The effects of site conditions and browsing on natural tree regeneration in protected areas of southern Sweden

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Independent project • 15 credits
Swedish University of Agricultural Sciences, SLU
Southern Swedish Forest Research Centre
Forest and Landscape Bachelor´s programme
Alnarp, 2025

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Credits:	15 credits
Level:	First cycle, G2E
Course title:	Independent project in Forestry science
Course code:	EX1012
Programme/education:	Forest and Landscape Bachelor's Programme
Course coordinating dept:	Southern Swedish Forest Research Centre
Place of publication:	Alnarp
Year of publication:	2025
Copyright:	All featured images are used with permission from the copyright owner.
Keywords:	Broadleaf forest, Light and edaphic gradients, Herbivory

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Faculty of Forest Sciences
Southern Swedish Forest Research Centre

Abstract

The homogeneous structures of Swedish forest limits and threats biodiversity. To protect and preserve the biodiversity found in the country, land is set aside. In southern Sweden, broadleaf forest is often suitable for such set asides due to their limited abundance and high associated biodiversity values. In order to preserve forests in the long-term, regeneration is a prerequisite. However, old broadleaf forest found in protected areas often are observed to have a limited natural regeneration. Broadleaf forest tree species compositions change along gradients in site conditions due to differences in tree species adaptations. Site conditions are among other things edaphic gradients which are spatial changes in moisture, nitrogen availability, and pH. Other factors which influence broadleaf tree species compositions are variations in light conditions, as well as selective browsing pressure that may alter how the species compositions of tree regeneration changes along these gradients.

This thesis´ aim was to test if browsing affects how the natural regeneration of trees varies along gradients of light and soil in protected broadleaf forests in southern Sweden. This was done by inventorying fenced and unfenced plots in three protected areas in the county Skåne. The collected data was the number of seedlings found, as well as the plots´ light and edaphic conditions indicated by the plots´ ground vegetation. Thereafter, Generalized Linear Models were created to test how the general number of seedlings and the number of beech and ash seedlings shifted with changing gradients of light and site conditions, and how this shift changed when exposed to browsing in un-fenced plots and when browsing was excluded in fenced plots.

The results indicate that the total number of seedlings and beech seedlings increased with increased nitrogen availability and lower pH. Additionally, lower pH was found to increase the total number of ash seedlings. Furthermore, increased light conditions increased both the total number of seedlings and beech seedlings. The results did not clearly indicate that browsing changes the expression of the light and edaphic gradients. There was rather a tendency that the effects of nitrogen availability and pH effect was more pronounced in un-fenced plots on the general number of seedlings and beech seedlings compared to fenced plots. The variable shade index indicated an increased number of beech seedlings with decreasing shade index in un-fenced plots compared to fenced plots. The single effect of fencing on the number of seedlings was not significant in this study but indicated an increase in seedling number in fenced plots.

This research shows tendencies that browsing influences how some edaphic and light gradients are expressed. However, the pattern is not consistent in the created models. The results still show that gradients of light and soil conditions effects natural regeneration. If fencing is implemented, sites which have a high variation of site conditions are expected to yield high variation in tree species regeneration. Research in this field of study is needed to understand how browsing influences natural regeneration expressed by certain site conditions. With a more well-rounded understanding, recommendations to protected areas which struggle with natural regeneration can be given.

Keywords: Broadleaf forest, Light and edaphic gradients, Herbivory

Table of contents

List of figures

1. Introduction

1.1 Broadleaf forest in Sweden

Rotational forest management in Sweden has resulted in a relatively uniform forested landscape where 80% of the country's standing forest volume consists of conifers, either Norway spruce (*Picea abies*) or Scots pine (*Pinus sylvestris)* (Felton et al., 2020; Lindbladh et al., 2014). Rotational forest management results in uniform species composition and homogeneous structures which limit and threat the biodiversity values of Swedish forests (Felton et al., 2020; Felton, Nilsson, et al., 2016; Lindbladh et al., 2014). To combat these threats to biodiversity and forest ecosystems, land is set-aside and preserved by creating protected areas such as nature reserves, national parks, or voluntary set asides (Götmark et al., 2000; Larsson & Danell, 2001).

Sweden had in 2023 formally protected approximately 6 % of the productive forest land and 9 % of the total forest land (SCB, 2024). Protected areas come with different purposes, sizes, structures, and species compositions. The different purposes of protected areas are often linked to preservation of biodiversity, cultural values or other valuable landscape elements (Angelstam, 1998; Götmark et al., 2000; Larsson & Danell, 2001). In southern Sweden, broadleaf trees and forest often meet these requirements.

Trees like oak (*Quercus spp.*), ash (*Fraxinus excelsior*) beech (*Fagus sylvatica*) and other broadleaf trees in southern Sweden are considered high in value for biodiversity as well as being associated with high cultural values (Hultberg, 2015; Leonardsson et al., 2015; Löf et al., 2016). The high biodiversity value of broadleaf forest is argued due to their high association with red listed species, as well as their relatively small distribution in Sweden (Berg et al. 1994, 1995). The distribution of broadleaf forest in Sweden was much different between 500 and 1000 years ago compared to present day (Björse & Bradshaw, 1998). The counties Småland, Halland, Blekinge and Skåne, Southern Sweden were mostly covered by beech forest and other mixed broadleaf forests. Scots pine forest was mostly found in western parts of Småland and Norway spruce was only present in northern Småland. The counties that had mainly broadleaf forest are today dominated by Norway spruce or Scots pine forests (Björse & Bradshaw, 1998). The decline of broadleaf forests has ultimately led to the associated and dependent species being affected and could be one of the reasons for broadleaf forests general high association with red listed species (SLU, 2020).

1.2 Habitat of broadleaved trees

Broadleaf tree species differ in site preferences and requirements for regeneration, survival, and growth. However, site conditions such as high nutrient and water availability are preferred by some species like beech, ash, lime (*Tilia spp.*), maple (*Acer spp.*), alder (*Alnus spp.*), hornbeam (*Carpinus betulus*), and some other broadleaves (Ellenberg, 2009). Beech, one of the most abundant broadleaf tree species in Europe, is a late successional tree species (Barna & Bosela, 2015). The species is shade tolerant while also producing deep shade (Ellenberg, 2009). It can be found in a variety of moisture conditions, but not on very dry or very wet sites. Additionally, beech can survive in a variety of pH ranges. Geographically, it can be found on slopes, hollows and all types of bedrock. This makes beech very competitive in natural conditions. However, beech is sensitive to hypoxia which makes it absent from waterlogged sites. Beech can also not grow on very high elevations (Ellenberg, 2009). Ash trees, similarly to beech, can grow on sites which have sufficient water availability without being waterlogged. Unlike beech, ash is relatively insensitive to drought and prefers more basic ph above 4.2 (Ellenberg, 2009). The ideal pH for ash in the UK was approximated to around 6 (Thomas, 2016). In central Europe, ash forest communities are considered highly productive in growth and can thus outcompete beech at young ages in site conditions they both are adapted to. Examples of ash habitats are on floodplains of rivers, humus rich slopes or ravines, as well as at the bottom of valleys which have nutrient rich soils and some moisture (Ellenberg, 2009).

Other broadleaf trees like lime and hornbeam tends to grow on sites which are both dryer and wetter than beech does. These species are often found more on sites where beech growth is reduced, and beech is less competitive (Ellenberg, 2009). Oak is in general a light demanding species and can be found on sites where beech is generally hindered by frost, drought, and or waterlogging. This includes habitats which are warm and dry, have acidic soils with low nutrient availability, and are wet or sometimes waterlogged (Ellenberg, 2009).

Broadleaf tree species composition changes along gradients in site conditions due to these differences in tree species´ adaptations (Ellenberg, 2009). Examples of site conditions are edaphic gradients which are spatial changes in moisture, nitrogen availability, and pH (Bigelow & Canham, 2002; Hedwall et al., 2018; Hedwall & Brunet, 2016). These gradients express the local site conditions and changing site conditions through a landscape (Bigelow & Canham, 2002; Hedwall et al., 2018; Hedwall & Brunet, 2016). Together, these gradients form varying natural forest with changing species compositions and associated biodiversity.

1.3 Regeneration problems of broadleaf forest

When aiming to sustainably protect and preserve the natural environment of broadleaf forests, natural regeneration of the different tree species is a long-term prerequisite. Regeneration provides a new generation of trees which ensures future habitat of the associated species in the ecosystem. However, studies have shown that natural regeneration of broadleaves species is limited in production forest, and in protected forested areas (Bobiec et al., 2011; Götmark et al., 2005; Turczański et al., 2021).

Protected broadleaf forests in southern Sweden often consists of old high closed canopy trees, providing shade and limiting the light availability. This results in hard competition for tree regeneration (Jensen et al., 2012). In addition to the edaphic gradients described above, variation in light conditions affects the composition of tree species in the forest (Hedwall & Brunet, 2016).

Browsing pressure is another factor which effects the tree species compositions (Hedwall et al., 2018; Götmark et al., 2005; Kuijper et al., 2010). Broadleaf species like oak, rowan (*Sorbus aucuparia*), beech, ash, lime, maple, and other, are exposed to browsing by herbivore species (Götmark et al., 2005). In southern Sweden the browsing species tend to be roe deer (*Capreolus capreolus L.*), moose (*Alces alces L.*), hares (*Lepus europeus, L. timidus L.*), red deer (*Cervus elaphus L.*) and fallow deer (*Cervus dama L.*) (Svenska Jägareförbundet, n.d.) (see Appendix 1). However, browsing pressure can be countered by fencing which is proven effective on oak regeneration (Götmark et al., 2005; Jensen et al., 2012). Previous research about browsing effects in Białowieża Primeval Forest, Poland, on natural regeneration indicated that browsing pressure is affecting the species compositions formed by the edaphic gradients (Hedwall et al., 2018). This is due to browsers being selective, browsing less, or making less impact on fast-growing trees with thick leaves, and low leaf nitrogen content (Hedwall et al., 2018). Therefore, due to browsing selection, some tree species may be favored, which changes and filters the expressions of gradients in site conditions.

Altogether, this means that the composition of natural tree regeneration in an area is affected by the combined conditions of the site, formed by the edaphic gradients (Hedwall et al., 2018), light availability resulting from competing vegetation (Jensen et al., 2012; Hedwall & Brunet, 2016), and the selective browsing pressure (Hedwall et al., 2018; Götmark et al., 2005). The combined effect of the browsing pressure that broadleaves are exposed to, and the strong competition from mature trees, which are often found in protected areas, is that regeneration of trees often is poor (Götmark et al., 2005; Jensen et al., 2012). This proposes a threat to the already limited broadleaf forest in southern Sweden as well as the biodiversity dependent on its continued existence. Therefore, there is a need to establish more knowledge about how browsing affects how gradients in site conditions are expressed in tree species composition.

1.4 Purpose and Hypothesis

The purpose of this thesis is to increase the knowledge about the effects that different site conditions and browsing have on natural regeneration in protected areas consisting of old broadleaf forest in southern Sweden. This will be achieved by answering the research question: How does browsing in protected areas in southern Sweden affect the variation in natural regeneration of tree species formed by light and edaphic gradients? The hypothesis is that the number of seedlings will vary along light and edaphic gradients when browsing is limited by fencing, while this variation will be less pronounced in unfenced plots where regeneration is constrained by browsing pressure.

2. Materials and methods

2.1 Project design

In the year 2000, a research team in Poland established a study in Białowieża Primeval Forest, Poland, with the aim to examine the effects that browsing have on natural regeneration in the highly protected area (Kuijper et al., 2010). With respect to this experiment conducted in Poland, the Swedish University of Agricultural Sciences (SLU) have during winter of 2017 and 2018, similarly to the polish research team, placed survey plots in three different protected areas in southern Sweden (section 2.2). The reasoning for replicating the polish method is because the method is already tested successfully and allows further comparisons between the two experiments.

To examine the effects that browsing has on natural regeneration of tree species in protected forested areas, a total of 60 survey plots were established with 20 plots in each of the three protected areas. The plots are of quadratic shape with a side of seven meters and covers an area of $49m^2$. Within each protected area, 10 plots have a 2-meter-high fence inclosing them. Near each fenced plot, and with similar site conditions, an un-fenced plot was established. The fenced plots aim to achieve conditions where browsing is not a factor influencing the regeneration (Figure 1). The unfenced plots aim to represent normal conditions of the protected area and will be used as control plots for comparisons.

Figure 1. Fenced plot in Fyledalen. Taken by Gustaf Kihlstedt (2025).

2.2 The studied protected areas

The protected areas are all broadleaf forest nature reserves and Natura 2000 locations indicating that they hold threatened species and habitats worthy of protection and preservation. The locations are Maltesholm, Hästhagen and Fyledalen, all located in the county Skåne, Sweden (Figure 2).

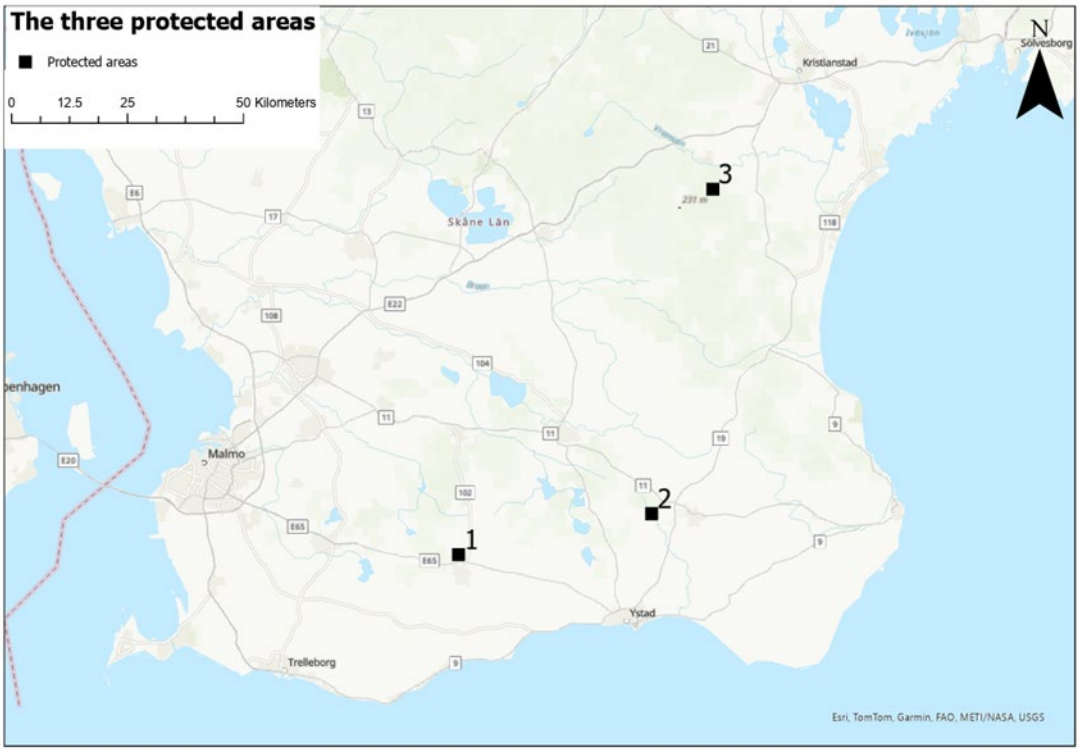

Figure 2. Map of southern Skåne, created in ArcGIS (version 3.1.0), black squares indicate where the nature reserves are located. 1) Hästhagen, 2) Fyledalen, 3) Maltesholm.

Maltesholm

The nature reserve Maltesholm is found in eastern Skåne in the municipality of Kristianstad and the area is 29 hectares in total. The 29 hectares in Maltesholm are mostly mixed broadleaf forest, mainly dominated by mature and old beech, but also ash, oak, elm (*Ulmus glabra*), birch and maple trees. The oldest trees in the nature reserve are approximately ~ 250 years old. The forest in Maltesholm hosts many different species including saproxylic invertebrates, different woodpeckers, wild boar and fallow deer (https://www.lansstyrelsen.se/).

Hästhagen

The nature reserve Hästhagen is in close quarters to the castle Svaneholm in the municipality of Skurup. The nature reserve is located on a small hill surrounded by open grazing and farmlands. The nature reserve is in total 56 hectares and is dominated by old beech forest. However, there are also oak, ash, and elm. Hornbeams dominate in the nature reserve´s edge zones (https://www.lansstyrelsen.se/).

Fyledalen

The nature reserve Fyledalen is in total 946 hectares and stretches over the municipalities of Tomelilla, Sjöbo and Ystad. Fyledalen encompasses a valley where the slopes leading to the bottom river are covered by mainly old beech forest but also hornbeam in the forests edge zones. Parts of the forests include ash, spruce, oak and maple trees. Fyledalen holds many different types of species, some examples are different beetles, frogs, salamanders, fungi, bats, and deer (https://www.lansstyrelsen.se/).

2.3 Potential browsers in protected areas

The browsers that are assumed to be present in the protected areas are roe deer, moose, hares, red deer, and fallow deer (Svenska Jägareförbundet, n.d.) (see Appendix 1). It is likely that the majority of the browsers in Maltesholm, Hästhagen, and Fyledalen are fallow deer and hares, due these species being observed during the data collection periods.

2.4 Inventory

Firstly, to describe the site conditions, an inventory of ground vegetation (including woody species) within the survey plots of each protected area was conducted in spring 2023. Five one by one-meter quadrats within each survey plot were inventoried. The data noted was the ground vegetation species and its approximated cover in percentage within the inventoried area. I then used the ground vegetation data as ecological indicators of the examined plots site characteristics using the species indicator values provided by Tyler et al. (2021). The indicator values I used when determining the site characteristics were those representing species adaptations to light availability, soil moisture, soil pH, and soil nitrogen availability. The scale of the indicators differ, light is measured on a scale one to seven, where one is deep shade and seven is always full sun conditions (Tyler et al. 2021). The moisture scale is from one to twelve, where one is very dry and twelve is deep water conditions (Tyler et al. 2021). The pH scale is between one to eight, where one is strongly acidic $pH < 4.5$ and eight is alkaline conditions with $pH > 7.5$ (Tyler et al. 2021). Lastly the scale of nitrogen is defined between one to nine, where one is nitrogen poor and nine is considered conditions where fertilization is involved in creating the nitrogen enriched conditions (Tyler et al. 2021).

To further investigate the survey plots site conditions, an inventory of the tree basal area was conducted in spring 2025 in all locations. During this inventory, I estimated the basal area from the centre of each plot, noting the basal area per species, using a relascope. I used the basal area to calculate basal area weighted shade indices of the survey plots. The shade index values per species were taken from Verheyen et al. (2012).

Furthermore, to examine the effects of browsing pressure and fencing treatments, an inventory of the survey plots was conducted previously during the spring in 2024 (Hästhagen and Maltesholm) and by myself in 2025 (Fyledalen). In this inventory, all established tree seedlings taller than 10 centimetres from ground level within each survey plot were inventoried. The data noted was species, height, browsed or non-browsed. Dead plants were not measured.

2.5 Data processing

The first parts of data analysis and processing involved calculating the total number of individuals per tree species in each plot. I did this by summarizing the collected data from the survey plots by location, plot, fencing treatment yes/no, species, in a sheet in Microsoft excel (version 16.89). Thereafter, by creating a pivot table from the whole summarised dataset, the total number of seedlings per species and total number of seedlings could be processed for each plot in each location.

Furthermore, the cover-weighted mean for each indicator value and plot was calculated. I did this by calculating the mean cover (across the five quadrats) of each ground vegetation species found in each of the 60 plots in Microsoft excel. Two plots were excluded at this stage since there was no ground vegetation present in them. Then for each species in each plot, I multiplied the mean cover of each species with that species´ indicator value (light, moisture, pH, and nitrogen). These products were then summed and divided by the sum of the mean covers per plot, giving the weighted mean indicator value for each indicator in each plot.

I calculated the basal-area weighted shade indices for each plot by multiplying the basal area for each tree species in each plot with the shade indicator value for the species, taken from Verheyen et al. (2012). These products were then summed for each plot and divided by the total basal area of each plot. This gave the basal-area weighted shade index for each plot.

Continuing, I put together these calculated variables in one database in Microsoft excel summarized by location, plot, fencing treatment yes/no, indicator for shade index, light, moisture, pH and nitrogen separately, total seedling count, and total seedling count for each species separately. I then checked these variables for corelation using the data analysis tool built into Microsoft excel. In the correlation test all continuous variables were checked together, not separating plots or locations. The major result of the correlation analysis was a strong correlation between light and the variables moisture (r=0.49), pH (r=-0.59) and nitrogen (r=-0.94).

Furthermore, I conducted a test of the site indicators´ effects on natural regeneration. This test included creating a Generalised Linear model (GLM) which was fitted using the glmmTMB function in the glmmTMB package (Brooks, 2025) in R (version 4.2.3). Three different response variables were used, the first was the total number of seedlings per plot, the second was the total number of beech seedlings per plot, and the third was the total number of ash seedlings per plot. The reasoning for comparing only the species ash and beech is due to their high abundance in the three locations and their differences in site preferences. These response variables were then tested for effects of site indicators (shade, light, moisture, pH, nitrogen).

I created two different GLMs for each of the three tested response variables, one model using soil dependent variables (soil model) and the other using light-indicating variables (competition model). The reasoning for creating two models was to avoid problems with multi-collinearity due to high corelations between different indicator variables (see above), as well as avoiding creating too advanced models in regard to the size of the database. At this stage of the analysis three plots were identified as outliers, having a disproportionally large influence on the GLMs. These plots had 490, 497 and 740 seedlings while all other observations were below 325. After evaluating the effects of different transformations, it was decided to exclude these observations, resulting in 55 observations. All GLMs used the Generalized Poisson distribution (genpois) and log-link to avoid overdispersion. The first full model included the indicator values for soil nitrogen, moisture and pH as well as fencing as a factor variable with two levels, unfenced (0) and fenced (1). The second full model included the competition dependent indicators light and shade index as variables and fencing as a factor. In both cases I included all possible two-way interactions between the continuous variables and the fencing factor in the full models. To select the best models based on these full models, the function buildglmmTMB in the package buildmer (Voeten, 2023) was used. This function performs stepwise eliminations of variables on complex GLM models based on their contribution to the explanatory power of the model, while punishing overly complex model alternatives. The result from the function is a suggested model structure which shows the effects of variables which have a clear effect on the response variable and excludes variables which does not have a clear effect on the response variable.

After all models were created, predictions of the models' effects were calculated using the function ggpredict in package ggeffects (Lüdecke, 2025). This function calculates expected outcomes of the response variable (total plant count per plot, total beech count per plot, total ash count per plot) by varying vital variables (shade, light, moisture, pH, nitrogen), while holding other variables in the model constant at their mean. The function also calculates a confidence interval (CI) of around 95% from the standard error (SE) of the predictions (CI = +/- 1.96 * SE). The created predicted effects and CI of each of the site indicators, developed from the six models, were then plotted together with the variables individual P-values calculated by the GLMs which uses a Wald chi-squared test. P-values below 0.05 in the plots indicate that the variable had a statistically significant effect.

3. Results

3.1 Effects of fencing and site conditions on total regeneration

The final soil model for total number of seedlings included pH, nitrogen, fencing and the interactions between nitrogen and fencing, and pH and fencing (total plant count ~ pH * fencing + nitrogen * fencing). The plotted model shows that increased nitrogen availability had a significantly positive effect on the number of seedlings found in both fenced and un-fenced plots (Figure 3a). Increased pH was found to have a significant negative effect on seedling number in both fenced and un-fenced plots (Figure 3b).

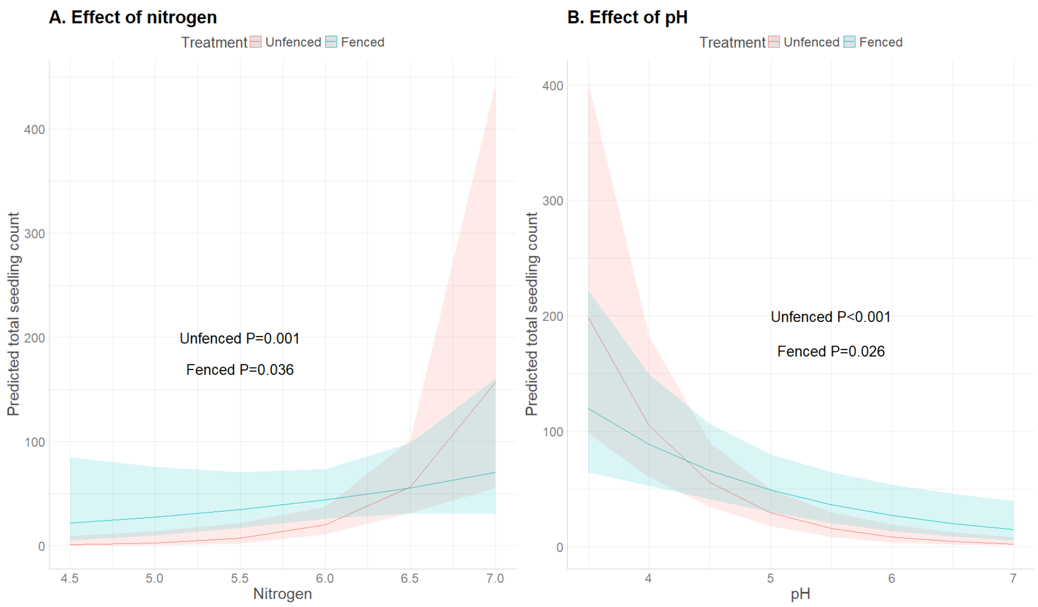

*Figure 3. Predicted effects of nitrogen (A) and pH (B) on total seedling count based on a Generalized Linear Model with the formula: total plant count ~ pH *fencing + nitrogen * fencing. Shaded areas around the lines indicate 95% CI.*

The final competition model for total number of seedlings included shade index and light (total plant count ~ shade index + light). The model shows that the number of seedlings decreases significantly with increasing shade index (Figure 4a). Increased light availability significantly increases the number of seedlings found (Figure 4b).

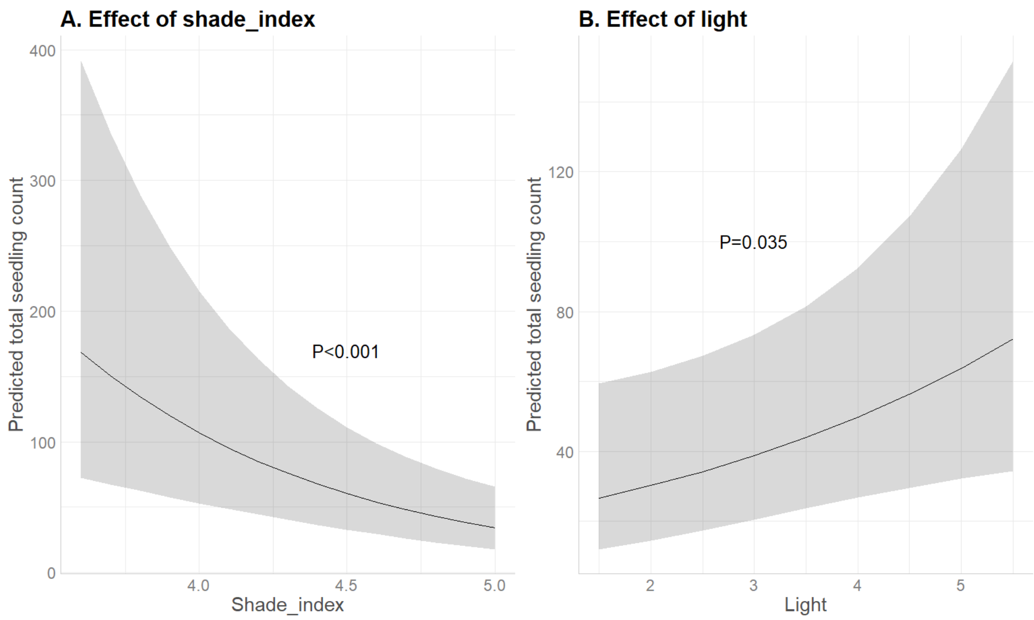

Figure 4. Predicted effects of shade index (A) and light (B) on total seedling count based on a Generalized Linear Model with the formula: total plant count ~ shade index + light. Shaded areas around the lines indicate 95% CI.

3.2 Effects of fencing and site conditions on beech natural regeneration

The final soil model for total number of beech seedlings included pH, nitrogen, fencing and the interactions between nitrogen and fencing, and pH and fencing (total beech count ~ pH * fencing + nitrogen * fencing). The plotted model shows that increased nitrogen availability has a positive effect on the number of beech seedlings in both fenced and un-fenced plots (Figure 5a). This effect was, however, just borderline significant in fenced plots (Figure 5a). Increased pH was found to have a significant negative effect on the number of beech seedlings found in both fenced and un-fenced plots (Figure 5b).

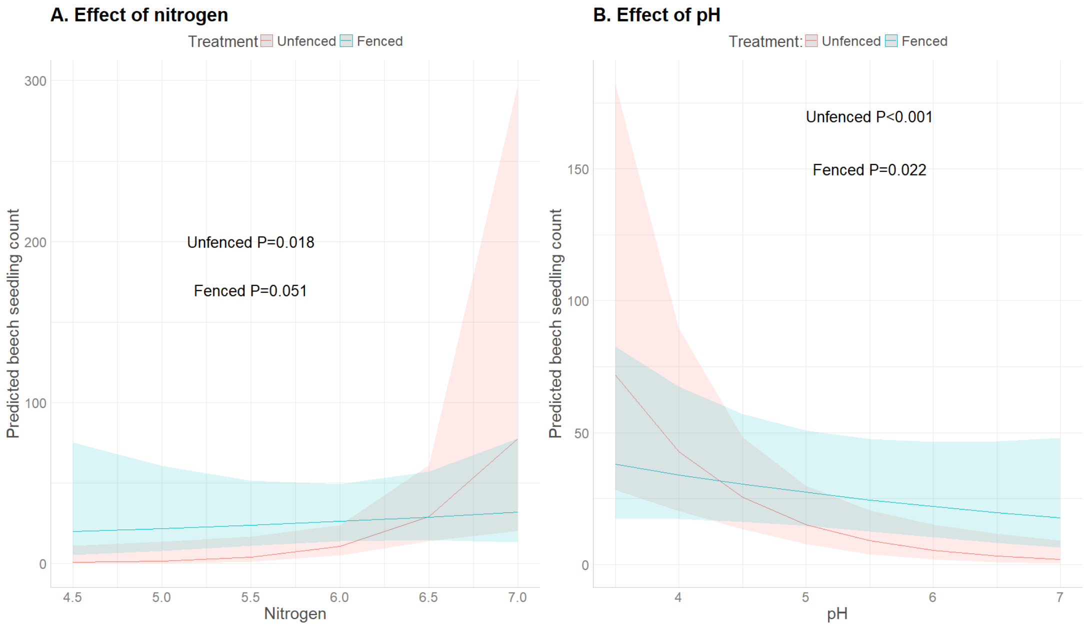

*Figure 5. Predicted effects of nitrogen (A) and pH (B) on total beech seedling count based on a Generalized Linear Model with the formula: total beech count ~ pH * fencing + nitrogen * fencing. Shaded areas around the lines indicate 95% CI.*

The final competition model for the total number of beech seedlings included shade index and fencing and the interaction between shade index and fencing (total beech count ~ shade index * fencing). The model shows that increased shade index has a significantly negative effect on the number of beech seedlings found in both fenced and un-fenced plots (Figure 6).

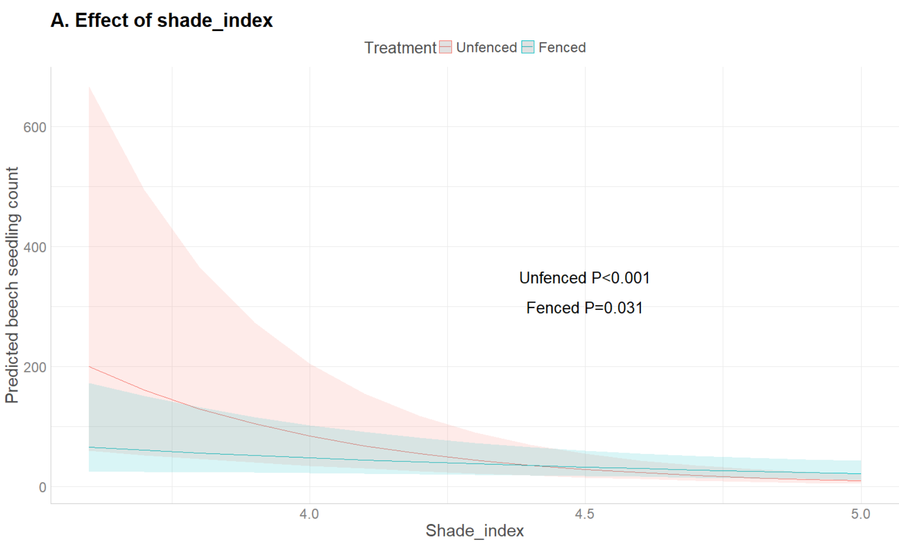

*Figure 6. Predicted effects of shade index on total beech seedling count based on a Generalized Linear Model with the formula: total beech count ~ shade index * fencing. Shaded areas around the lines indicate 95% CI.*

3.3 Effects of fencing and site conditions on ash natural regeneration

The final soil model for total number of ash seedlings included the variable pH (total ash count ~ pH). The model showed that the number of ash seedlings decreased significantly with increased pH (Figure 7).

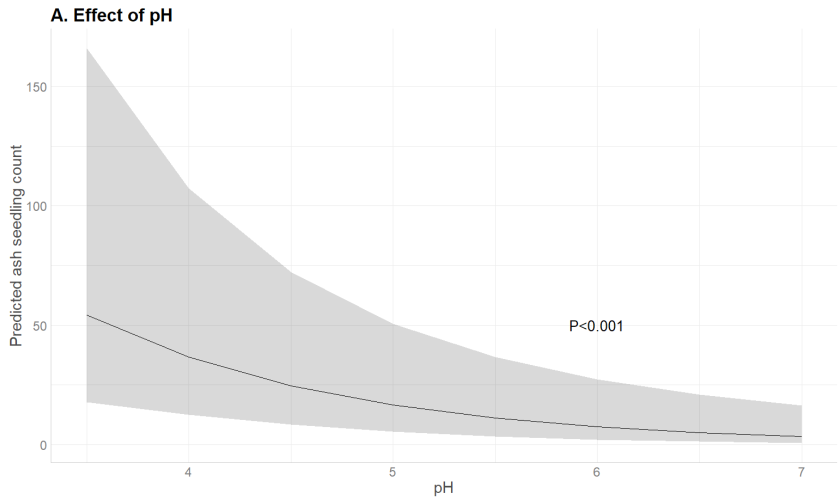

Figure 7. Predicted effects of pH on total ash plant count based on a Generalized Linear Model with the formula: total ash count ~ pH. Shaded areas around the lines indicate 95% CI.

The final competition model for total ash seedling count included the variable shade index (total ash count ~ shade index). The model indicated that increased shade index had a positive effect on the number of ash seedlings, but this effect was not statistically significant (Figure 8)

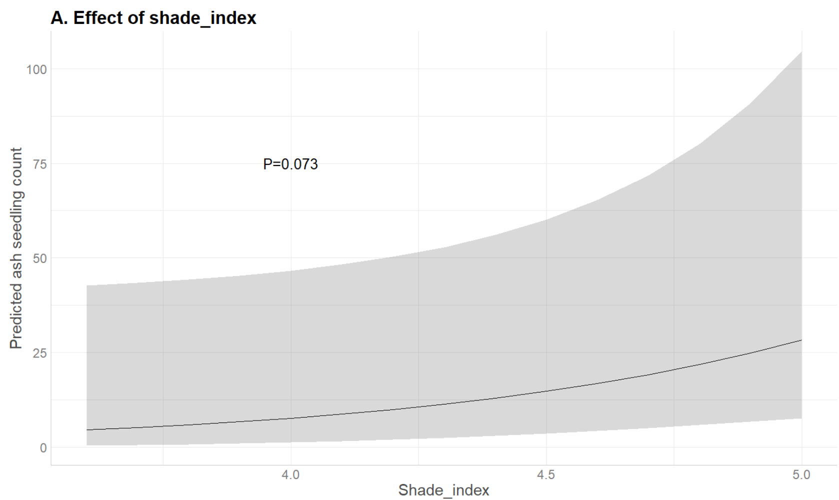

Figure 8. Predicted effects of shade index on total ash plant count based on a Generalized Linear Model with the formula: total ash count ~ shade index. Shaded areas around the lines indicate 95% CI.

3.4 Effects of fencing on the number of seedlings

The two final soil models for total seedling number and beech seedling number indicated that the number of seedlings were higher in fenced areas. Although, none of the models found the effect of fencing to be statistically significant (Figure 9).

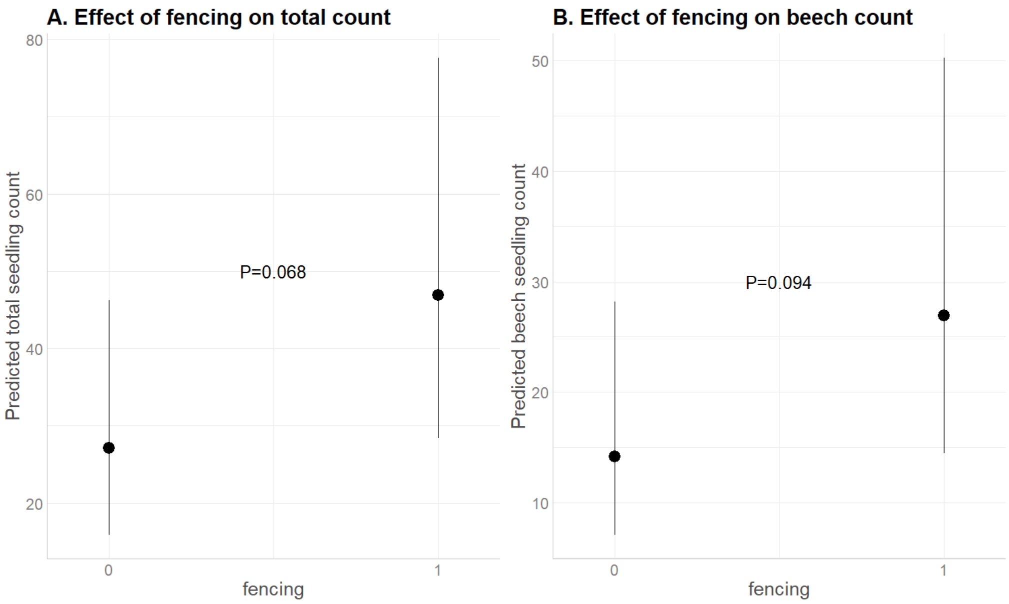

*Figure 9. Predicted effects of fencing on total plant count (A) and total beech plant count (B). Based on the two different soil Generalized Linear Models. The total seedling count formula: total plant count ~ pH *fencing + nitrogen * fencing. The total beech seedling count formula: total beech count ~ pH * fencing + nitrogen * fencing. Error bars indicate 95% CI.*

4. Discussion

4.1 Browsing effects on site condition expressions

To answer the research question, the results indicate that browsing to an extent can alter the expression of the edaphic nitrogen and pH gradients, but it cannot be concluded that browsing clearly limits the expression of these gradients. In contrast, the results concerning the effects of nitrogen and pH on the total number of seedlings (Figure 3), and the effect of pH and shade index on the number of beech seedlings (Figure 5b and 6), suggest that browsing does not limit but enhances the expression of these gradients. However, considering the CI of the plotted models, this cannot be definitively concluded. In all other models browsing had no significant effect on the expressions of the gradient tested, as indicated by the interactions between fencing and the continuous variables being excluded from the models. This concludes that the general hypothesis is rejected. However, the results still show that gradients of light and soil conditions are important for regeneration of broadleaf trees in protected areas, which have implications for both planning of forest production and management of protected areas.

The amount of research published on how browsing effects the variation formed by different light and edaphic gradients is limited. However, one study argues that browsing effects may reduce the expression of edaphic gradients (soil fertility), on functional trait compositions (Hedwall et al., 2018). The study also found that the expression of the indicators light and nitrogen was unaffected by browsing (Hedwall et al., 2018). The results of this thesis can partially agree on the gradient of light, on seedlings found in total (Figure 4), where the GLM did not find any significant difference in how light or shade index was expressed in fenced or unfenced areas. However, beech seedlings were indicated to occur more often in un-fenced areas at low levels of shade index, compared to fenced areas (Figure 6), which suggests a positive browsing effect on light gradient expression. This could potentially be explained by reduced local competition from ground flora by browsing, allowing more light availability to reach beech seedlings. Furthermore, the expression of nitrogen was found to have been affected by browsing on the total number of seedlings (Figure 3a). This effect was not found for beech seedlings in fenced plots (Figure 5a). This could also indicate that some disturbance is needed for beech seedlings to be able to access the nitrogen. Altogether, the results from this thesis neither support nor rejects the results provided from Hedwall et al. (2018). Worth noting is that the study provided by Hedwall et al. (2018) was conducted in Białowieża Primeval Forest. The setting in that forest is much different compared to the sites used in my study. Among others, beech which has a large amplitude along gradients of light, pH and nutrient availability is absent in Białowieża Primeval Forest. The nutrient gradient is also much longer, varying from poor conifer forest to land with very fertile tall-herb forest.

The number of tree seedlings did in general vary along the edaphic and light gradients as previous research has suggested. Previous research in Germany argue that the ideal pH for beech seed germination is approximately 4.3. Lower pH inhibits seed germination and pH>6 also present unfavourable conditions (Övergaard, 2010). These findings are in line with the effects of pH on beech seedlings on this study (Figure 5b). The effect of pH on beech seedlings compared with ash seedlings suggests that the species are, to a degree, adapted to similar pH conditions (Figure 5b and 7). The number of seedlings for both species decreases with increased pH. This found effect of pH contradicts previous research findings in Europe (Ellenberg, 2009; Thomas, 2016). This may be explained from interspecific competition by ground vegetation species which are associated with more basic pH, like wild garlic (*Allium ursinum*) (Tyler et al. 2021). Wild garlic has a vast cover in some of the survey plots in all three locations and thus increases the mean pH indicator value in these plots. In spring, wild garlic may provide interspecific competition to adjacent vegetation (Oborny et al., 2011). This could lead to the decreased number of seedlings in plots which have indications of more basic pH seen on all response variables (Figure 3b, 5b and 6).

Furthermore, high nutrient availability is one of many preferences among European broadleaf's (Ellenberg, 2009), where nitrogen is a key nutrient. Hence, the results of increased seedling numbers with increased nitrogen availability were expected. Increased light availability has also been found to have a positive effect on understory vegetation abundance (Couwenberghe et al., 2011; Tyler, 1989). In accordance with this previous research, this study found a positive effect on the number of seedlings found in all significant results of decreased shade index and increased light conditions.

Previous research in the same experiment has found that the single effect of fencing on the number of seedlings varies between the location and the species. They argue that the positive effect of fencing is mostly seen in Maltesholm and are indicated in Fyledalen and Hästhagen (Johansson, 2020; Olsson, 2024; Ramberg & Sjöqvist, 2023). The single effect of fencing on the total number of seedlings and beech seedlings in this thesis was not significant. Although my results indicate that more seedlings were present in fenced areas (Figure 9). This is likely due to the site effect being un-accounted for in the GLMs created. Therefore, the results are not unexpected and seen as further support of previous research findings in these locations.

4.2 Sources of error

This thesis methods allows for multiple sources of error, most of which can be traced back to data processing. The structure of the GLMs can have generated misleading P-values and estimated effects of the indicator variables due to too advanced model functions in relation to the size of the data (55 observations). The exclusion of the outliers has also affected the models results by decreasing the number of observations. However, by excluding them, the models became more reliable with less overpredictions. By increasing the number of survey plots where site conditions and number of seedlings are measured, this source of error will decrease. Furthermore, with more observations we may possibly find significant effects from the moisture gradient (now excluded from all models) and the interactions between fencing and the gradients.

The variable shade index is basal area weighted. Meaning that, for example the shade index in a beech forest monoculture, with a basal area of 20, consisting of only beech trees, has the same shade index as a beech forest monoculture with a basal area of 37. Therefore, the shade index may not only reflect the actual shade of the site, but also the species composition around each plot. This describes the site in one way but may not give the whole picture. In future research, the shade index may instead be used in combination with the basal area as an interaction or be calculated in another way which more reflects the plots actual shade.

This research only considered browsing as a factor. By reducing the likely varying browsing pressure in the locations and between the three locations (Johansson, 2020; Olsson, 2024; Ramberg & Sjöqvist, 2023), to a single factor with two levels, the results may be misleading. This is because some un-fenced plots may have been exposed to high browsing pressure, while other un-fenced plots could have experienced a lower pressure. By increasing the number of survey plots in each location, each location can have its own models. The factor of browsing would then be specific to a single location instead of a general factor for all three locations. There are of course also other variables which effect natural regeneration of seedlings. One example found by previous research is frost damage of seedlings, worth noting is that all studied locations have a covering shelter wood, which reduces this type of damage (Gemmel et al., 1996). Fungal infection of dropped beech seeds is another factor which can limit the number of beech seedlings regenerating (Övergaard, 2010). There are however no indications that these factors have affected seedlings differently in fenced and un-fenced plots.

Finally, the human error during both the inventories and data processing must be considered. The biggest one involves missing to count or double counting seedlings in the survey plots. Making this mistake leads to misleading results in how the indicator variables are expressed in either fenced or non-fenced areas. The data processing also involved major manual input which can lead to missing to count or double counting seedlings in certain plots, creating the same issue. However, these mistakes are likely random and thus not something that effects the results more than increased noise in the analysis.

4.3 Practical implications

Although the single effect of fencing on the number of seedlings was not found to be statistically significant, there was a tendency for such an effect (Figure 9). With the support of previous research (Johansson, 2020; Olsson, 2024; Ramberg & Sjöqvist, 2023), it may however be argued that fencing is needed to establish natural regeneration in some highly browsed protected areas.

The site conditions of potential fencing sites should be considered before establishment. The results clearly indicate an increased number of seedlings in increased light conditions (Figure 4 and 6). Therefore, potential fencing sites should be in already light areas. An alternative could be to perform a thinning or veteranization of trees to create lighter conditions. There is also a clear effect of the soil gradients nitrogen and pH (Figure 3, 5b, and 7). Potential fencing sites can be areas with pH around 4.2 and high nitrogen availability. If the goal is to preserve the landscape variation under heavy browsing, fencing of forest or sites which have a high variation of site conditions is recommended. One downside to fencing is of course the cost of establishing and maintaining them (Jensen et al., 2012). Furthermore, fencing limits the accessibility for users of the landscape, compromising potential cultural values, and managers of nature reserves like Fyledalen, Hästhagen or Maltesholm must weigh this cost against the benefits that fencing may have.

4.4 Conclusion and further development of research

In conclusion, this research shows that browsing may influence how some edaphic and light gradients, at certain levels, are pronounced. However, this is not a general pattern. By increasing the number of surveyed plots, potential errors from models may be reduced, allow for more comparisons of gradients in fenced or un-fenced plots, and sanction models specific for each of the locations. Further research in this field of study is needed to develop a more well-rounded understanding of how browsing influences the vegetation expressed by certain site conditions. Furthermore, research is important to be able to give better recommendations to protected areas which struggle with natural regeneration.

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Acknowledgments

I would like to express my acknowledgement to my supervisor, Per-Ola Hedwall, for his valuable guidance and constructive feedback throughout the development of this thesis. His knowledge in vegetation ecology, statistics, and R contributed to the depth of the analysis and clarity in the presentation of the results.

Appendix 1

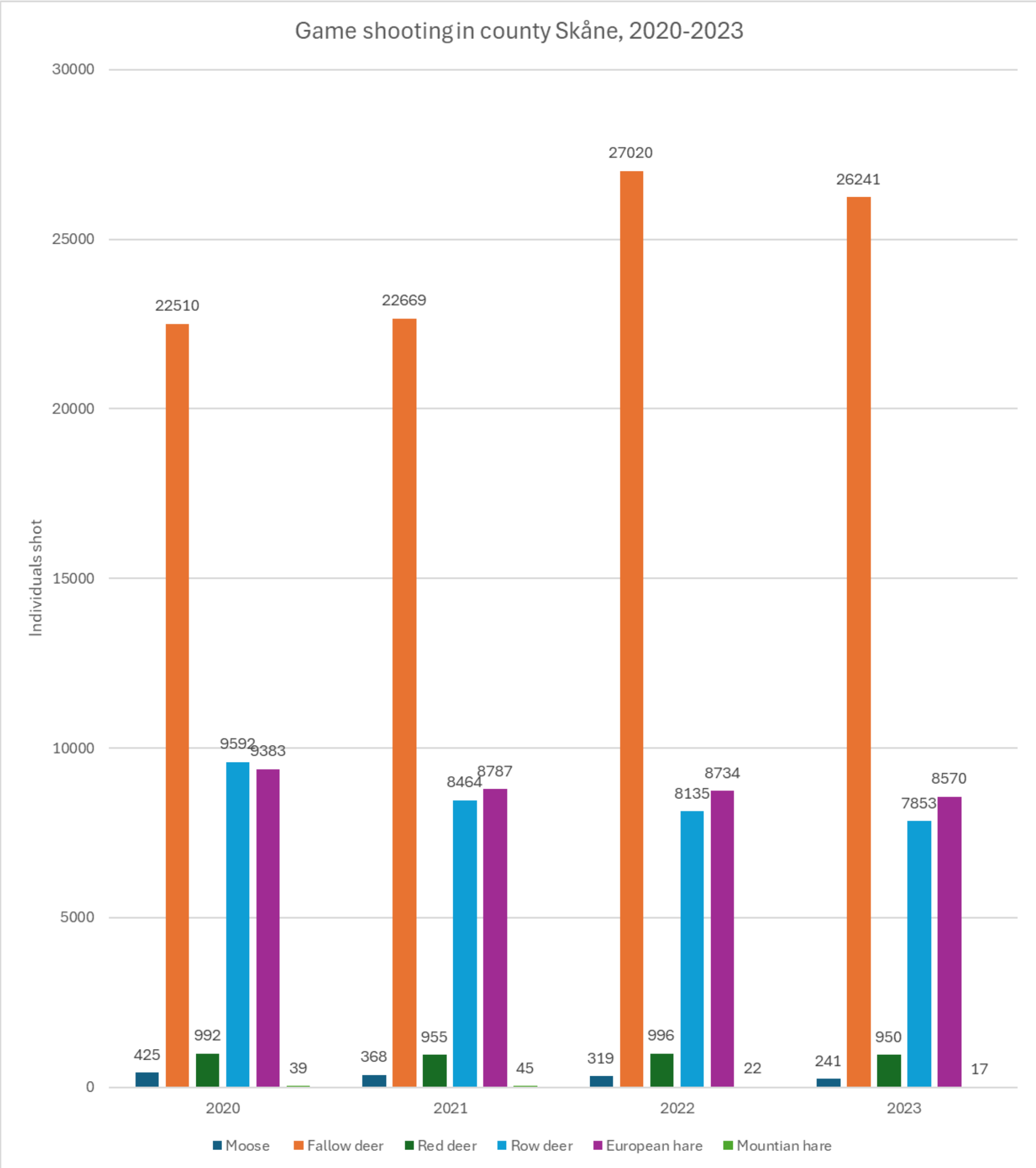

Figure 10. Hunting statistics of game shootings in the county Skåne (approximately 11 million hectares) between 2020-2023 (Svenska Jägareförbundet, n.d.).

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