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Effects of moose (*Alces alces*) browsing on naturally regenerated deciduous trees and field layer in Swedish pine stands

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Abstract

National and international forest biodiversity goals are not being met in Sweden, with 67% of productive forest area covered in even-aged monoculture coniferous forest stands. To diversify the forest management in order to increase, among other things, biodiversity in these stands, using natural deciduous regeneration can help in creating more mixed stands. Ungulate browsing can affect survival of this regeneration and possibly limit which trees forestry can select for. This thesis aimed to study the effects of ungulate browsing on the natural deciduous regeneration and field layer in young planted Scots pine (Pinus sylvestris) stands. This was done by comparing data from exclosure plots with unfenced plots, spanning a large part of the latitudinal range of Sweden. GLMM analyses showed that browsing affect the number of established (>2.5 m height) trees and the amount of deciduous forage biomass of the species silver birch Betula pendula, downy birch Betula pubescens, rowan Sorbus aucuparia, aspen Populus tremula and Salix spp. The abundance of RAS (i.e. rowan, aspen and Salix spp.) was low, even inside of the exclosures, which points out that regeneration of RAS is low even when browsers are excluded and thus other factors are also affecting abundance of RAS regeneration. The species composition as depicted by NMDS ordination and the Shannon diversity of different plots did not differ significantly, but did show patterns of more variation in species composition and diversity in the browsed plots.

These results imply that management of browsed stands is less predictable than that of unbrowsed stands and thus delaying precommerical thinning could provide management with a clearer idea of which trees could be selected as main stems in the mixed stand. Further research efforts should focus on disentangling different factors affecting deciduous tree regeneration.

Keywords: Herbivory, Ungulate browsing, Moose, Deciduous regeneration, RASO, Field layer, Tree diversity

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Abbreviations and definitions

F	Fenced – the plot with the fence around it, herbivores
Functional groups	Groups of species sharing some ecologically relevant characteristic
GLMM	Generalized Linear Mixed-effects Models
NMDS	Non-metric Multi-Dimensional Scaling
Pine	Scots pine (Pinus sylvestris)
RAS	Rowan (Sorbus aucuparia), Aspen (Populus tremula), Salix spp., adaption from the commonly used RASO (Rowan, Aspen, Salix spp., Oak), because no oak was found in the plots of this study
Salix	Salix spp.
SI	Site Index – a measurement of site fertility
SLU	Swedish University of Agricultural Sciences
Spruce	Norway spruce (Picea abies)
Total Birch	Silver birch (Betula pendula) + Downy birch (Betula pubescens)
Total Deciduous	Rowan, Aspen, Salix, Silver Birch, Downy Birch
UF	Unfenced – plots in the same site without fencing, thus browsing takes place here

1. Introduction

1.1 Swedish forests & forest management

Sweden has one of the highest forest covers in Europe, at 58% productive forest area (Skogsdata, 2022). This means a large part of biodiversity conservation for Sweden should take place in its forests, but Angelstam et al. (2020) as well as the Swedish Forest Agency (SFA) report that national and international forest biodiversity goals are not met (Karlsson et al., 2022). Instead, fulfilment of the environmental quality goals for "living forests" (Levande Skogar) have failed on several points, including negative developments for forest dependent species, insufficient quality of ecosystem services and lack and fragmentation of important habitats (Karlsson et al., 2022). It has been suggested that in order to secure longterm viability of Sweden's forest biodiversity, production forest stands need to better meet forest species habitat requirements, as it is risky to assume protected area's alone will suffice in meeting these habitat requirements (A. Felton et al., 2020). Therefore, forest management needs to diversify and adopt different approaches to restore forest habitat (Angelstam et al., 2020; Bergquist et al., 2016).

A way to better meet species habitat requirements is by diversifying the tree species in production stands, as many species groups rely on deciduous or mixed forest (as summarised by Johansson et al., 2013) and mixed species stands have been found to be more diverse in their fauna and flora than pure, single-species stands (Spiecker, 2003). The SFA reports that a higher consideration for biological diversity should be promoted as well as increasing of deciduous and mixed deciduous/coniferous stands (Bergquist et al., 2016). Demands for FSC forest certification also include aims for increased species diversity in production stands in their retention trees and species composition at final felling (FSC, 2010).

Besides providing habitat and improving forest biodiversity, increasing tree species diversity, especially the inclusion of more deciduous species in production forests, is recommended as a form of climate change adaptation and mitigation (Bolte et al., 2009; A. Felton et al., 2016; Kolström et al., 2011; Pawson et al., 2013). Additionally, mixed species stands have been found to be more resistant to various forms of damage (Spiecker, 2003).

Swedish forests are predominantly managed in a rotational system consisting of planting, pre-commercial thinning, thinning and clearcutting. This type of management and demands of the timber- and pulp industry have led to even-aged conifer stands. At present, 67% of the Swedish productive forest area is dominated by coniferous species, including 40% Scots pine (Pinus sylvestris) and 27% Norway spruce (Picea abies), while only a small proportion is mixed coniferous/deciduous (7%) or fully deciduous (9%) (Skogsdata, 2022). Currently the most abundant deciduous trees are silver birch (Betula pendula) and downy birch (Betula pubescens), together accounting for 10.5% of the growing stock on productive forest land. Other deciduous trees are much less represented, with for example 0.2% rowan (European mountain ash- Sorbus aucuparia), 2.8% aspen (European aspen - Populus tremula) and 0.4% Salix spp. (Skogsdata, 2022). Contemporary deciduous tree abundance may be a remaining result of historical forest management targeted at removing all deciduous trees by pre-commercial thinning or even using herbicides (Östlund et al., 2022), or of successful fire suppression (den Herder et al., 2009). To get from the current forest management to more diverse mixed forests, using the natural regeneration of deciduous trees in coniferous stands may form a practicable and cost-effective opportunity to increase tree species mixing (Götmark et al., 2005).

1.2 Ungulate browsing

Ungulate browsing is often mentioned as an important factor for natural regeneration, especially of deciduous and mixed forests (see Angelstam et al., 2000; Bergquist et al., 2016; Borowski et al., 2021; Edenius et al., 2002 among many others). Furthermore, ungulate browsing is a major driver in the functioning and dynamics of boreal forests because of selective herbivory, trampling and seed dispersal (Leroux et al., 2020; Pastor et al., 1988; Persson et al., 2000). For temperate forests, a meta-analysis by Ramirez et al. (2018) shows that ungulate browsing most often has been found to have a negative effect on forest regeneration (abundance, composition and diversity), forest structure and forest functioning. Similarly, in boreal forests, browsing by mostly moose (Alces alces) may negatively affect the forest structural measurements canopy height, vertical complexity, and above ground biomass (Petersen et al., 2023). Moose forage is found in largest proportion in the forested parts of the landscape, and browsing takes place accordingly (Hörnberg, 2001). In Sweden, moose browsing has large effects on the forest sector, with damages of approximately 1,15 billion Swedish Kronor/year (Bergquist et al., 2019).

The Swedish wild ungulate herbivore community includes moose, roe deer (*Capreolus capreolus*), red deer (*Cervus elaphus*) and fallow deer (*Dama dama*), while in the north it consists of mostly moose with low densities of roe deer. As

browsers, roe deer and moose are similar in their diets, foraging mostly on woody browse. Moose diet consists only for a limited part of grass (5% during the growing season and 1% in winter) (Spitzer et al., 2020). For roe deer, a diet containing >25% grass in the growing season is not uncommon. Fallow deer and red deer are more intermediate feeders, with diets consisting of grass and browse. In winter, the diets of all ungulates contain more woody browse (Spitzer et al., 2020). Direct effects of population size on amount of browsing have not always been strong (Bergqvist et al., 2014; Pfeffer et al., 2021). Instead, additional explanatory variables such as total browsing pressure (including all the browsers and all the forage) as well as climatic factors (e.g. snow, rain, drought) may also have effects on amount of damages caused by moose (Pfeffer et al., 2022).

In Sweden, moose diet consists of birch, Salix, pine, juniper (*Juniperus communis*), rowan and aspen. Spruce is only rarely consumed by moose, and not an important forage species (Hörnberg, 2001). Moose need a diet of mixed species in order to reach optimal nutritional value and avoid toxins (A. M. Felton et al., 2018). Even though studies on moose browsing show slightly different outcomes, the general tendency is that moose select, consume or utilize the deciduous trees rowan, aspen and Salix over birch and pine, and that the level of consumption is related to the amount of available forage (Bergqvist et al., 2018; Hörnberg, 2001; Månsson et al., 2007). Silver birch is found to be slightly preferred over pine, while downy birch might be preferred the same amount as pine (Månsson et al., 2007), however it is also possible that birch as a group has a lower utilisation rate than pine (Hörnberg, 2001). Bergqvist et al. (2018) showed that in winter browsing, aspen, Salix, rowan and oak were the most selected species, irrespective of forest- and land type.

Selection of both patch and food selection within a patch may follow optimal foraging theory, which would predict that in order to maximize fitness, ungulates try to maximize energy intake at the lowest energy costs (Charnov, 1976). Moose have been found to browse according to an ideal free distribution based on availability of forage on a landscape level. Even though young forests are not the only source of browse for moose, browsing does occur proportionally more in young stands, which also contain about three times more moose browse than older forests (Bergqvist et al., 2018). Young stands are also where moose may have the biggest effect on future species composition, as all trees are still within browsing height and browsing may therefore still largely affect survival rates and competition status.

1.3 Field layer

The field layer is another main component of biodiversity and provision of ecosystem services in the forest, potentially constituting numerous plant species in itself, as well as hosting and serving many pollinators and other organisms. Although different species in the field layer often have different requirements, several seem to be affected by forest management in one way or another; management actions in rotational forest management affect the cover of several species in the field layer (Hannerz & Hånell, 1993). Moose have also been found to affect the field layer cover indirectly through changing the light availability, with stronger effects in more productive areas (Mathisen et al., 2010), and potentially by direct browsing on some species in the field layer. The two most abundant species in the field layer in Sweden's productive forest area are bilberry (Vaccinium *myrtillus*) and lingonberry (*Vaccinium vitis-idaea*), with average covers of 11.1% and 7.4% respectively (Skogsdata, 2022). General cover of the field layer is about 40% (Skogsdata, 2022). Increased moose density leads to a decrease in the cover of bilberry, and an increased cover of a non-browsed graminoid (wavy hair-grass, Avenella flexuosa) (Mathisen et al., 2010). Meanwhile, an increased density of red deer, fallow deer and roe deer may increase feeding competition with moose over *Vaccinum* shrubs and therefore lead to moose increasing their pine consumption (Spitzer et al., 2021).

1.4 Research aim

There is an interest and need to diversify forest management and increase the amount of deciduous trees in production stands in Sweden (Angelstam et al., 2020; Bergquist et al., 2016), and using natural regeneration is a cost-effective way of working towards this goal (Götmark et al., 2005). Young stands contain most of the browse available to moose and other herbivores, and they may have a significant effect on survival and establishment of trees within browsing height, therefore also influencing the future stand species composition. 40% of productive forest area in Sweden is currently covered by pine stands (Skogsdata, 2022).

This study presents results from a 5-10 year exclosure experiment, focusing on the effects of primarily moose browsing on vegetation characteristics along a productivity gradient in Sweden. The overall aim was to study the effects of moose browsing on the development of naturally regenerating deciduous trees and field layer in young pine production stands. The effects on natural regeneration of deciduous trees were divided into the effects on the established trees (>2.5m) and the trees forming the deciduous forage resource (trees with forage within the height span of 0-2.5 m).

2. Methodology

2.1 Study area



Figure 1 – Location of the study area's in Sweden. Area 3 is not depicted because data were not collected there.

Data were collected between 2019-2022. The study plots range from the province of Småland in the south to Västerbotten in the north, roughly 850 km apart and covering a latitudinal gradient from 56°52' to 64°17' N (see figure 1). Annual precipitation ranges from 400 to 800 mm, falling year-round but mostly in summer and autumn. The annual mean temperature ranges from 2°C in the plots in Västerbotten to 7°C in Småland (SMHI, z.d.). study covers This the boreonemoral, southern boreal and middle boreal vegetation zones (Ahti et al., 1968). The soil types vary between glacial sediments and moraine soils, both with some additions of sand, postglacial sand or peat. The browser community in the southernmost surveyed areas (no. 6 and 7) is represented by moose, roe deer, red deer and fallow deer, while in the northernmost areas (1, 2,4 and 5) the dominating species is moose with low densities of roe deer. The moose population in Sweden is roughly stable at 340 000 individuals and is kept at roughly this level through yearly

harvest. Population density varies between 4 and 11.6 individuals per 1 000 hectares of forested land, with an average of 7.1 nationally after harvest (Widemo et al., 2022).

2.2 Study design

For this study, data has been collected at 11 sites, which is a subset of sites in which permanent plots were established in 2012-2014 to study pine growth under browsed, not-browsed and simulated browsed conditions (Wallgren, 2019). For the original study, seven areas with a distribution covering a major part of the country were selected, and for each area, sites with low, medium and high fertility ratings were established. The study sites were numbered per area from north to south (Västerbotten=1, Västernorrland=2, Dalarna=3, Värmland=4, Västmanland/Örebro=5, Östergötland=6 and Småland=7), with a second number showing the relative productivity rating (low=1, medium=2 and high=3) (Wallgren, 2019). In the present study I used study sites from all areas but 3.

Sites that were selected had to have a sufficiently large area (at least 7-9 ha) and harvesting maturity at time of selection. All sites are owned and managed by forest companies or larger forest owner associations. Grazing repellents are not used on the sites. The pines are planted according to industry standards, in rows that are 2 m apart and with 2 m between trees. This results in ~ 225 planted pines per 30 x 30 m plot. The exclosures are approximately 3 meters high and exclude larger mammals such as moose and deer, but not smaller animals such as rodents and hares (Wallgren, 2019).

The sites selected for this study were of pre-commercial thinning age (between 6 and 9 years) and were measured before pre-commercial thinning was executed. Each site contains a fenced plot (exclosure, from now on called the F plot) and one or two unfenced plots (from here onward the UF plots), permanently marked in the field by metal poles (figure 2). The plots measure 30 x 30 meters but there is a buffer of 5 meters around the F plot (thus a fence of 40 by 40 meters) to avoid edge effects. For more detailed measuring of the forage trees as well as field layer there are six 1-meter radius subplots at fixed positions within in each plot as depicted in figure 3.





Figure 2 – A study site (light green) with two unfenced and one fenced 30x30m plot (dark green) and six one meter radius subplots per plot (red dots).

Figure 3 – Location of the six subplots within the plot. Four subplots in the corners five meters from both edges, and two at the middle of the plot, 15m from one side and 10 m from the other.

2.3 Data collection

In the field, the following tree species were found; Scots pine, Norway Spruce, silver birch, downy birch, rowan, aspen and Salix spp (from now on Salix). All stems that were not touching above ground were counted as individual trees. The independent variable "fence" is directly connected to the plot number, latitude was retrieved from mapping of the plots and the site index (SI) was provided by the land owners.

2.3.1 All sites

Established trees (> 2.5 m)

The number of naturally regenerated trees over 2.5 m for each species in the whole plot (30 x 30 m) was counted. I consider these trees as established, having a high likelihood of forming the future stand (if not removed in pre-commercial thinning). At heights above 2 m the browsing itself is probably not deadly for the tree anymore (as shown for pine by Wallgren et al., 2014). The planted pines were not counted, as they were not naturally regenerated and were evenly distributed by planting at the same time as plot establishment.

Forage trees

In the subplots, measurements were taken on the forage trees and on the field layer. Forage trees are considered to be all trees of all species and sizes with branches available within browsing height 0-2.5 m, which in these young study sites were all tree individuals encountered. For these forage trees the following was noted: site-number, plot-number, subplot-number, tree-number (all trees found in the subplot were numbered consecutively), species (as listed above) and height in cm from ground to the highest living part.

Field layer

The field layer was surveyed by noting the cover (percentage) and representative height (cm) of the following species or functional groups: bilberry, lingonberry, common heather (*Calluna vulgaris*), other Ericaceae shrubs, fireweed (*Chamerion angustifolium*), other field layer (non-woody plants that do not fit in any other category, such as gras, herbs, ferns), European red raspberry (*Rubus idaeus*, later called "raspberry") and other woody plants up to 1.5 m height (excluding trees, later called "other woody plants").

2.3.2 Västerbotten sites (11, 12 & 13)

At site 11, 12 and 13, I took additional measurements on rowan, aspen and Salix in the whole plot, and clippings for forage quantification.

Rowan, aspen and Salix focus plots

For more detailed information on the RAS species, a complete plot inventory of all RAS trees was performed, noting their species and height. Seedlings <15 cm were excluded as the chance of detecting these in the field layer was too low.

Forage biomass

To obtain deciduous forage height-weight curves, forage samples were taken on all deciduous trees larger than 15 cm in all the subplots, using pruning shears to cut off all twigs identified as forage on a tree. Twigs with leaves were considered as forage up to a diameter of 3 mm (Fredriksson, E. and Wallgren, M., unpublished data), up to a height of 2.5 m (which was considered to be the browsing limit). If less than 10 trees of a species were acquired in all subplots in a plot, additional samples were taken in the rest of the plot. For all trees from which forage was taken, the species and height was noted.

Forage was collected in paper bags for individual trees. The samples were dried at 50 °C in drying ovens until the weight stabilised for a few (5-10) samples that were continuously weighed (\sim 8 days). Part of the forage samples were weighed the day of collection to acquire fresh-to-dry weight ratios so that comparing results to

literature using fresh weight is possible. All analyses on forage were done on dry weight to not introduce any errors due to different ratios.

In order to gather enough datapoints to create height-weight curves, sampling of additional forage trees outside of the subplots was conducted. The selection of these trees was subjective as the aim was to target a wide representation of species and height distributions. Hence, these samples are not representative of the actual distributions in the plots.

2.4 Data analysis

I used R version 4.2.1 (R Core Team, 2022) for all data analyses and visualisations. I used alpha <0.05 as the significance threshold for statistical tests. Normality testing was done using the Shapiro-Wilk test and visual inspection of the density plot and the Q-Q plot (using the functions *ggdensity* and *ggqqplot* from the package ggpubr (Kassambara, 2023)).

This is a study of traditional productive pine stands. Although spruces were present and included in data collection, they have been excluded in some of the analyses as they are rarely browsed and thus not a focal species of this study. Additionally, the soil-types of these stands are not traditionally suitable for spruce and spruce is also not the intended commercial crop in the sites. Lastly, the spruce trees observed were not necessarily of the same generation as the other trees observed (rather remnants from the previous stand). They have been included in diversity calculations and in the NMDS ordinations, and when analysed individually this was only to assess competition with the other species and functional groups.

2.4.1 Established trees

For this question, a dataset containing counts per tree species of all trees over 2.5 m in the plot was analysed.

Count

Some functional groups were created with pooled data of specific species:

- RAS: sum of rowan, aspen, Salix (no oak was found in any of the study plots, hence RAS instead of RASO)
- Total Birch: sum of silver birch and downy birch
- Total Deciduous: sum of silver birch, downy birch, rowan, aspen and Salix. The pooling was done because the RAS-group did not contain enough trees per species to perform analyses but grouping them made analysis possible. Total birch was calculated because silver birch and downy birch inhabit a similar ecological niche, so they are potentially in high competition with each other (Hynynen et al.,

2010). Grouping the birches may show clearer effects to the studied variables (fence and SI) because it takes away the possible competition between the two species. Total deciduous is interesting as a group because the combination of both the birches and the RAS provides a realistic main food source for browsers besides pine, and as a group they are competing with the production species pine.

The count of established trees contained many zeroes where species were not present, therefore data were not normally distributed. To find out whether species count differed between F and UF plots, I first performed Mann-Whitney U tests for each species and the functional groups.

Generalized Linear Mixed-effects Models (GLMM)

Because of the skewed distribution of the count data, I also used generalized linear mixed-effect models (GLMM) with a Poisson distribution using the function *lmer* from the lme4 package (Bates et al., 2023). I tested for differences in data distribution of the count between the F and UF plots, and for the effect of the SI on counts. All models included a random effect of site to account for the nesting of the data.

I also intended to test the effect of latitude and the interaction effects of latitude x fence and SI x fence. However, all these models were non-convergent because the size of the datasets was not sufficient for these more complicated models and thus these models were not analysed any further. Of the remaining model with only the independent variable fence, or both fence and SI as independent variables, the model with the lowest Akaike Information Criterion (AIC) was selected. If Δ AIC between models was smaller than 2, I selected the model with the least independent variables (thus the model with only fence).

I used the Dharma package (Hartig & Lohse, 2022) to test for overdispersion (function *testDispersion*) and zero inflation (function *testZeroInflation*). In case of a zero-inflation (p-value < 0.05), the model predicts significantly less zeroes than are found in the data set it is based on. I used the function *performance::check_Zeroinflation* from the performance package (Lüdecke et al., 2023) to see exactly how the zero-inflation was affecting the model predictions. For the species count data, the zero-inflation was significant for two cases (total birch and total deciduous), in both cases with one observed zero and no model predicted zeroes, which I deemed an acceptable difference and the models were used.

Non-metric Multidimensional Scaling (NMDS)

To investigate species composition of the plots established trees in reaction to browsing, I made a non-metric multidimensional scaling (NMDS) ordination. I used the function *metaMDS* from the vegan package (Oksanen et al., 2022) for the ordination, using the Bray-Curtis community dissimilarities based on species counts.

The stress value shows the goodness of fit of the NMDS to the original dimensionality of the data, it determines how well the fit of the limited dimensions ordination fits the original distance. Generally a stress value < 0.2 is accepted as a good fit (Clarke, 1993), but it has been suggested that in specific cases even a higher stress level would be acceptable (Dexter et al., 2018). I used two axes for the NMDS ordination (k=2).

To see if there was a difference between F and UF plots, I tested for a difference in centroids and dispersions between the groups. I used a PERMANOVA with the Bray-Curtis distances (*adonis2* function from the vegan package) to test for a difference in centroids and tested the difference in dispersions using the function *permutest*, also from the vegan package, which performs a permutation-based test of multivariate homogeneity of group dispersions (variances). The multivariate homogeneity of groups dispersion was calculated with the function *betadisper*.

Shannon Diversity Index

The Shannon diversity index (H) for all trees and for only the deciduous trees was calculated for each plot using the function *diversity* from the Vegan library (Oksanen et al., 2022) in R.

$$H = -\sum_{i=1}^{n} p_i \ln p_i$$

In which n is the total number of species and p_i is the relative abundance of the species *i*.

H was normally distributed and unbalanced for all tree species, so a Welch Two Sample t-test was performed to test for differences between F and UF plots. H for only the deciduous trees was not normally distributed and therefore a Mann-Whitney U test was performed.

2.4.2 Forage tree resource

The analyses on forage tree data were performed on trees of all heights and species in the subplots. The subplot data were pooled per plot to avoid pseudoreplication and analysed with the plot as sampling unit for the analyses on the counts and weights.

Count

The counts of forage trees were not normally distributed for any of the species / functional groups. To look at the difference between F and UF plots, I performed a Mann-Whitney U test for each species / functional group. To test for not only the mean but also the distribution of the data, I used a GLMM with a Poisson distribution, testing for the effect of fence and the effect of SI, with a random effect

of the site. As in question 1, I intended to test for the effect of latitude and interaction effects of SI and latitude with fence, but these models were nonconvergent and thus not used. Model selection and model testing for divergence and zero-inflation was done in the same way as for the GLMM in Q1. None of the significant factor-models was overdispersed or zero-inflated.

Species composition and diversity

To reveal possible differences in species composition between the F and the UF plots, I performed NMDS ordinations using the cumulative count of trees from the subplots. This was done with the same methodology as the NMDS for question 1.

The Shannon-diversity was also calculated for this dataset, for both all trees and only the deciduous trees. Shannon diversity was not normally distributed for both. To test for a difference between the F and UF plots a Mann-Whitney U test was used.

Weight

To calculate forage biomass for all the plots, I made height-weight curves for each species to predict forage weight based on the height of all the forage trees. These curves are based on the forage biomass dry weight of all trees collected for forage biomass from plot 11, 12 and 13.

By using a curve based on these data from Västerbotten to predict forage weight for each species in all plots, I made the assumptions that the height-weight curve of these plots is representative for trees in the other areas; that differences in climate and length of growing season do not affect the height-weight curve and that the fact that data were collected inside as well as outside of the fence, and from sites with 3 different SI do not affect the curves in a way that affects the results, since the assumptions were the same for all plots. Based on the scatterplots of height-weight distribution for each of the species, I decided to fit an exponential model. I used the function *lm*, with the log(weight) as the response variable to the independent variable height. This model was then used to predict the weight of trees based on their height. These curves can be found in appendix 1. The fit of the exponential curve is only good until the highest weight in the collected data, after that the model predicts unreasonably high values. I took a conservative approach and lowered all weights above the limit to the limit weight (see appendix 2 for these weight limits).

I summed the individual tree weights for the forage trees to a total forage weight per plot for each species and functional group. The weights were not normally distributed. I performed a Mann-Whitney U test to compare the F and UF plots. To better account for the data distribution (many zeroes and lower numbers), I rounded the weights off to integer values and analysed it with a Poisson-distribution GLMM. The Poisson-distribution is usually used for count-data (as it is in the rest of this study), but these weights follow the same distribution and I argue that you could see the weights as weight-units that were counted in the plot, albeit indirectly.

As for the previous two uses of Poisson-distributed GLMM, only a model with an independent factor of fence and model with a factor of both fence and SI were tested (both with a random effect of site). Model selection, testing for overdispersal and zero-inflation was done in the same way as for the GLMM's in question 1. The models for Total Birch and Total Deciduous gave warnings for zero-inflation, both predicting 0 zeroes while there were 3 zeroes in the dataset. These zeroes occurred in two of the UF plots and one of the F plots, I deemed this balanced enough to expect the significance of factors in the GLMM not to be affected by this probable zero-inflation. The model for downy birch was zero-inflated, with seven zeroes observed and two predicted.

2.4.3 Field layer

To study the effect of browsing on the field layer, the data with cover of fieldlayer vegetation species and functional groups were used. I calculated the average cover per plot for all species and functional groups from the six subplots. To analyse the plots as a whole, I used NMDS ordination to look at the species composition between the F and UF plots. I used the same method as for the NMDS on tree counts from question 1 and question 2. Shannon diversity was calculated in the same way as for question 1, but using cover percentages to determine the proportion of species instead of their counts. To analyse the potential difference in cover for the separate species and functional groups, I performed a Mann-Whitney U test as the data were not normally distributed for any of the species / functional groups.

3. Results

3.1 Established deciduous trees

A total of 22 plots were surveyed for established trees i.e. >2.5 m, and in total 1065 deciduous established trees were counted. The species composition of established trees differed visually between sites but also between F/UF plots, see figure 4 for an overview of all tree species counts in the F and UF plots.



Figure 4 – Count of established deciduous trees (height >2.5 m) in the whole plot ($30 \times 30m$). Mean count for unfenced plots on sites with two unfenced plots measured (site 11, 12, 13, 43).

It becomes clear that no matter the magnitude, one or both of the birch species are present in all sites, both in the F and UF plots. In total I counted 481 silver birches and 546 downy birches over 2.5 m. Only in one UF plot in site 11 birch was not found.

In all, 96% of the established deciduous trees counted were birch, both inside and outside of the fence. Contrastively, RAS species were only found in 3 out of 9 sites and made up 4% of all deciduous trees, both inside and outside of the fence. The biggest contributor to the RAS count for established trees were the 19 rowans, and 92% of those were found inside the fence. I found 1 aspen in an UF plot (site 23), and 1 aspen in a F plot (site 13). A total of 17 Salix were found, of which 11 in UF plots, 6 in F plots. Site 11 had low numbers of deciduous trees but a lot of naturally regenerated pines. Spruce numbers were generally low in all plots. In total 561 pines and 84 spruces were counted (see appendix 3).



Figure 5 – Count of established trees (self-regenerated trees >2.5m) in whole plot (30 x 30 m). Pine* includes only the self-regenerated pines and not the planted pines. *Mann-Whitney U test, p<0.05

A Mann-Whitney U comparison test of species-specific established tree counts (as seen in figure 5) showed that the fence had a significant effect on the number of total birch (p=0.011), and on the count of total deciduous (p=0.011). RAS did not show a significant difference between the F and UF plots, but because birch adds up to much higher numbers than RAS it is still unsurprising that counts of total deciduous were significantly higher in F compared to UF. In paired testing, total birch and total deciduous were also significantly different between F and UF plots (paired Mann-Whitney U test, p=0.008 for both functional groups).

For all species and functional groups as shown in figure 5, the Poissondistributed GLMM showed a significant positive effect of the fence on the count of established trees (table 2). The best fit (lowest AICc) was always the model with fence as a fixed factor (and site as a random factor), the model with an additional factor of SI did not improve model fit (these models can be found in appendix 4).

Table 1 – Results of best fit generalized linear mixed model for species or functional groups of established tree counts with significant factors (response – count, N=22, random effect of site). Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05

Surer Buen GEmini				
Variable	Estimate	SE	Ζ	Р
Intercept	1.688	0.701	2.407	0.016 *
Fence	0.822	0.094	8.763	< 0.001***
Downy Birch GLMM1				
Variable	Estimate	SE	Ζ	Р
Intercept	1.659	0.659	2.52	0.012 *
Fence	0.972	0.090	10.76	< 0.001***
Total Birch GLMM1				
Variable	Estimate	SE	Ζ	Р
Intercept	3.200	0.204	15.70	< 0.001***
Fence	0.902	0.065	13.85	<0.001***
RAS GLMM1				
Variable	Estimate	SE	Ζ	Р
Intercept	-4.996	4.401	-1.135	0.256
Fence	0.767	0.341	2.251	0.024 *
Total Deciduous GLMM1				
Variable	Estimate	SE	Ζ	Р
Intercept	3.251	0.199	16.30	< 0.001***
Fence	0.897	0.064	14.03	<0.001***

Silver Birch GLMM1

For species composition, the NMDS ordination of the plots in figure 6A shows that there is a larger spread of species compositions in the UF plots. A PERMANOVA showed that the fence did not have significant impact on the ordination (Pr(>F)=0.3) and a permutation test for homogeneity of multivariate dispersions showed that centroids and dispersions are not significantly different from each other between the F and UF plots (Pr(>F)=0.291). There is thus no statistically significant difference in the species compositions of the F compared to the UF plots.



Figure 6 - A) NMDS ordination of plots based on their naturally regenerated established (>2.5m) tree species composition. Dark grey hull and black letters display the spread for fenced plots and light grey hull and blue letters the spread for the unfenced plots. Labels are the site number and plot type (F or UF). Stress for this ordination is 0.134, which is considered a fair fit. **B**) Shannon Diversity (H) per plot for the established trees (>2.5m). F=Fenced plots, UF=Unfenced plots.

Figure 6B shows the Shannon diversity for all self-regenerated established trees. The difference between the mean of the F and UF plots is not significant for the complete tree diversity (Welch Two Sample T-test, p=0.563), but there are both higher and lower values for diversity in the UF plot.

3.2 Forage tree resource

3.2.1 Tree count

Within 24 plots, detailed measuring of forage trees was conducted in subplots, see figure 7 for cumulative counts per plot. These are trees of all heights, providing forage available at 0-2.5 m. Six subplots add up to a surface area of 18.85 m^2 , which is the area of comparison of forage tree counts per plot.



Figure 7 – Count of forage trees found in the six subplots (total area 18.85 m^2), Mean count per species for unfenced plots on sites with two unfenced plots measured (site 11, 12, 13, 43). Planted pines are included in this measurement.

In total there were 296 pines present across all the subplots, with pines found in every sampled plot (on average 12.33 pines per 18.85 m^2). A total of 8 spruces were counted over 5 sampled plots (18.85 m² per plot). Birch was found in all but 3 sampled plots, with a total of 365 birches. There were 249 downy birches spread over 17 plots and 116 silver birches spread over 20 plots. Especially site 13 had high numbers for downy birch, contributing to this high total compared to silver birch. Concerning the RAS group, I counted 44 Salix spread over 15 plots, 23 rowans over 10 plots, and 8 aspen in 7 plots, totalling at 75 individuals from the RAS functional group. In the UF plots, the amount of trees with browsing damage was highest for rowan (100% of trees browsed), then Salix (60%), downy birch (23%), and lastly silver birch (10%). Only 1 aspen was found in the UF plots, which had not been browsed.

I looked at individual species or functional groups reaction to the fence, as can be seen in figure 8. For the count of forage trees, there was no significant difference between F and UF plots for any of the species and functional groups (Mann-Whitney U, p>0.05 in all cases). In Poisson-distribution GLMM, pine and silver birch had a significant fixed factor of fence (table 2). The models with nonsignificant factors for the other species or functional groups can be found in appendix 5.



Figure 8 – Count of forage trees found in the six subplots (total area 18.85 m^2) for all species and functional groups Total Birch, RAS and Total Deciduous. *Planted pines are included.

Table 2 – Results of best fit generalized linear mixed model for pine and silver birch. (response – count, N=24, random effect of site). All other species and functional group models were non-significant and can be found in appendix 5. Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05

Pine GLMM1				
Variable	Estimate	SE	Ζ	Р
Intercept	1.956	0.278	7.033	<0.001***
Fence	0.504	0.116	4.330	<0.001***
Silver Birch GLMM1				
Variable	Estimate	SE	Z	Р
Intercept	0.753	0.447	1.686	0.092
Fence	0.390	0.185	2.108	0.035 *

In figure 9A, showing the NMDS ordination of the sampled 24 plots based on the forage trees, there is again a larger spread of the UF plots compared to the F plots. Both the PERMANOVA and permutation test for homogeneity of multivariate dispersions showed that centroids and dispersions are not significantly different between F and UF plots (Pr(>F)=0.965 and Pr(>F)=0.911 respectively).

The Shannon diversity per plot for the forage trees did not differ markedly between F and UF plots (figure 9B). The complete Shannon diversity per plot was not significantly different between F and UF plots (Mann-Whitney U, p=0.720).



Figure 9 - A) NMDS ordination of plots based on the forage trees (of all heights) in subplots. Dark grey hull and black letters display the spread for fenced plots and light grey hull and blue letters the spread for the unfenced plots. Labels are the site number and plot type (F or UF). Stress for this ordination is 0.093 which is considered a good fit. **B**) Shannon Diversity (H) per plot for forage trees of all heights found in the subplots. F=Fenced plots, UF=Unfenced plots.

3.2.2 Forage biomass

Using the heights of all forage trees, the biomasses of the species / functional groups were calculated with the height-weight distributions (appendix 1). The biomass of species and functional groups per plot are shown in figure 10. Differences in mean biomass between the F and UF plots were not significant for any species or functional group (Mann-Whitney U, p>0.05).



Figure 10 – Biomass (dry weight) of all species and the functional groups: Total Birch, RAS and Total Deciduous. Biomass was calculated based on the known height of all individual trees, using height-weight curves made for each of the species (appendix 1).

Analyses of the same biomasses with a GLMM show significant positive effect of fence for all species and functional groups. Total Birch and Total Deciduous also displayed significant positive effect of SI on forage biomass in the plot. The other models with lower AIC scores can be found in appendix 6.

Table 3 – Results of best fit generalized linear mixed models with significant fixed factors for forage species or functional group biomass (Poisson distribution, response – weight, N=24, random effect of site). Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05

Suver Birch GLMMI				
Variable	Estimate	SE	Ζ	Р
Intercept	2.225	1.224	1.818	0.069
Fence	1.609	0.033	48.237	< 0.001***
Downy Birch GLMM1				
Variable	Estimate	SE	Z	Р
Intercept	3.334	0.815	4.09	< 0.001***
Fence	0.541	0.031	17.20	< 0.001***
Total Birch GLMM2				
Variable	Estimate	SE	Z	Р
Intercept	-1.553	1.883	-0.825	0.409380
Fence	1.083	0.022	49.823	< 0.001***
SI	0.278	0.080	3.474	< 0.001***
Rowan GLMM1				
Variable	Estimate	SE	Z	Р
Intercept	-8.771	3.136	-2.797	0.00516**

|--|

Fence	2.628	0.213	12.319	< 0.001***
Salix GLMM1				
Variable	Estimate	SE	Ζ	Р
Intercept	0.289	0.903	0.319	0.749
Fence	0.691	0.146	4.728	<0.001***
RAS GLMM1				
Variable	Estimate	SE	Z	Р
Intercept	-0.118	1.011	-0.117	0.907
Fence	1.505	0.110	13.644	< 0.001***
Total Deciduous GLMM2				
Variable	Estimate	SE	Ζ	Р
Intercept	-1.414	1.923	-0.735	0.462
Fence	1.100	0.023	51.605	<0.001***
SI	0.273	0.082	3.347	<0.001***

At the sites in Västerbotten (11, 12 and 13), I did a more comprehensive inventory of RAS species, including all individuals in the entire 30 x 30 m plot. I found 721 individuals in total, of which 372 rowans, 9 aspens and 340 Salix. In the UF plots, 92% of Salix, all 3 of the aspens and 70% of the Salix had browsing damages of some degree. I calculated the dry weight biomass of these sites, as depicted in figure 11. Directly clear is that the biomass of RAS is higher within the F plots. Interestingly, no rowans were present inside the fence in site 13, which points out that the numbers of trees are not only affected by the browsing, but that there is a natural variation in the regeneration as well.



Figure 11 – Forage biomass in RAS focus plots, total plot surveyed (30 x 30 m).

3.3 Field layer

The field layer was inventoried in the same six subplots of 22 plots (distributed across 7 sites) as the forage resource data. The overall cover differs from 15% in plot 115 (F) to 73% in plot 627 (UF) (figure 12). There is not a clear pattern of increase or decrease of total cover between F and UF plots. The most common species was lingonberry, found in all sites, and second most common was bilberry, which was found in all sites except for site 11. Heather had the highest average cover at 15%, thereafter lingonberry (14%) and "other field layer" (10%) which mostly consisted of grasses and herbs.



Figure 12 - Average cover of all species and functional groups (FG) of the subplots in each plot. In case of two UF plots, the average cover is shown (site 11,12,13 and 41).

The cover per field layer species and functional groups can be seen in figure 12. None of the species / functional groups showed a significant difference between the F and UF plots in their mean cover (Mann-Whitney U, p>0.05).

In figure 14A, the NMDS ordination of plots based on their field layer composition is shown, with a stress of 0.169. Similar to the NMDS ordinations of the established trees (figure 6A) and the forage resource trees (figure 9A), the spread of F plots seems to display a smaller variation in species composition. However, there was no statistically significant difference in the species composition between the F and UF plots (PERMANOVA: Pr(>F)= 0.975, permutation test for homogeneity of multivariate dispersions: Pr(>F)=0.421).

As depicted in figure 14B, the UF plots show a bigger variation in Shannon diversity values, both having higher and lower diversity values than the F plots.

The difference between the means is not statistically significant (Welch Two Sample t-test, p=0.3372).



Figure 13 – Cover of all field layer species and functional groups. Other Ericaceae shrubs and other woody plants have only 5 and 2 plots with a cover >0% respectively.



Figure 14 – A) NMDS ordination of plots based on field layer species composition. Dark grey hull and black letters display the spread for fenced plots and light grey hull and blue letters the spread for the unfenced plots. Labels are the site number and plot type (F or UF). Stress for this ordination is 0.1685133, which is considered an acceptable fit. **B**) Shannon diversity per plot based on the field layer species cover. F=Fenced plots, UF=Unfenced plots.

4. Discussion

My study provides insight into the effect of browsing on the establishment of deciduous trees, the forage availability in stands and the field layer vegetation before pre-commercial thinning in young Scots pine production stands.

There was a lot of natural variation between sites, which I accounted for by using a random effect of site in the GLMM's. However, having more knowledge on this natural variation could provide further clarification of the results. This study provides a snapshot of the development of the natural regeneration in these stands. Prior to data collection, other factors might have affected the stand development. Such other factors have the same likelihood of affecting the fence and the unfenced plots, since the only difference induced by the fence is the exclusion of large animals, such as ungulate herbivores. The fence did not exclude hares and voles, and I did find these bitemarks on some of the seedlings. Hares and voles affecting seedling survival has been reported (den Herder et al., 2009; Lyly et al., 2014), thus this might have affected the regeneration in both the F and UF plots. Between the plots, there are differences in the herbivore communities between the northernmost and the southernmost plots, so only the effect of browsing in general can be assessed.

Looking at the established deciduous trees is a way of forecasting possibilities for the future stand, and I have found that browsing negatively affects the abundance of established deciduous trees. There was a higher number of established trees inside the fence for both the birches and the RAS species, but the ratio between birch and RAS (96:4) was the same both inside and outside of the fence. The fact that browsing does not seem to affect this ratio amongst the established trees could be related to optimal browsing strategies. Moose have a preference for RAS (Bergqvist et al., 2018; Hörnberg, 2001; Månsson, Andrén, et al., 2007), but due to their low abundance it may not be an optimal strategy to go out and select for these species, rather they continue to fulfil most of their diet with the more abundant birch and pine.

Browsing had a significant negative effect on the establishment of RAS, which mostly consisted of rowans. 92% of the rowans in the established tree data set were found inside the fence. For every site containing rowans among the forage trees,

their number was higher inside the fence. The percentages of browsed trees were much higher for RAS than for birch, and rowan was affected most when looking at the forage trees in all sites as well as in the focus plots in Västerbotten. Edenius & Ericsson (2015) found that browsing has negative effects on rowan and aspen trees transitioning from <1m to 1-2 m, but less so on transitioning onwards to the 2-3m class. It is possible that the effect of browsing on establishment of trees in my results reflects the same effect, as my data includes cumulative effects of browsing at all heights. Growth of rowan has also shown to be affected by browsing by another study in pine dominated forest (den Herder et al., 2009). Moreover, the effects on RAS are in line with studies showing that moose have a preference primarily for rowan but also for aspen and Salix ((Bergqvist et al., 2018; Hörnberg, 2001; Månsson, Andrén, et al., 2007). Low abundance of the RAS species is also reflected in the Swedish national forest inventory (Skogsdata, 2022).

The effect of the fence on the mean count of forage trees was not significant (figure 8), and only the GLMM for silver birch and pine were significant (table 2). Pine is also an important, albeit not highly selected, forage species, so a lower abundance in the unfenced plots could be expected. At the current stand age, the more pioneer deciduous trees are still competitively stronger, thus this difference in pine between the fenced and the unfenced plots should not impact the results.

Using the count of trees of all heights without any limits, may not be a good measure for the effect of browsing on these trees. The number may not be affected even if the height, cover and biomass are. Moose browsing has shown to affect growth and thus height, but not mortality of rowan in Scots pine stand (den Herder et al., 2009). Moose have been shown to affect the height of trees both directly by browsing on the top shoot, and indirectly by consuming/reducing leaf biomass, limiting photosynthetic capacity and thus growth (Wallgren et al., 2014). Therefore, including height limits, such as for the established trees, makes it possible to find an effect of browsing.

To better show the reality of forage availability as affected by browsing, the forage biomass was predicted and analysed. My results show that browsing lowers the forage biomass of all deciduous species and functional groups. For the functional groups "total birch" and "total deciduous", the SI also had a positive effect on the amount of forage biomass. Because the SI reflects the fertility of the soil, higher growth rates and therefore larger biomass are to be expected. Månsson, et al. (2007) have shown that site productivity explained a large part of the variation in forage consumption. Unfortunately, a possible interaction effect between SI and browsing could not be tested, but might be interesting because it could give opportunity to increase the level of finetuning in the management of moose and other deer species depending on their geographical context.

The effects of browsing and site fertility may have been stronger, if the biomass in these stands would not have been predicted using the height-weight curves of trees in Västerbotten. Generally, growth is faster in southern Sweden, therefore using trees from the sites in Västerbotten may have led to an underestimation of the effects of browsing in the southern sites. I found that forage biomass is a good and biologically relevant parameter to assess forage availability, and through assessing the RAS focus plots I found that surveying bigger area's is necessary in order to collect enough data for analysis of less abundant species.

There was no significant result showing that browsing affects the field layer cover. This might mean that browsing has no effect or that the browsing pressure might have been too low to directly affect the field layer. Another explanation might be that there is an effect of direct browsing in the unfenced plots but also an increased competition for light in the fenced plots which would both negatively affect cover of certain field layer species. However, the NMDS ordination and species diversity graph do show some effect of browsing.

Visual inspection of the NMDS ordinations of established trees (figure 6A), forage trees (figure 9A) and field layer vegetation (figure 14A) all show that the spread of the unfenced plots is larger than that of the fenced plots. The statistical tests do not support that this difference could not have been random for each of the ordinations. However, having this pattern in all tree ordinations suggests that there is more variation in species composition where there is browsing. In line with this, the Shannon diversity index has both lower and higher values for diversity in the unfenced plots for both established trees and field layer. Because the browsing pressure outside of the fence was variable, it is possible that values for the Shannon diversity index show indications of the intermediate disturbance hypothesis (Connell, 1978). Compared to the fenced plot, the higher diversity in some unfenced plots might be explained by an increase in browsing disturbance. The spatial heterogeneity of intermediate browsing pressure may be leading to more heterogeneity in the stand both in tree species and conditions for the field layer vegetation. A further increase in browsing could be linked to a lower diversity than that of the fenced plots, because high levels of browsing disturbance can cause a decrease in diversity of seedlings and vascular plants (Gill & Beardall, 2001; Martin et al., 2010). In this study I compared plots with a complete absence of browsing with varying levels of browsing outside of the exclosures, and I suggest that future studies should include a more detailed measure of browsing pressure within the study plots, to provide better insight into this suggested mechanism.

Implications for forest management

If browsing results in a wider variation in plant community species composition and diversity, managing stands with browsing is more unpredictable and difficult to plan ahead of time. Especially in order to create more mixed stands and saving RAS species, higher flexibility and expertise from forest planners is needed. The stands in this study were pre-commercially thinned after the data was collected. This may not truly reflect conventional forestry practice, where some of these stands probably would have been pre-commercially thinned at a younger age. The absence of thinning allowed me to see the effect of browsing on tree establishment without any effects of prior management in the stand. Browsing decreased the amount of established deciduous trees, and if the management goal is to create more mixed stands, it may be good practice to delay pre-commercial thinning. This would allow the forest planner to see which trees will actually establish despite browsing and may be selected as potential main stems in the stand. Delaying the precommercial thinning or lowering its intensity may also maintain a higher amount of forage in the stand, so that the effect of pre-commercial thinning on available forage is reduced.

Rowan, aspen and Salix

In a planted pine stand, biodiversity would benefit from intermixing with deciduous trees, especially stands with currently very low abundances. The current browsing pressure in my plots did affect the establishment and forage biomass of RAS, and might impact opportunities for selection for these trees in management. The abundance of RAS in the fence, however, are generally low, with some examples where RAS species were found outside the fence but not inside of it. This means that the low abundance of RAS in the Swedish forest is not only due to browsing and there may be other factors at play. One such factor may be the historical forest management, which was directed at completely eliminating deciduous trees in productions stands by pre-commercial thinning or by using herbicides (Östlund et al., 2022). This could have limited the amount of seed trees currently available in the landscape and therefore options for regeneration. Another factor may be the general biology and life history of the RAS species. Relative probability of presence maps show mid to low presence predicted for smaller area's throughout the whole distribution of all three species (Caudullo & de Rigo, 2016; Enescu et al., 2016; Räty et al., 2016), showing they are not highly abundant in other countries or climatic zones. RAS are all fast growing pioneer species that can also survive in the understory under more closed canopies (Caudullo & de Rigo, 2016; Enescu et al., 2016; Räty et al., 2016), but perhaps the conditions for regeneration are not optimal in planted pine stands. The opportunities to select birch for futures stands are limited by browsing, but because of birch' high abundance, this does not impose strong implications for management.

5. Conclusion

I found that browsing significantly affects the abundance of established deciduous trees and the forage resource biomass. The species composition and diversity was not significantly affected by browsing but there was a pattern suggesting that browsing might cause different species composition, as well as both higher and lower values for diversity of established trees and field layer. This means browsing might be a part of the filter determining what trees are available for selection for forest planners, and that browsing makes it more difficult to make assumptions about stand development and therefore plan ahead, since species composition and diversity can differ between browsed stands. The low number of RAS species in the forest is not improved by browsing, as browsing does negatively affect the establishment and forage biomass of these species, but even without browsing their abundance and biomass is lower than that of birch. Other factors, such as historical forest management, current forest management regime and the ecology of the RAS species need to be assessed to be able to disentangle the role of ungulate browsing on the naturally regenerating deciduous trees.

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Popular science summary

Sweden is one of the countries in Europe with the highest amount of its land area covered with forest. This forest is managed with the rotational system, which means that all trees harvested for production in forest aerial units called stands, are harvested in one go. After this, the stand is regenerated with new young trees, usually by planting. In Sweden the planted trees are usually the coniferous trees Norway spruce or Scots pine. Because of this management method most of the forest stands are, at mature age, heavily dominated by a single species, with all trees in the same age. Forest biodiversity goals of the Swedish forest agency as well as the European Union are not being reached, in part because of the lack of diversity within the forest stands. A good way to increase the diversity in the stands would be by growing more deciduous trees, such as birch, rowan, aspen and Salix in the stands. This would create more mixed stands. These deciduous trees are usually regenerating naturally in these locations and could be used to create some mixing among the planted coniferous trees. There are several big herbivores in the Swedish forests, for example moose, roe deer, red deer and fallow deer. Especially for moose and roe deer, a big part of their diet consists of leaves and twigs of trees. The eating of twigs and leaves of trees is called browsing, while the other herbivores are more of mixed-feeders, that also consume a substantial portion of grasses and herbs. Because of their diet, herbivores may affect the natural regeneration of deciduous trees. Browsing can also affect the field layer, which is the lower vegetation below the trees, of for example grasses, herbs, bilberry and lingonberry.

The goal of this thesis was to find out how browsing affects the natural regeneration of deciduous trees and the field layer, by comparing between fenced plots with no ungulate browsing and unfenced plots where browsing could take place as per usual. I found that browsing affects how many trees manage to reach a bigger size (>2.5m) and also the amount of forage biomass in the plots. Forage biomass is the weight of the eatable parts found on the trees and was predicted for all the plots based on a model line that used the heights and weights for many trees. Using a statistical tool displaying the plots based on their species composition showed that many of the plots that were browsed had a more divergent species composition. Looking at how diverse the species compositions in the plots. The proportions of rowan and Salix that were browsed were higher than those of the

birches. This could be explained by the fact that these trees have been shown to be preferred by moose in other studies. However, even in fenced plots (that had no browsing), the numbers for rowan, aspen and Salix were still low. This means that there are probably other reasons than browsing that also affect their natural regeneration.

My results showed that browsing affects which species are left to be selected by forest managers, and that browsing causes different paths of development for the stands. It could be a good idea to wait with pre-commercial thinning, so that it is clear which trees can actually be selected for. More research on this topic could investigate the different factors that can impact the natural regeneration of rowan, aspen and Salix, as it does not only seem to be browsing that keeps their numbers low.

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The limit for model usage was at 468.2 gram (g) for silver birch, 352.0 g for downy birch, 259.5 g for rowan, 175.1 g for aspen and 294.2 g for Salix. If the model did not predict a weight of 0 for a height of 0 (in case of a species not being present in a plot), this was also altered to 0.

Site	Pine		Sp	ruce
	F	UF	F	UF
11	121	162	0	0
12	0	3	1	1
13	1	11	7	2
23	0	0	8	5
43	37	16	2	0
52	2	45	19	25
53	1	4	2	1
62	0	0	0	2
63	0	0	0	0

Counts of naturally regenerated pine and spruce >2.5 m.

Non-selected results of generalized linear mixed model for species or group count established trees(response – count, N=22). Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05

Silver Birch GLMM	2			
Variable	Estimate	SE	Ζ	Р
Intercept	-1.163	5.789	-0.201	0.841
Fence	0.822	0.094	8.760	<0.001 ***
SI	0.118	0.236	0.499	0.618

AICc GLMM1 =227.2, AICc GLMM2 = 230.0, \triangle AICc=2.78

Downy	Birch	GLMM2
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Variable	Estimate	SE	Ζ	Р
Intercept	5.717	5.594	1.022	0.307
Fence	0.972	0.090	10.766	< 0.001 ***
SI	-0.167	0.229	-0.729	0.466

AICc GLMM1 =201.8, AICc GLMM2 = 230.0, ΔAICc=28.22

Total Birch GLMM2

Variable	Estimate	SE	Z	Р
Intercept	1.072	1.636	0.656	0.512
Fence	0.900	0.065	13.834	< 0.001 ***
SI	0.087	0.067	1.311	0.190

AICc GLMM1 =270.7 AICc GLMM2 = 272.2, Δ AICc=1.43

RAS GLMM2

Variable	Estimate	SE	Ζ	Р
Intercept	-19.082	16.194	-1.178	0.239
Fence	0.762	0.341	2.238	0.025 *
SI	0.647	0.626	1.033	0.302

AICc GLMM1 =62.4, AICc GLMM2 = 64.1, Δ AICc=1.73

All Deciduous GLMM2

In Deciauous GL	11/12			
Variable	Estimate	SE	Ζ	Р
Intercept	0.667	1.521	0.438	0.661
Fence	0.896	0.064	14.013	< 0.001 ***
SI	0.106	0.062	1.713	0.087

AICc GLMM1 =255.9, AICc GLMM2 = 256.364.1, ΔAICc=0.44

Non-selected results of generalized linear mixed model for species or group count of forage trees(response – count, N=24). Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05

Pine GLMM2				
Variable	Estimate	SE	Ζ	Р
Intercept	1.793	1.969	0.911	0.363
Fence	0.504	0.116	4.328	< 0.001***
SI	0.007	0.084	0.084	0.933

AICc GLMM1 =197.9, AICc GLMM2 = 200.8, Δ AICc=2.9

Silver Birch GLMM2				
Variable	Estimate	SE	Ζ	Р
Intercept	0.519	3.160	0.164	0.870
Fence	0.390	0.185	2.106	0.035 *
SI	0.010	0.134	0.075	0.940

AICc GLMM1 =129.1, AICc GLMM2 = 132.0, Δ AICc=2.9

Downy Birch GLMM1

Variable	Estimate	SE	Ζ	Р
Intercept	1.188	0.643	1.846	0.065
Fence	-0.156	0.136	-1.143	0.253
Downy Birch GLMM2				
Variable	Estimate	SE	Ζ	Р
Variable Intercept	Estimate 6.225	SE 4.741	Z 1.313	P 0.189
Variable Intercept Fence	Estimate 6.225 -0.155	SE 4.741 0.137	Z 1.313 -1.127	P 0.189 0.260
Variable Intercept Fence SI	Estimate 6.225 -0.155 -0.218	SE 4.741 0.137 0.205	Z 1.313 -1.127 -1.063	P 0.189 0.260 0.288

AICc GLMM1 =201.5, AICc GLMM2 = 203.2, Δ AICc=1.72

Total Birch GLMM1

Variable	Estimate	SE	Ζ	Р
Intercept	2.017	0.458	4.405	< 0.001 ***
Fence	0.027	0.109	0.251	0.802

Estimate	SE	Ζ	Р
3.215	3.300	0.974	0.330
0.028	0.109	0.254	0.799
-0.051	0.140	-0.366	0.714
	Estimate 3.215 0.028 -0.051	Estimate SE 3.215 3.300 0.028 0.109 -0.051 0.140	Estimate SE Z 3.215 3.300 0.974 0.028 0.109 0.254 -0.051 0.140 -0.366

AICc GLMM1 =234.4, AICc GLMM2 = 237.1, ΔAICc=2.77

RAS GLMM1

Variable	Estimate	SE	Ζ	Р
Intercept	0.053	0.726	0.073	0.942
Fence	0.184	0.237	0.776	0.438
RAS GLMM2				
Variable	Estimate	SE	Z	Р
Variable Intercept	Estimate 0.512	SE 4.668	Z 0.110	P 0.913
Variable Intercept Fence	Estimate 0.512 0.185	SE 4.668 0.237	Z 0.110 0.778	P 0.913 0.437
Variable Intercept Fence SI	Estimate 0.512 0.185 -0.020	SE 4.668 0.237 0.201	Z 0.110 0.778 -0.099	P 0.913 0.437 0.921

AICc GLMM1 =102.5, AICc GLMM2 =105.4, \triangle AICc=2.9

Total Deciduous GLMM1

Variable	Estimate	SE	Ζ	Р
Intercept	2.178	0.472	4.611	< 0.001 ***
Fence	0.056	0.099	0.566	0.572
Total Deciduous GLMM2				
Variable	Estimate	SE	Ζ	Р
Intercept	3.116	3.413	0.913	0.361
Fence	0.056	0.099	0.568	0.570
SI	-0.040	0.145	-0.277	0.782

AICc GLMM1 =235.4, AICc GLMM2 = 238.3, ΔAICc=2.83

Non-selected results of generalized linear mixed model for species or functional group forage weight (response – weight, N=24). Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05

Silver Birch GLMM2	2			
Variable	Estimate	SE	Z	Р
Intercept	-8.093	7.821	-1.035	0.301
Fence	1.609	0.033	48.236	< 0.001***
SI	0.445	0.331	1.344	0.179

AICc GLMM1 =3202.8, AICc GLMM2 = 3204.2, \triangle AICc=1.35

Downy Birch GLMM2				
Variable	Estimate	SE	Z	Р
Intercept	9.688	5.729	1.691	0.091
Fence	0.541	0.031	17.198	<0.001***
SI	0.273	0.244	-1.117	0.264

AICc GLMM1 =22114.2, AICc GLMM2 = 2115.9, ΔAICc=1.69

Zero-inflated with 7 observed zeroes and 2 predicted zeroes.

Total Birch GLMM1

Variable	Estimate	SE	Ζ	Р
Intercept	4.923	0.395	12.47	< 0.001***
Fence	1.083	0.022	49.83	< 0.001***

AICc GLMM1 =5133.8, AICc GLMM2 = 5129.0, ΔAICc=4.78

Zero-inflated with 3 observed and 0 predicted zeroes.

Rowan GLMM2

Variable	Estimate	SE	Ζ	Р
Intercept	-26.508	17.864	-1.484	0.138
Fence	2.627	0.213	12.316	< 0.001*
SI	0.885	0.728	1.216	0.224

AICc GLMM1 =219.7, AICc GLMM2 =221.4, ΔAICc=1.69

Salix GLMM2				
Variable	Estimate	SE	Ζ	Р
Intercept	1.195	6.016	0.199	0.843
Fence	0.691	0.146	4.730	<0.001***
SI	-0.040	0.260	-0.152	0.879

AICc GLMM1 =180.3, AICc GLMM2 =183.1, ΔAICc=2.88

RAS GLMM1

KAS GLMMI				
Variable	Estimate	SE	Ζ	Р
Intercept	-0.118	1.011	-0.117	0.907
Fence	1.505	0.110	13.644	< 0.001***

Total Deciduous GLMM1

Variable	Estimate	SE	Ζ	Р
Intercept	4.956	0.395	12.56	< 0.001***
Fence	1.101	0.021	51.61	< 0.001***

AICc GLMM1 =4517.1, AICc GLMM2 = 4512.7, ΔAICc=4.4

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