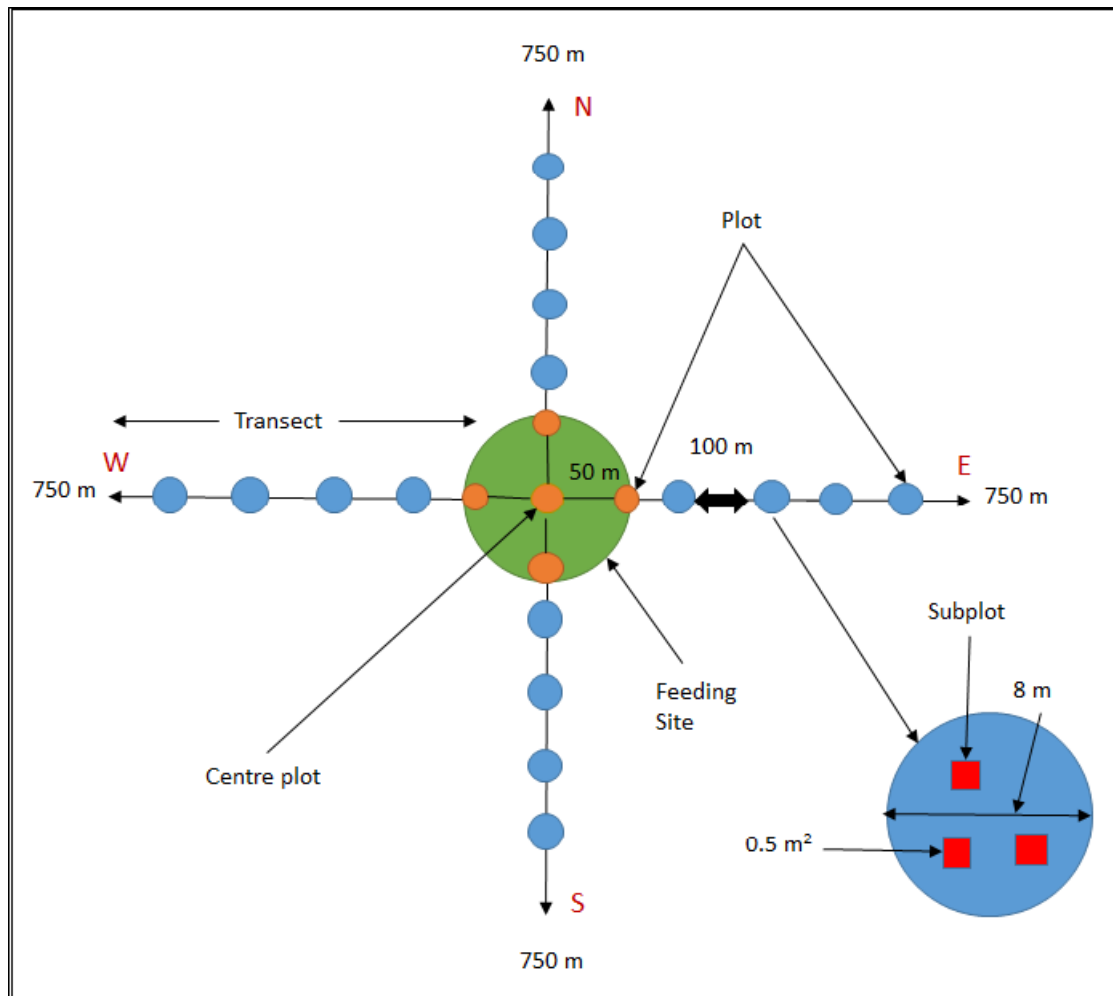
Red deer is as a mixed feeder that switches between a grazing and browsing diet (Gebert & Verheyden-Tixier 2001). Sogn og Fjordane county have high red deer densities at approximately 1.5 harvested animals per km<sup>2</sup> forest area (Solberg et al. 2012), and according to Statistics Norway 10.459 red deer were culled during hunting season in 2013-2014

(Statistics Norway 2015). In Kaupanger, 173 and 184 red deer were culled during hunting season in 2013 and 2014, respectively (Hjorteviltregisteret).

Supplementary winter-feeding of local red deer populations has been ongoing in Kaupanger since ca 1994 (Pers. comm. J. Haukås 2014). Landowners feed the animals with grass silage at selected locations during winter (November – March), mainly for diverting the animals away from roads, agricultural fields, attractive forest areas, in addition to improve winter condition for the animals (Pers. comm. S.J. Hegland 2014).

## ***2.2 Study design***

I performed a hierarchical, nested sampling design at five supplementary feeding sites. At each location, I first established a centre and a 50 m radius buffer zone for covering effects from the feeding site. Transects were systematically placed in each cardinal direction (north, south, east and west) with a maximum length of 750 m. Along transect lines, plots were evenly distributed every 100 m. In addition, I placed the first plot at the centre of the feeding site and the second plot at 50 m, adjusting for effects from the feeding site itself. All plots were circular with a diameter of 8 m (ca 50 m<sup>2</sup>), and each plot consisted of three subplots of 0.5 m<sup>2</sup> (Fig. 2). Subplots were randomly placed by throwing a stick, and its landing point was used as the subplot's centre. To avoid potential effects from surrounding trees and tree stumps, I adjusted the position of subplots ca 0.5 m from closest tree and tree stump.



**Figure 2:** Sketch of the hierarchical, nested sampling design for each of five locations.

Due to occasionally steep and rocky terrain and physical barriers, such as roads and agricultural fields, the actual length of transect lines and distance between the plots differed. Of 20 transects, 12 were 750 m, whereas the rest ranged from 150 m – 650 m. Because roads, agricultural fields and other physical barriers may affect patterns of red deer herbivory and vegetation, I decided to place plots 15 m from the disturbance.

### ***2.3 Data collection***

To estimate bilberry performance, I measured bilberry biomass, abundance and berry production at subplot level, whereas occurrences of young understory trees were estimated at plot level.



To estimate bilberry biomass, I randomly selected four individual plants and measured the height of ramets from ground to the highest point (cm) with a ruler, stem diameter at the woody structure at ground level (mm) with a calliper, and counted number of annual shoots (stems with leaves) (see Hegland et al. 2010). Within each subplot, mean values of the ramet height, stem diameter and number of shoots were calculated and added in a multiple regression model. The model explained 94% ( $R^2 = 0.94$ ) of the variation for the biomass estimation. This is an easy and rapid way for estimating biomass and one consequently avoids impacting the vegetation by data collection (Hegland et al. 2010).

Bilberry abundance was measured at subplot level as a frequency between 0 – 16 based on the subdivision of the plot (Fig.3). Within some subplots, there were no bilberry plants and bilberry abundance was registered as zero. To avoid many zeroes for biomass-estimation, I measured ramets at the closest bilberry plants in relation to the subplot.



**Figure 3:** Bilberry sampling at subplot level.

I estimated berry production at subplot levels by counting berries on the four plants selected for biomass-estimation. However, numbers of berries per subplot were few and consisted of

many zeroes. Therefore, I added the numbers of berries from each subplot, and used the total berry count at plot level for statistical analyses.

I estimated density of young understory trees by counting them at plot level. Both juveniles (< 20 cm) and understory trees (20 – 300 cm), browsed and unbrowsed young trees, were included in a total count. As regeneration of deciduous tree species were of greater interest in this study, I chose to exclude saplings of both Scots pine and Norway spruce from the total count. Thus, juniper was added to the total counts for decreasing amount of zeroes for the statistical analyses.

I registered distance from feeding station (in m) as a proxy for browsing intensity. Distance from feeding stations is an accurate estimate and less time consuming than specific estimates like pellet counts and browsing impact (Andrew 1988; Fernandez-Gimenez & Allen-Diaz 2001; Manthey & Peper 2010; Sasaki et al. 2008; Todd 2006). Sheep (*Ovis aries*) were observed in the study area and some browsing impact might originate from them, as red deer and sheep might have similar browsing impact upon the vegetation (Albon et al. 2007). Sheep grazing typically occur from June to September, a time when both red deer and sheep show less preference for bilberry and young trees (Welch et al. 1994). Therefore, sheep grazing is of less importance in this study.

I measured slope, altitude, tree density and forest type at plot level as proxies for general habitat characteristics that might affect bilberry and density of young trees. Slope (in °) was measured with a clinometer (Suunto PM-5/360 PC Clinometer), whereas altitude was measured with a GPS. Tree density was registered by counting numbers of trees over 3 m. I categorized forest type into either pine or spruce, depending on which tree species dominated the plot and the surrounding area.

Light availability (in %) at plot level is a general proxy for forestry activities and was measured with a densiometer (Lemmon 1956). Light levels reflects how forests differs between open and exposed clear-cut areas, to denser and shady areas.

## ***2.4 Statistical analysis***

To investigate how red deer herbivory, forestry and habitat variables affected bilberry performance and occurrences of young trees, I used generalized linear mixed models

(GLMM) with the lme4 package (Bates et al. 2014) and the glmmADMB package (Skaug et al. 2014) in R version 3.1.2 (R Development Core Team 2014).

Bilberry biomass, abundance and total berry counts were used as response variables for bilberry performance. For occurrences of young trees, I decided to use a total count of young trees within plots as a response variable as there were too few observations to perform species-specific analyses.

In accordance with Zuur et al (2010), I performed data exploration on both response and predictor variables, and compared individual variable relationships by visual means for assessing potential collinearity. Correlation matrixes were applied for comparing continuous predictor variables against each other, whereas boxplots were applied for comparing continuous predictor variables against categorical predictor variables (Zuur et al. 2010). Slope was moderate correlated with both distance from feeding site and light availability, so I decided to exclude slope from the models. Forest type was excluded from models as spruce was registered in few plots ( $n = 4$ ), in relation to pine which was registered in majority of plots ( $n = 135$ ). A correlation was found between tree density and light availability, so tree density was excluded from models. As there was no collinearity between distance and light availability, I therefore used light availability as a general proxy for forestry. Scatterplots only revealed a weak correlation between altitude and distance, so I decided to use distance, altitude and light availability as explanatory variables in all models.

To prevent misinterpretation due to different numeric estimates, the continuous predictor variables (distance, altitude and light availability) were scaled. By scaling continuous predictor variables, it is easier to compare different numeric effect sizes, especially in models with interactions (Muller et al. 2005; West et al. 1996).

Due to strong heterogeneity and outliers, I log-transformed bilberry biomass to obtain normality and for stabilizing the variance. Models were fitted with the lmer function in the lme4 package. Models with different fixed structures (but same random structure) were fitted with maximum likelihood (ML) as default. The final model with the optimal fixed structure was fitted with restricted maximum likelihood (REML) (Zuur et al. 2009). I fitted bilberry abundance with the glmer function in the lme4 package and a binomial distribution.

As berry production and occurrences of young trees are count data, they were first fitted with the glmer function and a poisson distribution, but due to many zeros and overdispersion, I fitted both response variables with the glmmadmb function in the glmmADMB package using

a negative binomial distribution. I used a negative binomial distribution as it is known for better handling excess zeroes than the poisson distribution (Crawley 2013; Zuur et al. 2009). Generalised Pearson statistic was used to check for overdispersion in the models (Crawley 2013).

To correct for dependency, spatial pseudoreplication and the unbalanced sampling design, I nested plots within transects within sites (1 | Site/Transect/Plot) in random effects for models with response variables measured at subplot level (bilberry biomass and abundance). For models with response variables measured at plot level (total berry count and total young tree count), I nested transects within sites (1 | Site/Transect) as random effects (Gillies et al. 2006)

For model selection, I used a backward stepwise elimination method, and subsequently rejected or accepted models according to Akaike's information Criteria (AIC) values (Crawley 2013; Zuur et al. 2009).

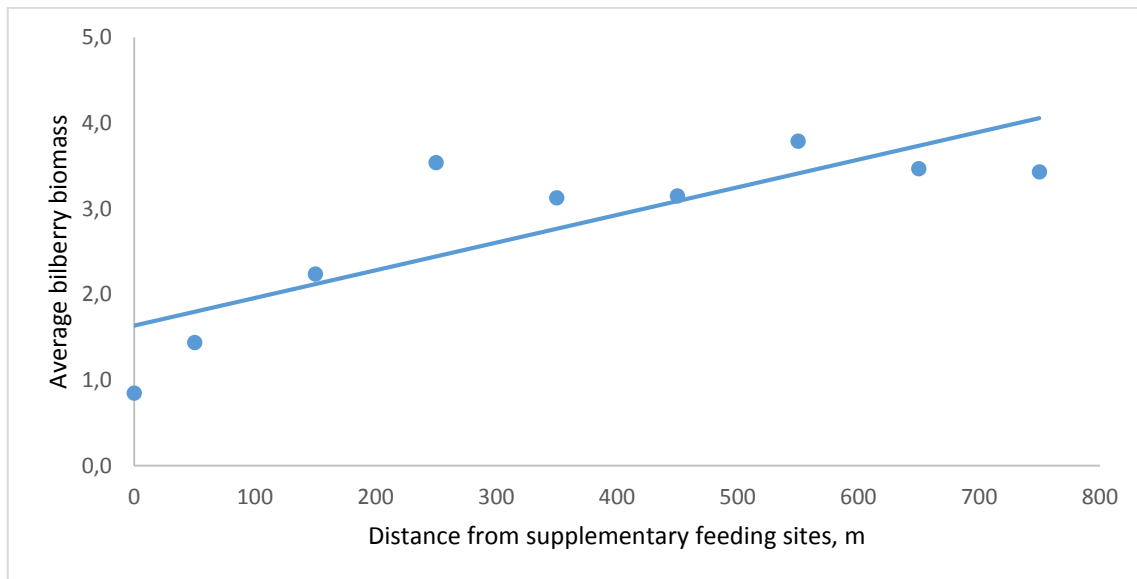
### 3. RESULTS

#### 3.1 *Bilberry biomass*

Bilberry biomass increased significantly with reduced browsing intensity away from supplementary feeding sites (Table 1). Light availability, as an estimate of forestry activities, had a slightly positive effect on bilberry biomass, although the effect seems to be of less importance than browsing intensity (Table 1). The positive effects from the reduced browsing intensity on bilberry biomass increased at higher light levels (Fig.4; Table 1). Altitude alone had no apparent effect on bilberry biomass, but it tended to interact positively with browsing intensity (Table 1).

**Table 1:** The most parsimonious generalized linear mixed model that predicted bilberry biomass (log-transformed) as a function of browsing intensity (scaled) from the feeding site, light availability (scaled) and altitude (scaled).

<b>Variable</b>	<b>Estimate</b>	<b>SE</b>	<b>df</b>	<b>t-value</b>	<b>P-value</b>
Intercept	0.721	0.124	3	5.818	0.011
Browsing	0.481	0.073	118	6.582	< <b>0.001</b>
Light	0.108	0.052	129	2.049	<b>0.043</b>
Altitude	0.135	0.123	27	1.098	0.282
Browsing x Light	0.191	0.076	120	2.510	<b>0.013</b>
Browsing x Altitude	0.155	0.098	117	1.589	0.115



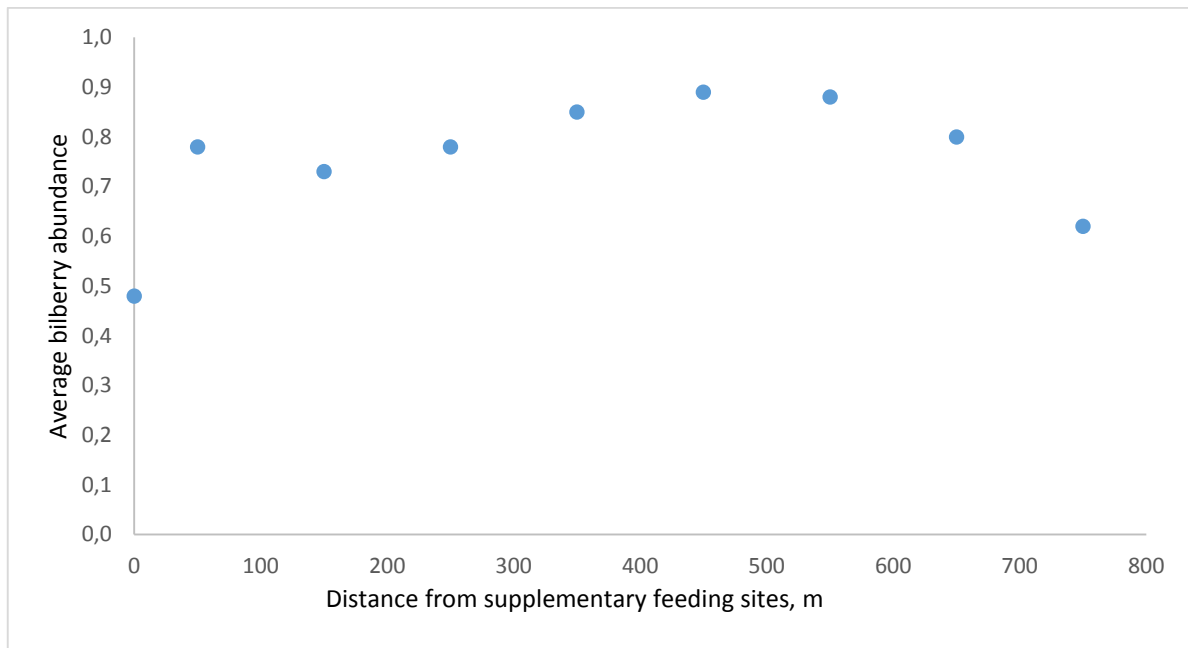
**Figure 4:** Average bilberry biomass in relation to distance (m) from supplementary feeding sites. Plotted raw data points are means for per distance plot (0, 50, 150, 250, 350, 450, 550, 650, and 750 m).

### 3.2 Bilberry abundance

In contrast to biomass, bilberry abundance did not increase significantly with reduced browsing intensity away from supplementary feeding sites (Fig. 5; Table 2). However, bilberry abundance showed a significantly negative trend with higher light intensities (Fig. 5; Table 2). Altitude alone had no apparent influence upon bilberry abundance, although it showed a strong significant negative trend in the interaction with browsing intensity (Table 2).

**Table 2:** The most parsimonious generalized linear mixed model for predicting bilberry abundance in relation to browsing intensity (scaled), light availability (scaled) and altitude (scaled).

Variable	Estimate	SE	z-value	P-value
Intercept	2.294	0.238	9.642	< 0.001
Browsing	0.132	0.317	0.418	0.676
Light	-0.483	0.199	-2.434	<b>0.015</b>
Altitude	-0.196	0.341	-0.575	0.566
Browsing x Altitude	-1.072	0.422	-2.541	<b>0.011</b>



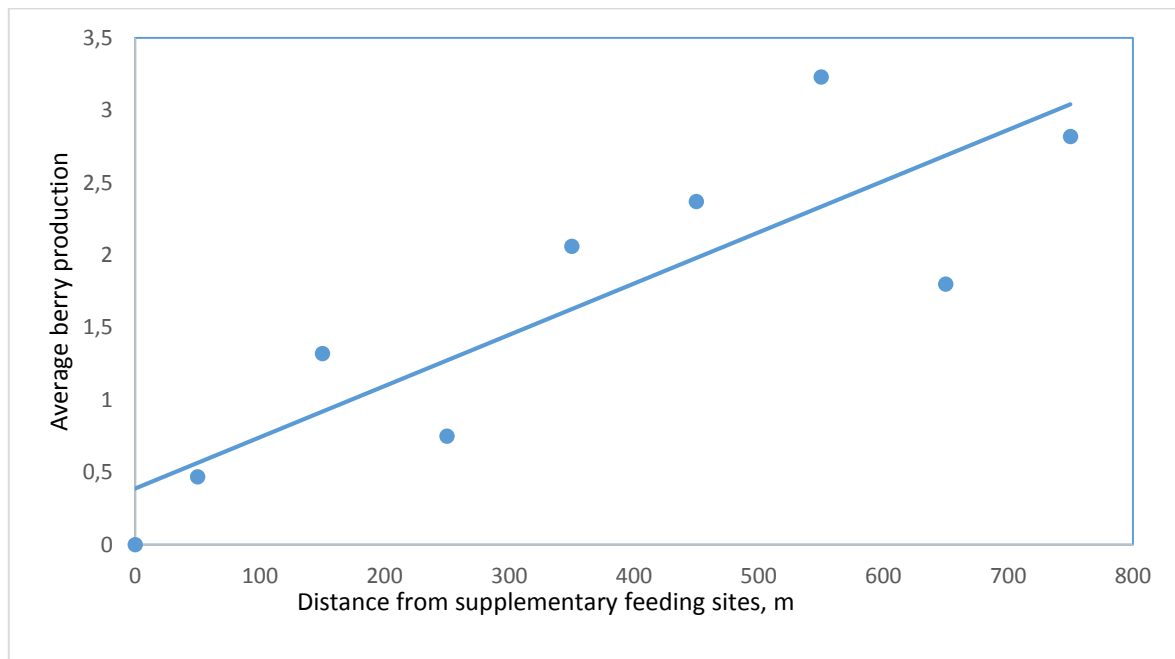
**Figure 5:** Average bilberry abundance in relation to distance (m) from supplementary feeding sites. Plotted raw data points are means for per distance plot (0, 50, 150, 250, 350, 450, 550, 650, and 750 m).

### **3.3 Berry production**

Berry production increased significantly with reduced browsing intensity away from supplementary feeding sites (Fig. 6; Table 3) at local scale. In addition, berry production improved significantly with increased light availability (Table 3). Within the local scale, the interaction between browsing intensity and light availability only showed a tendency toward significance (Table 3). Altitude at local scale had no influence upon berry production ( $p = 0.77$ ), and was not significant in the interaction with browsing either ( $p = 0.39$ ).

**Table 3:** Best generalized linear mixed model for predicting berry production in relation to browsing intensity (scaled) and light (scaled).

Variable	Estimate	SE	z-value	P-value
Intercept	0.045	0.264	0.170	0.866
Browsing	1.025	0.297	3.450	< 0.001
Light	0.784	0.214	3.660	< 0.001
Browsing x Light	0.438	0.317	1.380	0.167



**Figure 6:** Average berry production in relation to distance from feeding sites. Plotted raw data points are means for per distance plot (0, 50, 150, 250, 350, 450, 550, 650, and 750 m)

### 3.4 Occurrences of young understory trees

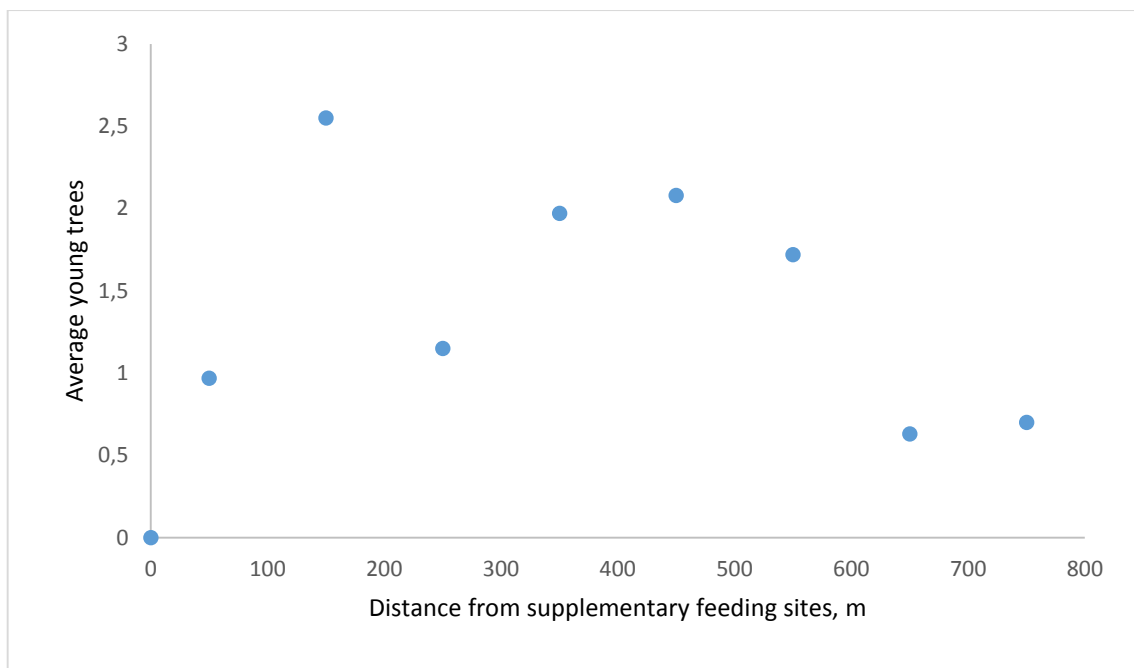
At local scale, browsing intensity appear to have no significant influence on occurrences of young trees, although the raw data points shows an almost convex trend ( $p = 0.90$ ; Fig.7).



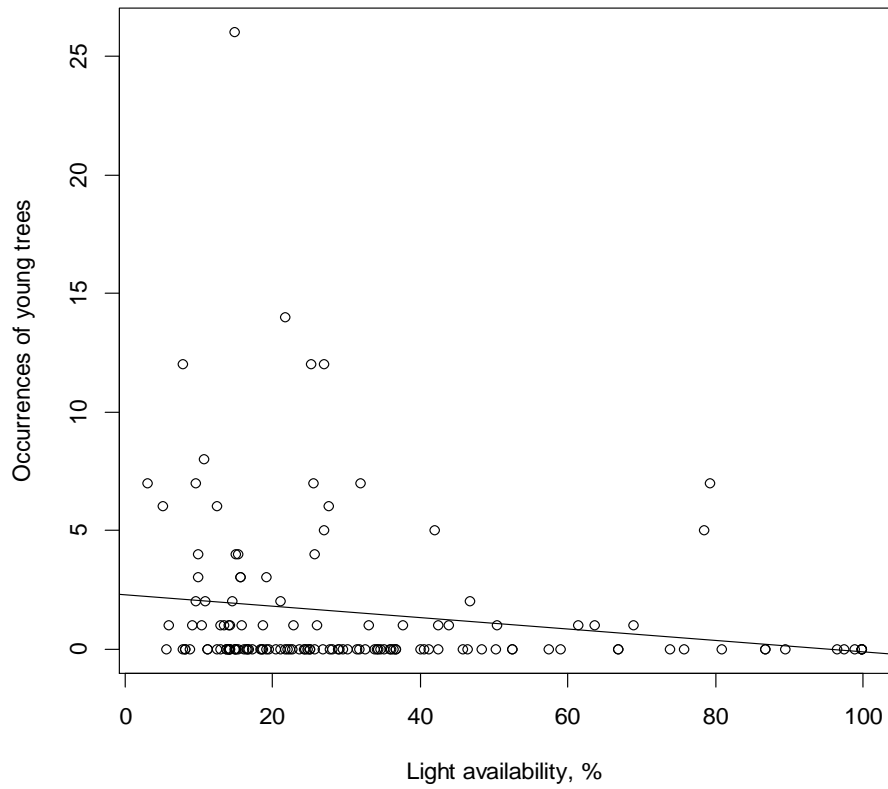
Variations in browsing intensity was not significant in the interactions with altitude ( $p = 0.29$ ) or light availability ( $p = 0.22$ ) at local scale. Increased light availability appear to have a negative significant effect upon occurrences of young understory trees (Fig. 8; Table 4), whereas altitude had no influence upon occurrences of young understory trees at local scale ( $p = 0.26$ ).

**Table 4:** Best generalized linear mixed model for predicting occurrences of young understory trees in relation to light availability (scaled).

Variable	Estimate	SE	z-value	P-value
Intercept	0.224	0.260	0.860	0.388
Light	-0.552	0.231	-2.390	<b>0.017</b>



**Figure 7:** Average young tree density in relation to distance from supplementary feeding site. Plotted raw data points are means for per distance plot (0, 50, 150, 250, 350, 450, 550, 650, and 750 m).



**Figure 8:** Raw data points showing young tree density in relation to light availability (%).

## 4. DISCUSSION

### *4.1 Bilberry performance*

My results revealed contrasting findings for bilberry performance characteristics. Berry production showed an approximately linear response along the browsing gradient away from supplementary feeding sites (Fig. 6), which supports prediction 1). The interaction between browsing intensity and light availability had a significant effect upon bilberry biomass, which modifies interpretations for the main factors (Table 1). This means that neither browsing intensity nor light levels alone cannot properly explain the trend for bilberry biomass. Reduced browsing impacts had a positive effect upon bilberry biomass, and the interaction with light levels was positive. Indicating that the positive effects from the reduced browsing intensity on bilberry biomass increased with higher light levels (Fig. 4), and supports for prediction 1). Both increased light levels and the interaction between browsing intensity and altitude had a negative impact on bilberry abundance (Fig. 5; Table 2). The interaction between browsing intensity and altitude indicates that bilberry abundance decreases with increased elevations along the browsing gradient. Therefore, there is no support for the predictions on bilberry abundance, as they assumed a positive trend.

Studies have shown that red deer browsing have negative effects on bilberry height, abundance and berry production (Hegland et al. 2005; Parlane et al. 2006; Welch et al. 1994). Hegland et al. (2010) found that red deer browsing affects bilberry biomass more than abundance. Indicating that the plant itself handles browsing well due to undergrowth structures and clonal growth, whereas the aboveground biomass is reduced (Hegland et al. 2010; Hegland et al. 2013). A review indicated that browsers have a less impact upon long-lived plant species with an enduring seedbank, as they have energy reserves as buffers to compensate for biomass reduction (Maron & Crone 2006). Bilberry have an enduring seedbank as seedlings are rare (Welch et al. 1994). These finding corresponds with my own results as red deer reduced bilberry biomass and berry production within and in proximity to supplementary feeding sites, whereas browsing impact alone had less of an effect upon bilberry abundance.

Parlane et al. (2006) found that bilberry abundance and height had a light optima ranging between 35 – 40 %, and decreased at both lower and higher light intensities. A national report from Finland evaluated changes upon understory vegetation in different forestry areas from

1985 to 2006, and found that bilberry cover both increased and decreased with enhanced light availability in different forest stands (Tonteri et al. 2013). They found that bilberry cover decreased in regeneration forest areas, due to very dry soil and enhanced light levels, whereas in thinned forests bilberry cover improved with increased light levels (Tonteri et al. 2013). Which probably occurred as thinning creates gaps in the canopy and increases light levels toward the understory vegetation (Ricard et al. 2003). According to my own results, enhanced light levels decreased bilberry abundance. This was most pronounced within clear-cut areas in Kaupanger, where the ground was drier and exposed to light and I mostly observed bilberry plants in proximity to tree stumps and interspersed trees. In addition, due to warm and dry summer in 2014 (NMI 2014a), the ground was very dry at several places within the fieldwork area, and hence had less bilberry cover. Whereas higher light levels positively affected bilberry biomass along the browsing gradient. Berry production only occurred at higher elevations in summer 2014 at Kaupanger (Pers. comm. S.J. Hegland, 2015), which does not corresponds with my results as altitude had no significant effect for berry production in my study. This corresponds with a study from Spain, where they observed that berry production increased with altitude (Pato & Ramón Obeso 2012). In addition, drought and dry conditions also impedes berry production (Selås 2000).

The interaction between browsing intensity and altitude had a negative influence upon bilberry abundance. Bilberry occurs in elevations ranging up to 2000 m.a.s.l. (Pato & Ramón Obeso 2012), and plots in my study area ranged between 150 – 540 m.a.s.l, which indicates that this interaction is not consistent. An alternative explanation is that altitude correlates with temperature and humidity, two variables that I did not measure in this study (Gamfeldt et al. 2013).

#### ***4.2 Occurrences of young understory trees***

Distance as a proxy for browsing intensity, had no significant effect on young understory trees. Yet, the raw data points indicate differently (Fig. 7). In fact, light availability was the only variable showing a significantly negative influence upon young tree densities (Fig. 8; Table 4). Thus, I have no support for either predictions on occurrences of young understory trees.

A possible explanation as for why young understory trees showed a distinct pattern with distance from feeding sites, is that red deer particularly select for them (Gill 2000; Mysterud et al. 2010). A study from southern Norway found that moose (*Alces alces*) highly selected for deciduous tree species, regardless of distance from supplementary feeding sites (Mathisen et al. 2014). Besides, Mathisen et al. (2014) used specific estimates like pellet count as proxy for moose density and estimated browsing impact upon understory trees. Indicating that using distance as a proxy for browsing intensity might not be applicable on young understory trees.

Except for herbivory impact, growth and regeneration of understory trees also depends upon light availability and canopy composition (Delagrange et al. 2004; Roberts 1992). Light availability is a limiting factor for growth of understory trees (Ricard et al. 2003). Which is in contrast with my own results, where light availability had a negative impact upon understory trees. A logic explanation as for why deciduous young tree species and juniper decreased with enhanced light intensities in this study is that they were not present in plots within clear-cut areas. Clear-cut areas have highest light levels and several of them were plantations with young trees of Scots pine and Norway spruce (Pers. obs.).

#### ***4.3 Potential limitations***

During this study, I had no control over the positioning of the feeding sites. Studies with similar study design perform surveys in similar areas, for example with small variations in altitude and habitat (Hegland et al. 2013; Wesuls et al. 2013). In my study, the five locations were situated at different elevations and plots were sampled at ranges between 150m – 540m. Local topography and forest stands varied along transects. In such cases, it is challenging to apply distance from feeding sites as a proxy for browsing intensity, as it might show unavoidable collinearity with variables like slope, altitude and pellet counts (Brits et al. 2000; Fernandez-Gimenez & Allen-Diaz 2001). Light availability correlated with both tree density and slope.

Another limitation in this study was the unusual warm weather and dry conditions in the area (NOAA National Climatic Data Center 2014). As climatic factors like temperature and moisture also affects plant dynamics (Moen 1999), I cannot really tell if this is ‘normal’ conditions for the vegetation dynamics in the study area.

## 5. CONCLUSION

Berry production improved with decreased browsing intensity as in accordance with prediction 1). Enhanced light levels, in interaction with reduced browsing intensity had a positive effect upon bilberry biomass, as in accordance with prediction 1).

On the other hand, browsing intensity were of less importance for bilberry abundance, indicating that bilberry are resistant to a certain browsing pressure. Therefore, not supporting predictions 1 and 2. Instead, bilberry abundance declined with enhanced light levels in clear-cut areas, which indicates that bilberry have an approximate intermediate light optima. The results indicated that enhanced light levels had a negative influence upon young understory trees. A most likely explanation is that there were no deciduous understory trees or juniper present in clear-cut areas, which have the highest light levels. Browsing intensity appeared to have no significant influence upon young tree density, yet the raw data points indicated differently. This indicates that distance from supplementary feeding sites may not be a suitable proxy for browsing intensity when studying the effect of browsers toward highly selected plant species.

I recommend conducting surveys within a landscape-scale for comparing with effects from supplementary feeding stations at the local scale. In addition, to include other environmental and habitat variables like nitrogen content, temperature and humidity for evaluating their effect upon plant responses.

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