Scots pine for fika

The role of local moose density in determining browsing damages to pine across commercial forests in Sweden

Rebecca Partemi

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Abstract

By browsing on young Scots pine (*Pinus sylvestris*), moose (*Alces alces*) can cause significant damage to commercial forests. The National Forest Agency monitors browsing damage and moose faecal pellet groups annually on pre-defined plots throughout Sweden. Here, we investigated the relationship between moose pellet groups and the proportion of pine trees with fresh (< 1 year) browsing damages. We used mixed-effects logistic regression models with proportion of damaged stems as response and moose pellet group density, presence of other deer pellet groups, Scots pine and birch (Betula spp.) numbers, and site productivity as predictors. We used data collected nationwide and did analyses first for the whole of Sweden and secondly for each separate region by subdividing the same dataset. Overall, the results were consistent across the regions and for Sweden as a whole, with some differences. We found that moose pellet group density was positively correlated with damage in every region and was especially important in explaining damage levels in the north of Sweden. Presence of other ungulates was positively related to pine damage in the Southern region only, and it is unclear to what extent their effect on young pine trees is direct through browsing or indirect through competition. Contrary to recent studies, pine abundance had a secondary role in explaining browsing damage. Instead, browsing damage was positively associated to site productivity and number of birch trees, the latter with a systematic higher importance than moose local density. Plots where birch is abundant might be attractive to moose and therefore indirectly lead to increased browsing damage on pine. Given the consistent positive association found between moose pellet groups and level of damage, we conclude that moose pellet counts on browsing survey plots are an important add-on for the adaptive management of moose and forests. However, pellet count should be made more systematically and should not be limited to young forest stands to properly capture moose density.

Keywords: Moose, Ungulates, Scots pine, browsing damage, forestry, Äbin

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Abbreviations

SFA   Swedish Forest Agency (*sv: Skogsstyrelsen*)

MMA   Moose Management Area (*sv: Älgförvaltningsområde, Äfo)*

1.
Introduction

1.1 Wild ungulates and forestry in Sweden

Large herbivores, such as ungulates, are known to be important ecosystem engineers as they actively modify the vegetational systems from individuals to communities (Putman et al., 2011). Ungulates modify their habitat through selective foraging, trampling, defecation, and urination (Hobbs 1996). Through foraging and habitat use, they reshape the architecture and composition of plant communities often increasing species richness and plant productivity when grazing is moderate (Putman et al., 2011). When high ungulate densities occur in human-dominated landscapes, the two sectors that are usually most affected are agriculture and forestry (Reimoser & Putman 2011). Due to a general lack of systematic damage surveys and monitoring, it is often not easy to quantify the economic loss that wild ungulate populations can inflict to these human activities, especially because not all types of ungulate damage result in crops and trees being negatively affected (Reimoser & Putman 2011). However, damage by ungulates on commercially important tree species generally increases with their increasing density and it is identified as a common problem in young forest stands (Pfeffer et al., 2021).

Moose (*Alces alces*) is the largest herbivore found in Fennoscandia and as such it is a key species in boreal forests. Selective feeding by moose affects canopy structure (opening) and tree composition, favouring less browsed species. A study by Kolstad et al. (2018) concerning secondary succession found that intensive browsing suppresses a key stone species like rowan (*Sorbus aucuparia*) (Bendiksen et al., 2008) but also other more common tree species like downy (*Betula pubescens*) and silver birch (*Betula pendula*) to fail to recruit into taller height classes. The study also found that conifers tend to be the dominant trees where moose is present while deciduous trees systematically prevail in areas where moose is excluded (Kolstad et al.,2018). In addition, trampling and canopy modifications have both direct and indirect effects on soil quality and composition. For example, removal of lateral twigs and branches has been found to alter decomposition rates and general site productivity by letting more light reach the lower forest levels

(Persson et al., 2000). Similarly, Mathisen et al. (2010) found in their experiment that simulated browsing changed the field layer from a shrub (*Vaccinium myrtillus*) to a graminoid-dominated community because of increased light availability.

In recent years, the wild ungulate populations across Europe have been showing a positive trend (Apollonio et al., 2010). The causes are multiple but in general, ungulates tend to benefit from a variety of anthropogenic modifications to natural habitats. For example, agriculture and forestry techniques increase forage quantity and quality (Kuijper et al., 2009, Edenius et al., 2015) and often improve habitat suitability for ungulates (Presley et al., 2019). These suitable conditions combined with a lack of natural predators, who were mostly hunted to near extinction in Europe (Linnell & Cretois, 2018), can largely explain the rise of ungulates populations. In Sweden, the moose population has shown a positive trend since the early 20th century (Hörnberg 2001) and is currently one with the highest densities in the world (Jensen et al., 2020). The current pre-harvest population estimates are between 240.000-360.000 animals (Jägareförbundet, 2021). Change in forestry practices, absence of natural predators, and sex- and age-specific hunting quotas were the main causes behind the strong increase of the Swedish moose populations between 1980-1990 (Lavsund et al., 2003). Similar reasons also explain the rise of other deer species present in Sweden such as roe deer (*Capreolus capreolus*), red deer (*Cervus elaphus*), and fallow deer (*Dama dama*) (Apollonio et al., 2010). From now on in the text, we refer to these three species simply as "deer".

These increasing ungulate densities signify higher levels of damage by browsing on commercial forests (Pfeffer et al., 2021). Across Scandinavia, moose is the main consumer of Scots pine (*Pinus sylvestris*) (Bergqvist et al., 2001, Nichols & Spong 2014) which is the primary food source in winter (Bergström and Hjeljord, 1987; Lavsund, 1987). In reality, conifers are less preferred by moose compared to deciduous species such as aspen (*Populus tremula*), rowan, willow (*Salix* spp.) and birch (*Betula* spp.) (Hörnberg 2001, Cassing et al., 2006, Månsson et al., 2007b) and consumption of pine seems to be inversely proportional to the availability of these deciduous species (Bergqvist et al., 2018). Nevertheless, Scots pine (hereafter "pine") is made widely available and abundant by silviculture, especially in young forests (Cederlund et al., 1980; Bergström and Hjeljord 1987). Inter-specific competition is another key factor as it appears to increase the rate of pine intake by moose due to competitive exclusion (Spitzer et al., 2021) and might be exacerbated by increased density of competing ungulate species.

1.1.1 1.2 The moose management strategy

Traditionally, moose has always been an important game species in Sweden and hunting holds significant economical and recreational value (Mattsson et al., 2008)

with approximately 300.000 hunters registered in 2019 (Jägareförbundet, 2019). Whereas hunters usually strive for high moose densities and yield, this is usually in stark contrast with forestry goals to minimize browsing damages to young pine trees. Thus, in recent years, the booming population of moose in Sweden has made necessary to rethink the moose management strategy and make it more adaptive to ecological, societal, and economical interests (Sandström et al., 2013, Lindqvist et al., 2014).

Today, moose regulation policy strives to accommodate multiple stakeholders' interests involved (Lindqvist et al., 2014) and criteria for harvesting quotas now include, for example, data on local levels of herbivore-induced damage to commercial forests. Forestry is of great importance for the Swedish economy and damage to forests can be costly. In 2020, forest-based products accounted for 10 % of Sweden's total exports with a total approximated value of 143 billion SEK. Moreover, the industry employs 11% of the total workforce in the country (SFIF 2020). In a report from 2019, ungulate game damage to young pine forest was estimated to an annual cost of approximately SEK 1.15 billion (Bergqvist et al., 2019). Furthermore, high moose densities also cause a higher risk of moose-car collisions and it is therefore an issue for public safety (Seiler 2005).

The Swedish Environmental Agency (EPA, Naturvårdsverket) holds the main responsibility of wildlife management in Sweden. The balance between multiple important interests such as hunting and forestry is achieved by a cooperation between the EPA, the various County Administrative Boards (CAB, Länsstyrelsen) and the Swedish Forest Agency (SFA, Skogsstyrelsen). The SFA has the responsibility for conducting and compiling data on ungulate damages across commercial forests to support the CABs in making informed decisions in regulating moose densities (Naturvårdsverket 2015). The CABs' role is to bring together different stakeholders' interests and therefore it is in charge of most of the decisions regarding regulation of moose populations.

Moose management areas (MMA, *älgförvaltningsområde*) are the key organisational unit used to manage and regulate moose numbers according to the interests of all parties involved. According to guidelines, MMAs must cover at least one migratory population of moose (Naturvårdsverket 2011). Moose migratory patterns, however, vary considerably across Sweden and this means that MMAs also vary in size and they are larger in the north where animals cover larger distances when migrating (Singh et al., 2012). Originally, MMA boundaries were set to follow moose populations and landscape features regardless of administrative borders (Naturvårdsverket 2011; Naturvårdsverket, 2015). In practice, MMAs are often delineated by administrative borders for management purposes. Sweden is

currently divided in 131 MMAs across 20 counties (Fig.1) and the island of Gotland is the only county where no moose are found. Each MMA is administered by a moose management group (MMG) with representatives of hunters and forest owners. The MMG is responsible of the evaluation of the status of the moose population in relation to the amount of available forage, of level of browsing damage, and ultimately of the construction of moose management plans. Including multiple stakeholders in the MMG is vital to facilitate wildlife management policies and decisions and resolve conflicts (Naturvårdsverket, 2015). This new management strategy for moose in Sweden was adopted in 2012 (Prop 2009/10:239).
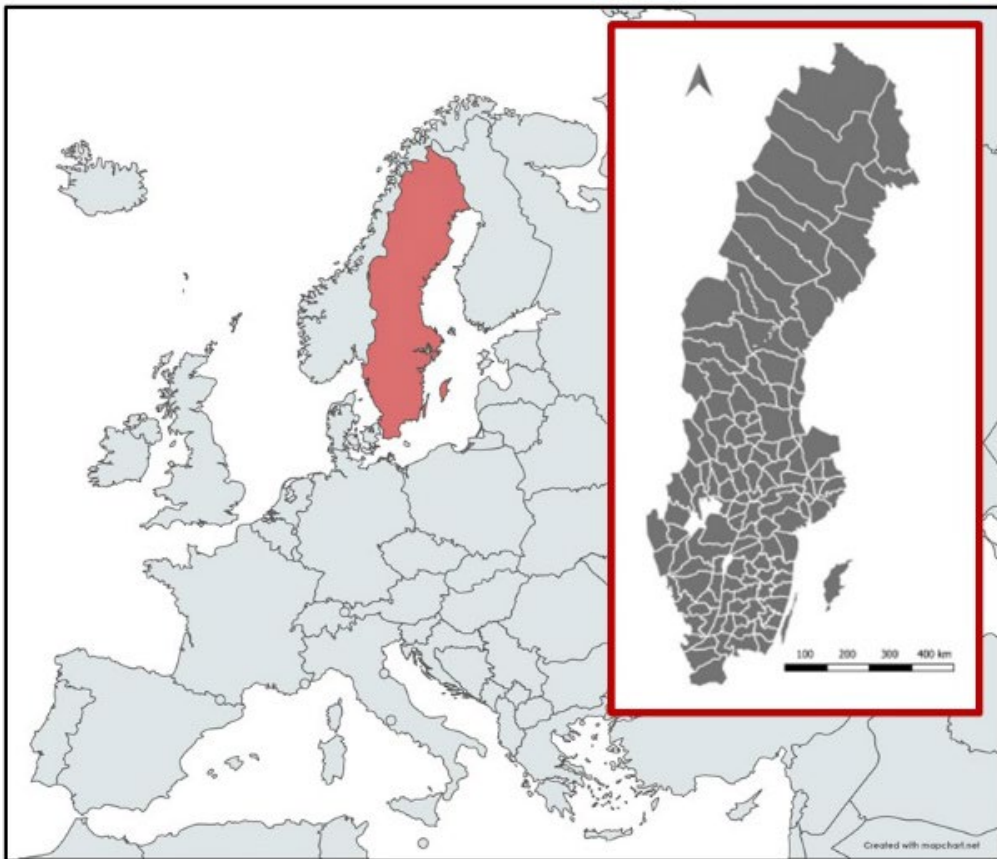
Figure 1. Map of Europe with a zoomed-in map of Sweden divided into moose management areas (MMA, n= 131). MMAs vary considerably in size and become larger from south to north. Map of Europe was created with mapchart.net. The MMA map credit: Swedish forest agency.

1.2 This study

This study focuses on the browsing damage caused by moose across young forest stands (i.e., first phase after reforestation) in Swedish commercial forests. For the first time in 2021, moose and deer pellet groups were included in the browsing damage survey. Moose pellet group counts can be used as moose density index

within young forest stands (Månsson 2009). Adding this feature to the data collection made it possible to better explore how the use of young forest stands by herbivores is linked to the damage. In this study we wanted to investigate the following questions: 1. What is the type of relationship between damage levels to pine ad moose density? And how does the relationship vary across the different MMAs in Sweden? 2. What other factors are important in explaining damage to pine in concert with moose density? and 3. What role do other wild herbivore species have on the level of browsing damages? Initially, we made a global analysis including all plots sampled throughout Sweden. Secondly, we subdivided the entire dataset according to the three regions of Sweden and repeated the analysis for each of them separately (Fig. 4). Plots were our observational unit throughout all the analyses. We expect moose density index to be an important predictor of pine damage in both cases (national and regional). On the opposite, we expect other deer species to have a spatially limited impact on the level of pine damage since their distribution is limited to south central Sweden. Moreover, studies on deer diet have shown that other deer occurring in Sweden do not consume pine and and woody species to the same extent as moose (Spitzer et al., 2020). In particular, fallow deer is almost exclusively a grazer according to its dietary preferences (Spitzer et al., 2020) and red deer includes pine in its diet only to a limited extent (Bergqvist et al., 2004; Lavsund, 1976). Roe deer browses on pine more than the other two deer species but only up to about 100 cm of height and therefore it has a limited impact (Palmer & Truscott 2003). It is also a second consumer of pine compared to moose (Spitzer et al., 2020).

For question 2, we chose variables that were found to be relevant drivers of pine damage in previous studies concerning ungulate damage in boreal forests. Ultimately, we chose to include the number of pines, number of birches, average tree height, and vegetation class (a proxy for site productivity) (Table 1). We expect the number of pines to be negatively associated with browsing damage since pine abundance can be seen as a proxy for forage availability and hence reduces the proportion of damaged trees in a stand through a "dilution effect" (Bergqvist et al., 2014, Herfindal et al., 2015, Pfeffer et al., 2021). The presence of deciduous trees has been shown to have a role in driving damage on pine and therefore we included birch which is a dominant deciduous species in boreal forests (Kolstad et al., 2018). Based on previous findings (Härkönen et al., 2008, Wallgren et al., 2013) we expect birch numbers to be positively correlated to damage as, in general, deciduous trees presence seem to drive higher levels of damage on pine possibly confirming the associational susceptibility hypothesis (Milligan & Koricheva 2013). On the other hand, abundance of birch trees could increase total forage availability and help lowering the total proportion of damaged pine trees with a "dilution effect" as mentioned previously for pine. Selection of average tree height as a predictor is

directly connected to moose browsing habits (Edenius 1993; Faber and Lavsund) and modern forestry management. Even-aged management is the dominating management system in Swedish forests today (Felton et al., 2020) and it is a good example of how certain forestry practices effectively improve habitat quality and forage availability for ungulates (Lavsund 1987, Felton et al., 2020). A forest stand is labelled as "young" during the first regeneration phase after reforestation (Roberge et al., 2020) and these stands, made available by final felling, are attractive foraging sites for ungulates, especially moose (Pfeffer et al., 2021).

According to previous studies (Edenius 1993; Faber & Lavsund 1999), we predict that the level of damage will be lower on plots with trees above 2.5 meters of mean height since damage decreases as trees grow out of reach for browsing. The intensity of this association could however vary between regions since, for example, at high latitudes trees tend to be shorter on average and with slower growth rate than their conspecific at lower latitudes (Moles et al., 2009). It could be possible that in the north, tree height is more homogenous and hence, with less detectable difference than in the south where height could be more heterogeneous. Finally, we included site productivity which was classified into three categories according to the prevalent plant species in the field layer. We expect moose to select stands and plants that are more nutritious (Danell et al.,1991b). However, since forest owners grow pine in sites with lower site productivity index as compared to spruce and birch (Roberge et al., 2020) moose could be drawn to sites with poor or medium productivity levels where pine is made more abundant and therefore productivity could be of secondary importance.
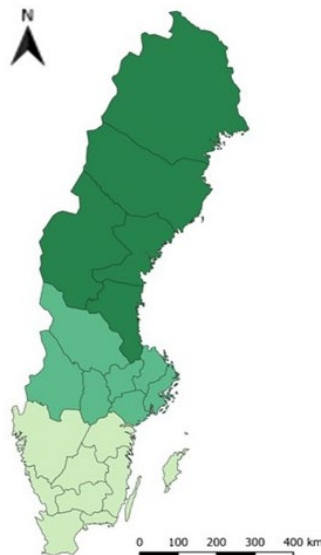

Figure 2. Representation of the subdivision of Sweden in the three regions that was adopted in this study for the analyses. From north to south: Norrland (27 MMAs, 13548 plots sampled), Svealand (21 MMAs, 5477 plots sampled) and Götaland (30 MMAs, 3798 plots sampled). Map was created with mapchart.net.

2. Materials and Methods

2.1 Study Area

Sweden encompasses a significant latitudinal gradient, ranging from 59°N to 69°N. This large-scale gradient translates in different climate, vegetation, forest composition and productivity levels. Winter severity is a particularly important latitudinal factor. In the north, we have longer and colder winters compared to the south and growing season at high latitudes is shorter (~170 days) than at lower ones (~210 days; SMHI, 2020). This can affect the availability and accessibility of forage and movement possibilities (Pfeffer et al., 2021). For example, it is energy consuming for animals to move through deep snow and moose in the north might spend relatively more time in a particular forest stand compared to their conspecific in the south. In Sweden, we can distinguish three main forest vegetation zones: boreal, hemiboreal and nemoral. (Roberge et al., 2020). The dominant zone is the boreal that stretches from North to South-Central Sweden. In the southernmost part we find nemoral zone and in between of them there is a large transition zone defined as hemiboreal (Roberge et al., 2020). Boreal and hemi-boreal forests are the dominant ecosystem types (Ahti et al., 1968) and are also the natural habitat of moose. The boreal forests of Sweden are dominated by conifers, mainly Scots pine *(Pinus sylvestris)* and Norway spruce (*Picea abies*). For deciduous species, the most common ones are silver birch (*Betula pendula*), downy birch (*Betula pubescens*), European aspen (*Populus tremula*), rowan (*Sorbus aucuparia*), grey alder (*Alnus incana*) and willows (*Salix* spp.) (Roberge et al., 2020). Pine, spruce and birch dominate the current timber production where 80% is made up by the two conifer species and another 12% is represented by birch (Roberge et al., 2020).

2.2 Data collection

Data was collected in spring 2021 between snowmelt and bud burst by personnel employed and trained by the SFA. Sampling is done following protocols of the national moose browsing damage survey "Äbin" (Skogsstyrelsen, 2019). Data collection is done in pre-defined plots within moose management areas (MMA). For each MMA, at least 45 squares of 1 km^2 are placed randomly and within them a maximum of 5 stands that meet the criteria (>=0.5 ha, average height of productive stems should be between 1-4 meters) are selected per each grid square. For every stand, the age and average height are recorded together with a qualitative assessment of the tree species proportion in the stand. A site productivity evaluation on plot level is done by observing the understory vegetation and classifying it into three categories (Table 1). Within the young forest stands, another grid of 80x80 meters is placed and a maximum of 15 circular plots are selected randomly. Each plot has a radius of 3.5 m (38.5 m^2 circa) (Fig. 3).
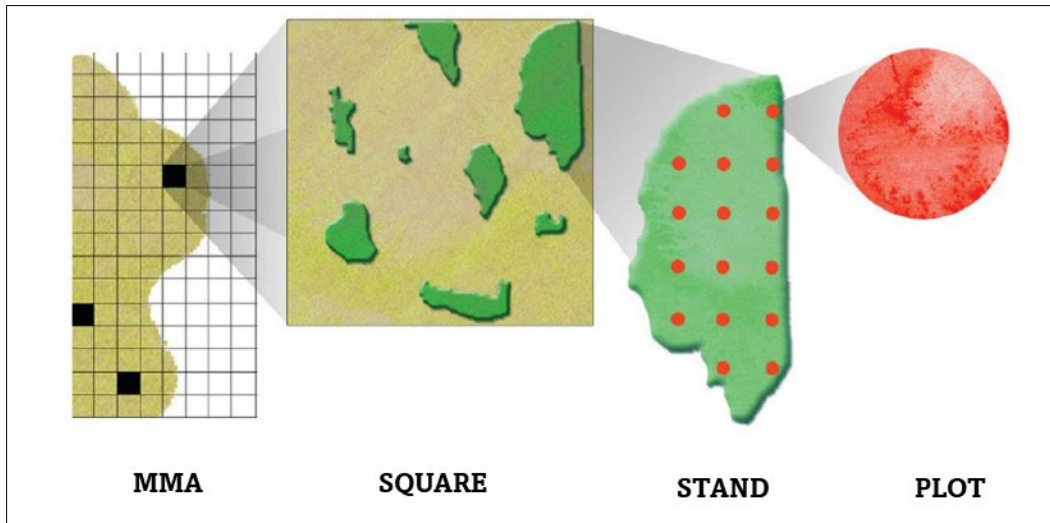
Figure 3. Graphical illustration of the sampling structure of the Äbin inventory method. Source: Skogsstyrelsen.

2.3 Proportion of damaged pines – the response variable

Figure 4. The three types of damage that moose can cause to trees. From left to right: Top shoot browsing, Bark damage (or stripping) and trunk breakage. Pictures: Sabine Pfeffer.

Damage on pine by ungulates can be of three types: top shoot browsing, trunk breakage (also reported as *stem* breakage) and bark damage caused by fraying or gnawing (Fig.4). Any of these damage types affect the wood quality and volume growth therefore causing economic loss to the forest owners (Edenius et al., 2002, Bergqvist et al., 2013). The Äbin inventory method registers a tree as "damaged" if it shows any of the three afore-mentioned damages. This study solely concerns *winter* damage which is damage occurred after the previous vegetation period and

up to the moment of inventory. The response variable in all the analyses (level of damage) is defined as the proportion of pines damaged in a plot during the last year.

2.4 Moose pellet counts as estimators for density

Pellet group counts can be used to estimate animal density and investigate habitat use by ungulates (Neff 1968). They also have been proved to be a useful tool in monitoring ungulate population trends (Rönnegård et al., 2008). In this study, ungulate pellet groups presence and numbers were recorded within the same plots as tree damage. Pellet groups are a good indicator of how much time moose have spent in the area (i.e., area utilization) (Bergqvist et al., 2018). From now on, we refer to number of moose pellet groups as "moose density index" following similar studies (Månsson 2009, Bergqvist et al., 2018). However, the term "density" needs to be interpreted with caution. Pellet group counts need to be integrated with additional information regarding animal defecation rate and animal abundance in the area in order to give reliable density estimations at a larger scale (Rönnegård et al., 2008, Månsson 2009). However, moose density index has been shown to correlate well with other methods used for estimating moose densities (Angelstam et al., 2000). Since only young forest stands were sampled in this study, our moose density index can only be considered as a "local" density limited to these areas and habitats and cannot be extrapolated to MMA or regional level.

2.5 The dataset

A total of 33207 plots spanning 80 MMAs and 20 counties were sampled in the 2021 inventory. We excluded plots where pine was not present from the statistical analyses as we are interested in damage to this species. Gotland county was excluded as there are no moose on the island. The county of Blekinge was also excluded since there were no plots where pine and ungulate pellets were co-occurring there. The structure of the dataset made possible to do analyses for Sweden and the three regions by just sub-setting specific counties that belonged to each one (Fig.4). (For a detailed list of which counties belong to each region see Appendix Table A.1). The subdivision in three regions: Norrland, Svealand and Götaland follows the broad climatic and land-use gradient across the country (Pfeffer et al., 2021). It is widely adopted in forestry and management (Roberge et al., 2020) and it is useful to investigate differences within Sweden with a higher spatial resolution. It also helps reducing the considerable variation that nationwide datasets usually contain. Götaland region comprised a total of 30 MMAs, Svealand region covered 21 MMAs and the remaining 27 belonged to Norrland. We first conducted analysis at the national level (78 MMAs) and in a second moment we investigated the three Swedish regions separately.

In table 1 we report a short description of every variable that was included in our analyses. To answer our second question: "What other drivers are important in explaining driving browsing damage by moose?" we chose four variables that were important in previous studies and were also available in the dataset. These 4 variables were added to the moose density index and the number of deer pellet groups that helped address question 1 and 3 of this study. "Vegclass" is used as a proxy for site productivity which is labelled as "Rich", "Middle" or "Poor" depending on the vegetation type of the field layer (Table 1). As mentioned, this is a ranking adopted by the SFA based on vegetation layer present in the plot and it is used to help decide which species to grow according to soil quality. Pine is mostly grown on poor soils (Roberge et al., 2020). Number of pine and birch trees that were above the half average height of the two highest conifers trees (or deciduous if conifers were absent) on the plots were included. Birch trees were the only deciduous species included in the analysis. Average tree height was included in the analysis but only forest stands within the 1-4 meters height range were surveyed.

Regarding spatial information, we included longitudinal coordinates for Svealand because of the climatic gradient present in central Sweden. In the west, we find a predominant boreal zone with dominance of conifer trees, as compared to the Stockholm area which is boreo-nemoral where conifers and deciduous trees are both present. We also included latitudinal coordinates for the analysis at country level. Latitudinal information for the analysis of Sweden was included to account for the large latitudinal gradient of the country and the variation within the dataset since several stand characteristics like site productivity (Gillman et al., 2015) and average tree height (Moles et al., 2009) show distinct latitudinal patterns.

Table 1 Short description of the variables used in the analyses. We report the names of the variables in the dataset and the analysis, a short description of how they are measured and their category (i.e., continuous or categorical)

Variable	Name in the analysis	Description	Category
PLOT VARIABLES			
Site productivity	Vegclass	Poor (low soil quality; lingonberry is the dominant vegetation layer) Middle (intermediate soil quality; blueberry is the dominant vegetation layer) Rich (high soil quality; grass is the dominant vegetation layer)	Factor
Average tree height	Treeheight	Mean height of the two highest conifer trees within the sampling plot before any fresh game damage divided by 2. Calculate half-height by dividing average height by 2.	Continuous
Number of birch trees present	Nrofirch	Number of birch stems above half average height	Continuous
Number of pine trees present	Nrofpines	Number of pine stems above half average height	Continuous
Moose density index	Moosepellets	Number of moose pellet groups from past winter recorded	Continuous
Deer pellets	Deerpellets	Number of other deer species pellet groups from past winter recorded.	Continuous
SQUARE VARIABLES			
Geographical coordinates	CoordNorth CoordEast	Coordinates were recorded for squares and stands	Continuous

2.6 Statistical analysis

All statistical analyses were done with the R software version 4.2.0 (R Core Team, 2022). We used generalised linear mixed models (GLMM) (Bolker et al., 2009) with a binomial error distribution in package glmmTMB (Brooks et al., 2017). Pearson correlation coefficients were computed for each set of variables and no variables with a correlation above 0.5 were included in the same model to avoid collinearity (see Appendix figure A.1 for correlation plots). To check correlation between site productivity and the other variables we plotted boxplot graphs. Our response variable was the proportion of pines with fresh damages versus undamaged ones. We formulated the proportion with the *cbind* function to offset for total number of pines per plot. In all our models a random intercept of forest squares nested within moose management areas (MMA/Squares) was included. This was necessary to account for the different sampling effort in different MMAs (MMAs in the north cover considerably larger areas than MMAs in the south) and for the general nested nature of our data. All continuous variables were standardised and centred on their z-scores prior to analysis.

We modelled zero-inflation explicitly to account for the high number of zeros that ecological surveys at small spatial scales usually contain. Diagnostics on scaled residuals were performed using DHARMa package (Hartig, 2021) and tests for dispersion, presence of outliers and zero-inflation in the simulated residuals were performed for every model. We kept the combination of variables constant for every model except for Sweden where we included latitude and for Svealand where we included longitude. A model selection was adopted by using a top-down selection strategy and selected the best model according to Akaike Information Criterion (AIC) and Bayesian Information Criterion (BIC). We then employed the *dredge* function in MuMIn package (Barton, 2018) to generate model selection tables with combinations (subsets) of fixed effect terms ranked by second order Akaike Information Criterion (AICc). We only considered models that were returned within the ΔAIC < 2 threshold (Burnham & Anderson, 2002). Final model outputs after this selection for Sweden and the three regions are available in Table 2.

Once model selection was concluded, we tested the accuracy of the final model for Sweden with a train-validation process. This technique is best suited for large amount of data (Christin et al., 2019) and we therefore applied it only to the global model for Sweden. Test-train validation method requires splitting the dataset in two: 75% of the dataset is used as "training data" and the remaining 25% is used as "testing data". We employed the 75% of the data to train our final model. Afterwards, the train-model predictions were tested on the test data (the remaining 25% that was not used for modelling). As a result, the model predictions were

compared to a known value and the performance of the model was then assessed by calculating root mean square error (RMSE) with function *rmse* in package Metrics (Hamner & Frasco, 2018) and correlation coefficients between the test data and the model predictions. The higher the correlation with the test data the better the predictions. The lower the RMSE the closer our predictions are to the actual data since it indicates the spread of the residual errors.

Finally, to investigate how the relationship moose density index-level of damages varied across different MMAs we included moose density index as a slope in the random effect to account for different moose densities in the different MMAs at country level (MoosePellets_sc | MMA/Square). Having moose density index as a random slope allowed us to have different slopes for each of the 80 MMAs and we extracted them with the ranef function in glmmTMB package to consequently plotting them in a forest graph (see Appendix figure A.2).

Due to the large size of the dataset, significance levels (p-value) are to be interpreted with caution (Stephens et al., 2007). P-values are affected by sample size and the larger the number the observations the faster p-values tend to deflate to 0 (Lin et al., 2013). Therefore, for each of our final models, we report forest plots with Odds Ratios on the x axis (Fig. 5, 10) that report the real effect size of our model parameters. While interpreting the results and discussing them we refer to our variables' importance not according to p values but to their Odds ratios values.

3. Results

After removing the two counties and the plots where pine was absent, we had 22823 plots distributed over 18 counties and 78 MMAs in total. Moose pellets were absent in 88.9 % of the plots and the majority of them had mostly one (8.9%) or two pellet groups (1.6%) recorded. Other deer pellets were recorded in 2% of the plots. Fresh damage on pine was recorded in 30.4% of the plots. Most plots belonged to either the "middle" (58%) or "poor" (36%) productivity classes.

Overall, moose pellet groups were also mostly found in plots (n. of plots = 2521) belonging to middle or poor productivity levels (rich= 7%; middle= 57 %; poor= 36 %) and this is true also for the occurrence of birch trees (rich= 8%; middle= 61 %; poor = 31%). Most damages were found in plots between 100-300 cm of average tree height.

3.1 Sweden

At the national level, the main predictors for browsing damage were (in order of decreasing absolute beta coefficients of scaled variables): vegetation class (a proxy for site productivity), latitude, and the number of birch trees present (Table 2; Fig. 5). Plots within the "rich" productivity level showed higher levels of damage (33%) compared to "poor" (26%) and "middle" (25%) categories (Fig.8A). However, the "rich" category had very few observations (n=1439 out of 22823). Beta coefficients of moose density index and number of birch trees were similar and equally important in explaining the level of damage. They were both positively associated with pine fresh damage and they also showed higher level of damage in more productive stands according to model predictions (Fig. 6A; Fig.7B). Presence of other ungulate species was also positively related to browsing damage (Fig.6B), but weakly (Fig.5). Number of pines present and the average tree height were less important than the presence of birch trees or site productivity and were both negatively related to browsing damage (Fig.7A; Fig.8B). Latitude displayed a negative slope meaning that proportion of damaged pines decreased at higher latitudes (fig.9).
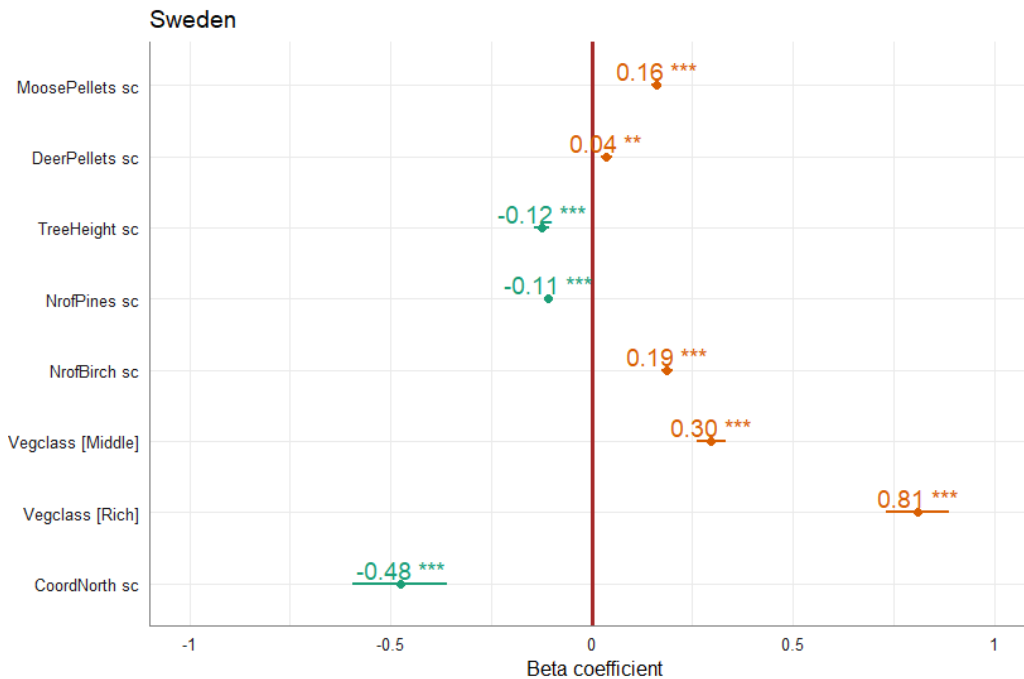

*Figure 5. Forest plot of the top-ranked model for Sweden. The numbers report beta coefficients. Symbol * indicates level of significance (0.05*, 0.01**, 0.001***) and the horizontal bars are the standard errors (SE). The position of the variables to the left or right of the middle vertical line (brown) shows the slope orientation (left is negative and right is positive). Bars overlapping the vertical line indicate a non-significant effect. The response variable (not shown) was the proportion of pines damaged in the plot. For Sweden, the top three covariates (with highest beta coefficient and further from the line of null significance) were: Site productivity, latitude and number of birch trees.*

Due to the high amount of zeros and very low variation within the moose density index variable (mostly 0s and 1s), it was not possible to investigate in detail how the relationship between moose density and level of damage varied across MMAs at country level. (See Appendix Fig. A.2 for further details).

Furthermore, predictions of the train-model showed a Pearson correlation of 0.39 to the test data meaning that there is a good degree of association between what the model predicts and the actual data. RMSE between predictions and test data was 0.26 meaning that the spread of the residual errors is reasonably low.
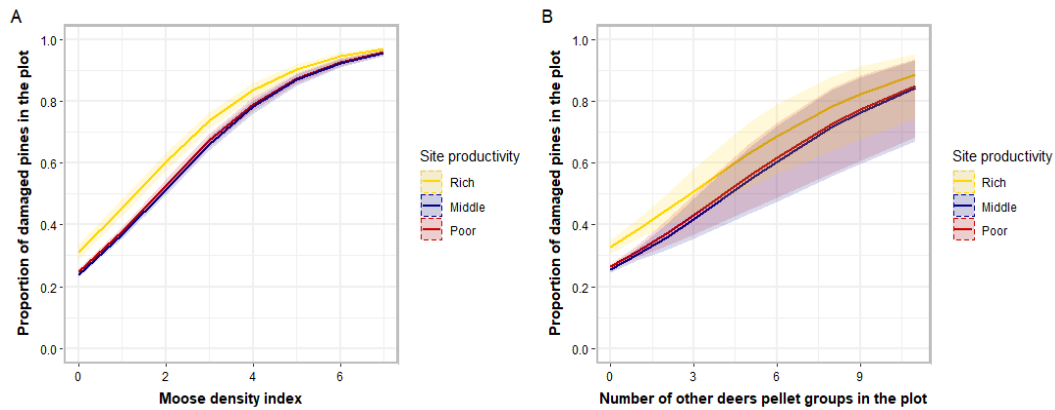

Figure 6. Predictive plots based on the top-ranked model for Sweden. Ribbons represent 95% confidence intervals. O the y axis we represent predicted proportion of damaged pine trees in the plot according to moose density index (left) and number of other deer pellet groups (right). The three prediction slopes represent three different productivity levels. Sites with high productivity levels consistently report a higher share of damaged pine trees while middle and poor sites are more similar.
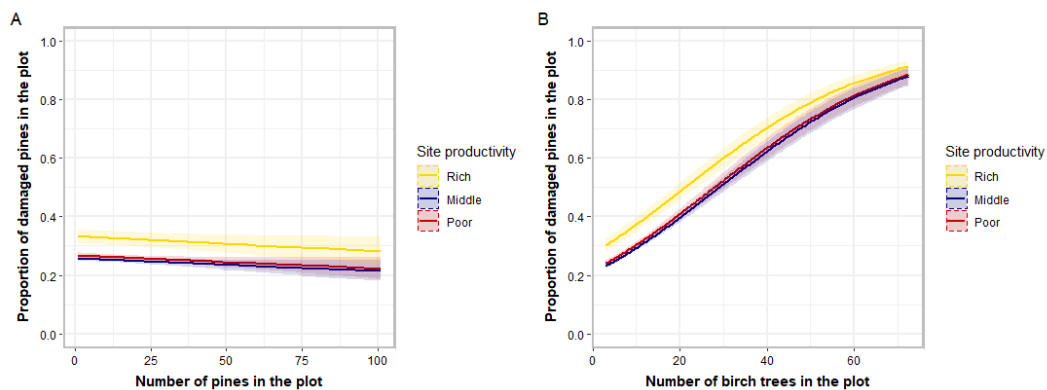

Figure 7. Predictive plots based on the top-ranked model for Sweden. Ribbons represent 95% confidence intervals. On the y axis we report the predicted proportion of damaged pine trees in the plot according to number of pine trees (left) and number of birch trees (right). The three prediction slopes represent three different productivity levels. Sites with high productivity levels report a higher share of damaged pine trees while middle and poor sites are more similar.
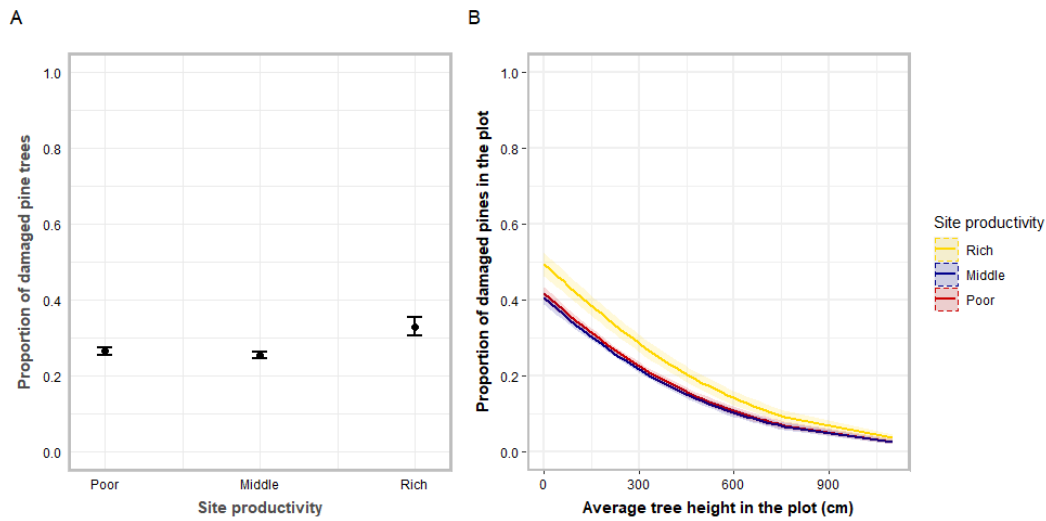
Figure 8. Predictive plots based on the top-ranked model for Sweden. Ribbons represent 95% confidence intervals. On the y axis we report the predicted proportion of damaged pine trees in the plot according to site productivity (left) and average tree height (cm) in the plot (right). On the left we can see that the tree levels of productivity report similar proportions of predicted damage. According to the model predictions, we expect 26% of pines damaged in the sites labelled as "poor", 25% in the ones labelled as "middle" and 33% in the "rich" ones. On the right, the three prediction slopes represent three different productivity levels. Sites with high productivity levels report a slightly higher share of damaged pine trees while middle and poor sites are more similar.
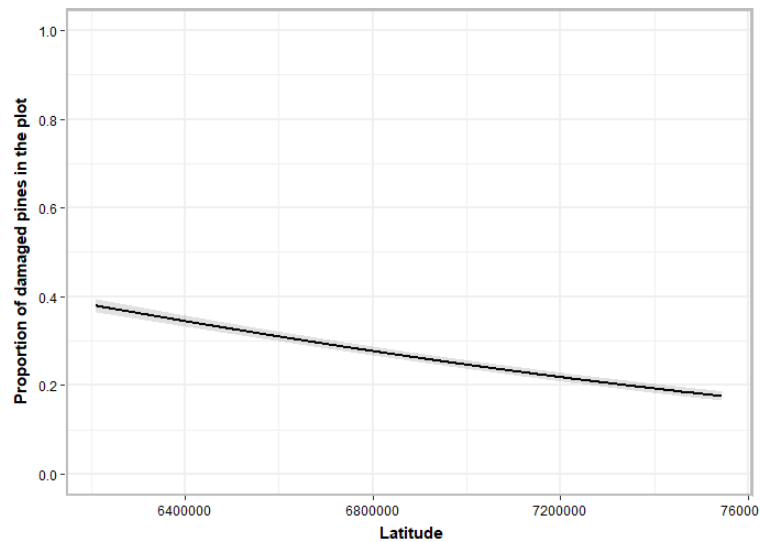

Figure 9. Predictive plot based on the top-ranked model for Sweden. Ribbons represent 95% confidence intervals. On the y axis we report the predicted proportion of damaged pine trees in the plot according to latitude. We can see that as latitude increases (towards north) the proportion of damaged pines decreases.

3.2 Götaland, Svealand and Norrland

The percentage of plots where moose pellets were found (total number=2521) varied among regions. In Norrland we had the highest share of plots with recorded moose pellets (52%) whereas in Götaland and Svealand the proportion was significantly lower (20% and 27% respectively). Deer pellets (total plots= 469) were almost only present in Götaland (66% of the plots, versus 22% of plots in Svealand and 12% in Norrland). The tree height classes that had most damage fell between 100-300 cm.

The three regions were modelled separately while keeping the same set of variables. The top-ranked model for Norrland included only site productivity, moose density index, number of birches and pines (table 2, fig.10.A). Deer pellets were included only in the model for Götaland (table 2; fig. 10.C). Similarly, average tree height in the plot was retained after model selection for Svealand and Götaland but not for Norrland.

The variables that were systematically relevant in predicting level of damage to pine across all three regions were: Site productivity, the number of birches, the number of pines, and moose density index.

Presence of birch showed consistent beta estimates across the three regions and remained an important covariate in all parts of Sweden. In contrast, site productivity showed less consistent beta coefficients but always showed a robust association with damage and was always within the top two covariates in the models. Moose density index systematically showed a positive association to damage in all three regions and with similar beta coefficients. Effect of other deer density was limited to Götaland but the effect was close to negligible even there (very close to the line of null effect as seen in fig.10.C). The number of pines displayed a constant negative relationship with damage across all the three regions, but its importance varied across them. Tree height was negatively associated to damage except for Norrland where it was not included in the final model. Longitude was an important covariate in Svealand (fig.10.B) and reported a negative slope meaning that level of damage increased towards the west. Overall, the main differences were found between Götaland and Norrland. In the southern region, average tree height and number of pines had higher beta coefficients than moose density index while it was the opposite for Norrland. Svealand was closer to Götaland than to Norrland for beta coefficients and relative relevance of predictors.
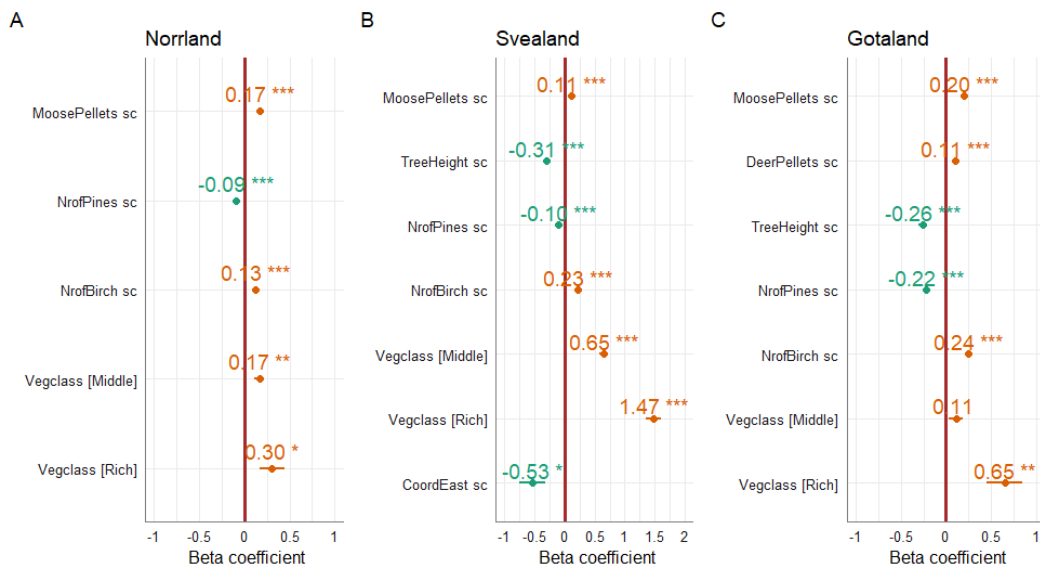
*Figure 10. Forest plots of the top-ranked model for Norrland (A), Svealand (B) and Götaland (C). The numbers report model coefficients. Symbol * shows level of significance (0.05*, 0.01**, 0.001***) and the horizontal bars are the standard errors (SE). The position of the variables to the left or right of the middle vertical line (brown) shows the slope orientation (left is negative and right is positive). Bars overlapping the vertical line indicate a non-significant effect. The response variable (not shown) was always the proportion of pines damaged in the plot.*

(A) Norrland. Deer pellets and average tree height here were excluded during model selection. For Norrland, the top three covariates (with highest beta coefficient and further from the line of null significance) were: Site productivity, moose density index and number of birch trees.

(B) Svealand. Deer pellets here were excluded during the model selection. The top three covariates (with highest beta coefficient and further from the line of null significance) were: Site productivity ("Rich"), longitude and average tree height in the plot.

(C) Götaland. For Götaland, the top three covariates (with highest beta coefficient and further from the line of null significance) were: Site productivity ("Rich"), average tree height in the plot and number of birch trees.

Table 2. Model outputs of the top-ranked models for Sweden, Götaland, Svealand and Norrland. Model estimates, standard error (SE) and level of significance (p value) are reported. Variables were all scaled ("_sc" suffix stands for "scaled") and centred around their z scores before modelling. The response variable was the proportion of damaged pines in the plot. Spatial information (coordinates) was only included in Svealand and Sweden. Number of deer pellets was excluded by model selection in Svealand and Norrland. Average tree height in the plot was excluded by model selection in Norrland.

	Estimate	SE	p value	
Sweden				
MoosePellets_sc	0.160	0.010	< 2e-16	***
DeerPellets_sc	0.037	0.013	0.005	**
TreeHeight_sc	-0.124	0.020	< 2e-16	***
NrofPines_sc	-0.108	0.009	< 2e-16	***
NrofBirch_sc	0.187	0.015	< 2e-16	***
VegclassMiddle	0.297	0.037	< 2e-16	***
VegclassRich	0.810	0.079	< 2e-16	***
CoordNorth_sc	-0.477	0.117	< 2e-16	***
Gotaland				
MoosePellets_sc	0.196	0.026	< 2e-16	***
DeerPellets_sc	0.109	0.032	0.001	***
TreeHeight_sc	-0.257	0.045	< 2e-16	***
NrofPines_sc	-0.223	0.026	< 2e-16	***
NrofBirch_sc	0.243	0.037	< 2e-16	***
VegclassMiddle	0.114	0.078	0.144	
VegclassRich	0.653	0.199	0.001	**
Svealand				
MoosePellets_sc	0.107	0.019	< 2e-16	***
TreeHeight_sc	-0.305	0.038	< 2e-16	***
NrofPines_sc	-0.096	0.019	< 2e-16	***
NrofBirch_sc	0.225	0.030	< 2e-16	***
VegclassMiddle	0.652	0.073	< 2e-16	***
VegclassRich	1.473	0.130	< 2e-16	***
CoordEast_sc	-0.533	0.213	0.012	*
Norrland				
MoosePellets_sc	0.165	0.014	< 2e-16	***
NrofPines_sc	-0.089	0.011	< 2e-16	***
NrofBirch_sc	0.126	0.019	< 2e-16	***
VegclassMiddle	0.167	0.055	0.002	**
VegclassRich	0.303	0.138	0.028	*

4. Discussion

Patterns and processes of browsing damage on young pine trees assessed during the Swedish browsing survey 2021 had many similarities between regions (global model for Sweden and within each of the three regions Götaland, Svealand and Norrland). Moose density index was always positively related to damage levels and with a stronger association to damage levels than the number of pines in the global model and in model including Norrland. Norrland was also the only case where the local moose density index was a more important driver than the number of birches in explaining pine damage levels. However, even though moose density index was significantly related to damage, other variables explained more of the variation. Aside from spatial coordinates (when included), site productivity, and presence of birch trees were among the top three covariates in all our analyses, and they were positively associated with damage. The average height of the trees in the plot was a relevant predictor of damage in Svealand and Götaland but not at all for Norrland and was secondary for Sweden as a whole. However, it always showed a negative association with the response variable, as expected. In Svealand and Götaland, the central and southern regions, moose and deer densities had distinct smaller effects compared to the variables that described forest stand characteristics like the number of birches, pines, site productivity, and average tree height.

Site productivity was the first and most important covariate that came up in every model in this study. In line with our predictions, the highest productivity level was correlated to higher levels of damage in all our analyses regardless of the fact that pines are mostly grown on poor productivity sites. This is similar to what (Danell et al., 1991b, Edenius 1993) found and can be explained by the fact that higher productivity sites offer a higher quality of nutrients and more biomass. Previous studies found that site productivity and nutrient quality are important factors related to browsing damage at small spatial scales (Danell et al., 1991b, Månsson et al., 2007a). Additionally, lower damage levels recorded in lower productivity levels are probably connected to the presence of foraging alternatives. Middle and poor productivity levels were categorized according to presence of blueberry (*Vaccinium myrtillus*) or lingonberry (*Vaccinium vitis-idaea*) and we know that ericaceous shrubs in the forest understory represent an important food source for all four deer species throughout the year (Spitzer et al., 2021). Their presence may therefore represent alternative forage that could help decrease browsing impact on trees (Putman 1989).

The number of birches was an important covariate in all our analyses and this confirms the importance of deciduous trees as drivers for browsing damage. Birch

is not a favored foraging species in any season. During winter, moose mainly forages on pine and birch trees as these are the most abundant and relatively palatable species occurring (Cederlund et al., 1980). Usually, other tree species such as aspen, rowan and willows are preferred (Månsson et al., 2007b) but they are less widespread and abundant. Our findings confirm those of (Härkönen et al., 2008) where the number of broadleaf trees on the sample plots were positively related to damage. Moreover, below the 3 meters height-range, which is where most browsing occurs in this study, pine has been shown to have more biomass than birch trees (Kalén & Bergquist 2004). Thus, there is a possibility that moose are attracted to sites where birch is present, but they still prioritize pine as a winter resource over birch since it offers more biomass. This would confirm the associational susceptibility hypothesis (Milligan & Koricheva 2013, Wallgren et al., 2013) and could be a possible explanation of why proportion of damaged pines is higher when they co-occur with birch trees. Additionally, inter specific competition between these tree species could be driving higher levels of damage on pine. Birches are pioneers in early successional stages such as clear cuts and other open areas (Fischer et al., 2002) (i.e. post felling) and since they grow faster than pine, they easily overshadow them and limit pine height and diameter growth within the same stand, therefore exposing the pine trees for a longer time within moose browsing range (Danell et al., 1991a). Bergqvist et al., (2014) also found that damage increased when birch overtopped pine. Previous studies (Heikkilä & Härkönen 1993, Heikkilä & Härkönen 1996) have also found that palatability of pines increases when they are overshadowed by birch although this in contrast with what Danell et al. (1991a) found previously.

As expected, density of other deer was not a driver for damage on pine in Norrland. Interestingly, it was not relevant in Svealand either. In the south, deer density was positively associated with level of pine damage, but it is unclear whether the effect is indirect (competition) or direct (consumption). Other deer species are secondary consumers of pine compared to moose (Spitzer et al., 2020). Moreover, it is necessary to account for the different detectability rates of other ungulate species pellet groups compared to moose (due to their smaller size). Deer pellets were absent in 98% of the plots (countrywide) and hence other deer numbers might be underestimated if we rely on pellet counts (Pfeffer et al., 2018). This is also the reason we can't talk about a local deer density like we did for moose. Unlike (Pfeffer et al., 2021) we did not find deer pellets to be a better predictor than moose for pine damage in any of the regions. It is important to remember that the Äbin inventory method is designed to capture moose damage and suitable forest stands have a height range of 1-4 meters which is likely a too high range to correctly quantify the extent of deer damage (Palmer & Truscott 2003).

Average tree height showed a constant negative association with damage, in line with predictions. Most damaged pines occurred within height ranges of 100-300 cm countrywide. This is in line with previous findings by Edenius (1993) who found trees of 150 cm of height to have the highest risk of being browsed. Similarly, Faber and Lavsund (1999) found in their study that the preferred browsing height fell between 90 and 160 cm and no browsing was found above 230 cm. However, tree height was not included in the final model for Norrland. This is not easily explained as the data collection is limited to stands within 1-4 meters height range. It could be that trees in the north are on average shorter and more homogeneous in height (Moles et al., 2009) and this could be diminishing the difference in height classes across the forests. It is also interesting to note that tree height was a more important predictor in Götaland and Svealand than moose density index, and the number of birch and pines. Moreover, in Götaland and Svealand, plots with pines in the first height class (50-100 cm) reported more damage compared to the north region which is probably due to the higher densities of the other deer species, roe deer in particular (Spitzer et al., 2020) found there. Climate change is pushing many species to expand their current ranges at higher latitudes (Chen et al., 2011). A recent Norwegian study concerning red deer predicted large increases in future winter habitat suitability for this species due to anticipated climate change (Rivrud et al., 2019) and this can probably be applied to other Scandinavian ungulate populations. If roe deer and other ungulates expand their ranges northward, it is reasonable to expect a higher proportion of damage in lower tree height classes as currently seen in Götaland.

The number of pines present was of less importance in explaining pine damage in our analyses compared to earlier studies (Andren & Angelstam 1993, Månsson et al., 2007, Bergqvist et al., 2014, Pfeffer et al., 2021) where pine density was to be the main driver. In figure 7.A, the slope of predicted damage according to pine numbers is almost horizontal, meaning a weak relationship. Still, the negative association with damage supports a possible "dilution effect" on overall damage (Bergqvist et al., 2014, Herfindal et al., 2015, Díaz-Yáñez et al., 2017). A likely reason for the limited importance of pines in this study compared to a recent study by Pfeffer et al. (2021) is that in our dataset, browsing damages, the number of pines, and moose density were all sampled at the same scale (plot). Forage availability, as represented by abundance of pines, probably gains more importance at wider spatial scales (i.e., landscape or moose home range levels) as it was shown in previous studies (Månsson et al., 2007a, Jarnemo et al., 2014, Herfindal et al., 2015).

Finally, we can observe that at the plot level, local moose density index is closely associated with damage throughout the whole of Sweden. However, the moose

pellet count survey in this study solely concerned young forest stands and therefore the moose density index used here cannot be interpreted to represent a regional estimate of moose density but rather as a measure of activity and use of surveyed stands (i.e., how much time they spend in a young forest stand). It is known that the negative effect on vegetation by large herbivores generally increases with herbivore density (Gill 1992, Hornberg 2001), as is the case for other herbivore-induced processes, such as trampling, defecation and browsing pressure (Hobbs 1996). The importance of moose population density on browsing damage in Sweden has been shown to be scale-dependent: at small spatial scales moose density was shown to be a key predictor for browsing pressure (Månsson et al., 2007a, Wallgren et al., 2013, Jarnemo et al., 2014, Pfeffer et al., 2021) and increasing moose densities have been shown to be correlated to increased browsing on pine (Månsson 2009, Hörnberg 2001). Therefore, our results can be considered indirectly in line with these findings.

We were not able to investigate in detail the relationship between moose density index and level of damage across MMAs. As we mentioned, moose pellets were only recorded in 12% of the plots nationwide and most of them had only 1 or 2 pellet groups. This meant too little variation to detect any patterns across MMAs and hence we cannot draw any clear conclusions at this spatial level. Pfeffer et al. (2021) previously raised the issue of whether animal harvest quotas are possibly better suited than pellet counts for moose density estimations at wider spatial scales like MMAs or higher. We can conclude that including moose pellet counts on browsing survey plots was an important add-on since it was a systematically important predictor for browsing damage at the plot level throughout the analysis. However, pellet count surveys should be conducted systematically and not be limited to young forest stands to obtain a more reliable and unbiased moose density index.

Based on our findings, we could conclude that the best management actions to reduce moose damage to pine should aim at decreasing moose local density and local abundance of birch trees. However, simply reducing the moose population might not be the most efficient solution. Moose selects young forest stands (where most damage occurs) regardless of density and population reduction may not consistently reduce browsing damage (Reimoser and Gossow 1996). Concerning birch, it is likely that stands with abundant deciduous trees are attractive to moose. These stands could be used to draw the animals to specific desired locations and possibly concentrate most of the browsing damage in "expendable" stands of commercial forest (diversionary feeding; Geisser and Reyer 2004). However, our findings alone cannot be used to implement any management decision unless they are integrated with information from wider spatial scales. To take suitable and

effective management actions it is key to integrate findings from different spatial levels because moose foraging decisions are dictated by different factors at different spatial scales (Månsson et al., 2007a, Herfindal et al., 2015). Finally, it is also essential to understand browsing dynamics in relation to other important external factors that actively influence moose habitat use such as human infrastructure (i.e., roads), predator presence, snow cover and depth.

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Popular science summary

In recent years, the wild deer (Cervidae) populations of Sweden have increased and expanded in their distribution. The causes are multiple but in general, deer species tend to benefit from a variety of anthropogenic modifications to natural habitats such as forestry and agriculture.

In Sweden, the moose (*Alces alces*) population has currently reached one of the highest densities in the world. The main winter food source for moose is Scots pine which is also a commercially valuable species. By browsing on young Scots pine (*Pinus sylvestris*), moose can cause significant damage to commercial forests and these damages can be costly for the forestry sector which is an important part of Swedish economy. On the other hand, moose is an important game species in Sweden and hunting holds significant economical and recreational value. The diverging interests of hunters and forest owners are a source of conflict regarding moose population regulation and management strategy.

To monitor damage levels, the Swedish Forest Agency (Skogsstyrelsen) conducts every year a game damage survey (Äbin) of young forest stands (i.e., after felling). The survey takes place every year across the whole country, and it includes detailed information about the current status of young forest stands at different spatial scales. For the first time in 2021, the survey also included moose and other deer faecal pellet group counts to see how these relate to the number of damaged pines at plot level.

In this study, I used data from the damage survey to investigate what is the relationship between moose density (extrapolated from pellet group counts) and level of browsing damage on young Scots pine trees across commercial forests. Level of damage was formulated as the proportion of pines damaged in the plot (the observational unit where data was collected). Additionally, I investigated which other possible factors affects this relationship and these questions were analysed for Sweden and for the three regions of Norrland, Svealand and Götaland, separately.

We found a consistent positive relationship between level of damage to pine and moose density across the three regions and Sweden as a whole. Among the investigated factors, those that consistently seem to drive a higher level of damage on pine were number of birch (*Betula* spp.) trees and productivity level (a proxy for soil quality) in the plots. Presence of other deer species such as roe deer (*Capreolus capreolus*), red deer (*Cervus elaphus*), and fallow deer (*Dama dama*) also showed

a positive association with pine damage, but this effect was limited to the southern region of Götaland where these deer species are mostly distributed. Factors that, on the opposite, seem to decrease damage levels were total number of pines in the plot and the recorded average tree height.

For the first time, we could investigate effects of moose local density recorded at the same level that tree damage and we found a consistent association. We can conclude that including ungulate pellet group counts are a potential important addiction to the game damage survey although to have reliable moose and other deer density estimates the pellet group counts should be made systematically and should not be limited to young forest stands. Moreover, our results are limited to a small spatial scale (plot) and should be incorporated with information from higher scales as we know that moose habitat utilisation and foraging strategy are a result of factors operating at multiple spatial scales.

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Appendix

Table A.1 Counties belonging to each of the three regions in which we divided Sweden for the analysis.

Region	County
Norrland (13548 plots)	21 - Gävleborg 22 - Västernorrland 23 - Jämtland

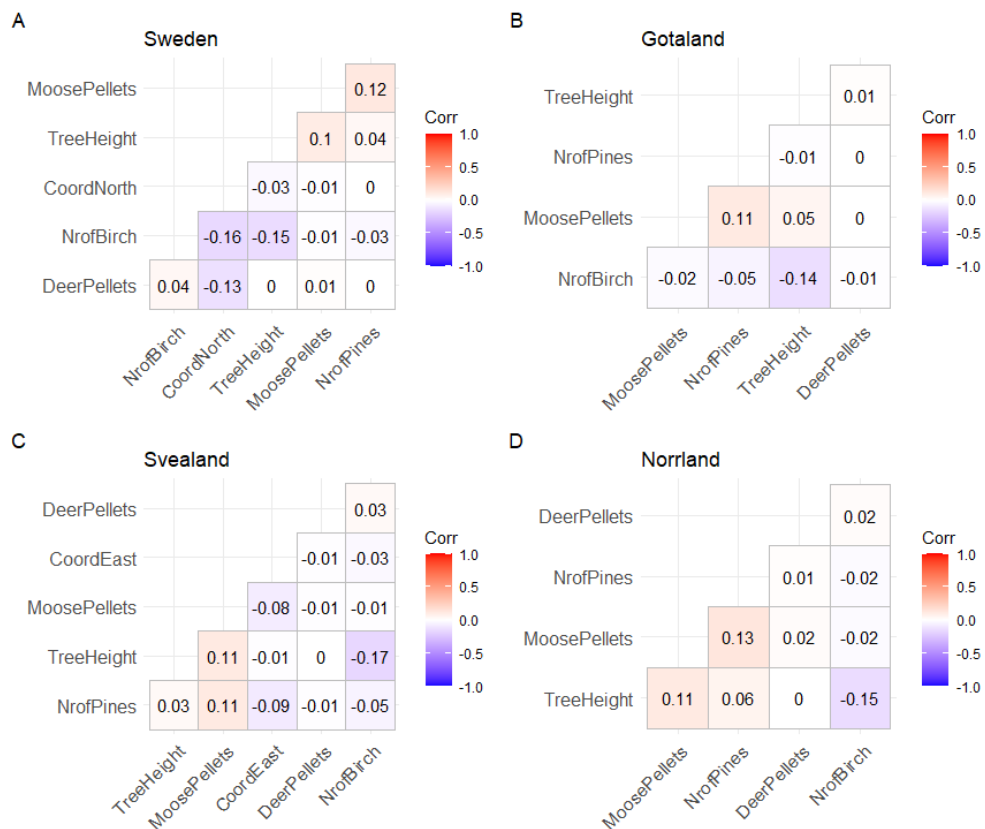| | 24 - Västerbotten |
	25 – Norrbotten
Svealand	3 - Uppsala
(5477 plots)	4 – Södermanland
	17 - Värmland
	18 - Örebro
	19 - Västmanland
	20 – Dalarna
Götaland	5 - Östergötland
(3798 plots)	6 - Jönköping
	7 - Kronoberg
	8 – Kalmar
	9 – Blekinge
	10 - Gotland
	12 - Skåne
	13 - Halland
	14 - Västra Götaland

Figure A.1. Correlation plots between explanatory variables for Sweden (A), Götaland (B), Svealand (C) and Norrland (D). Correlation was calculated using Pearson correlation coefficient before modeling to exclude collinearity.
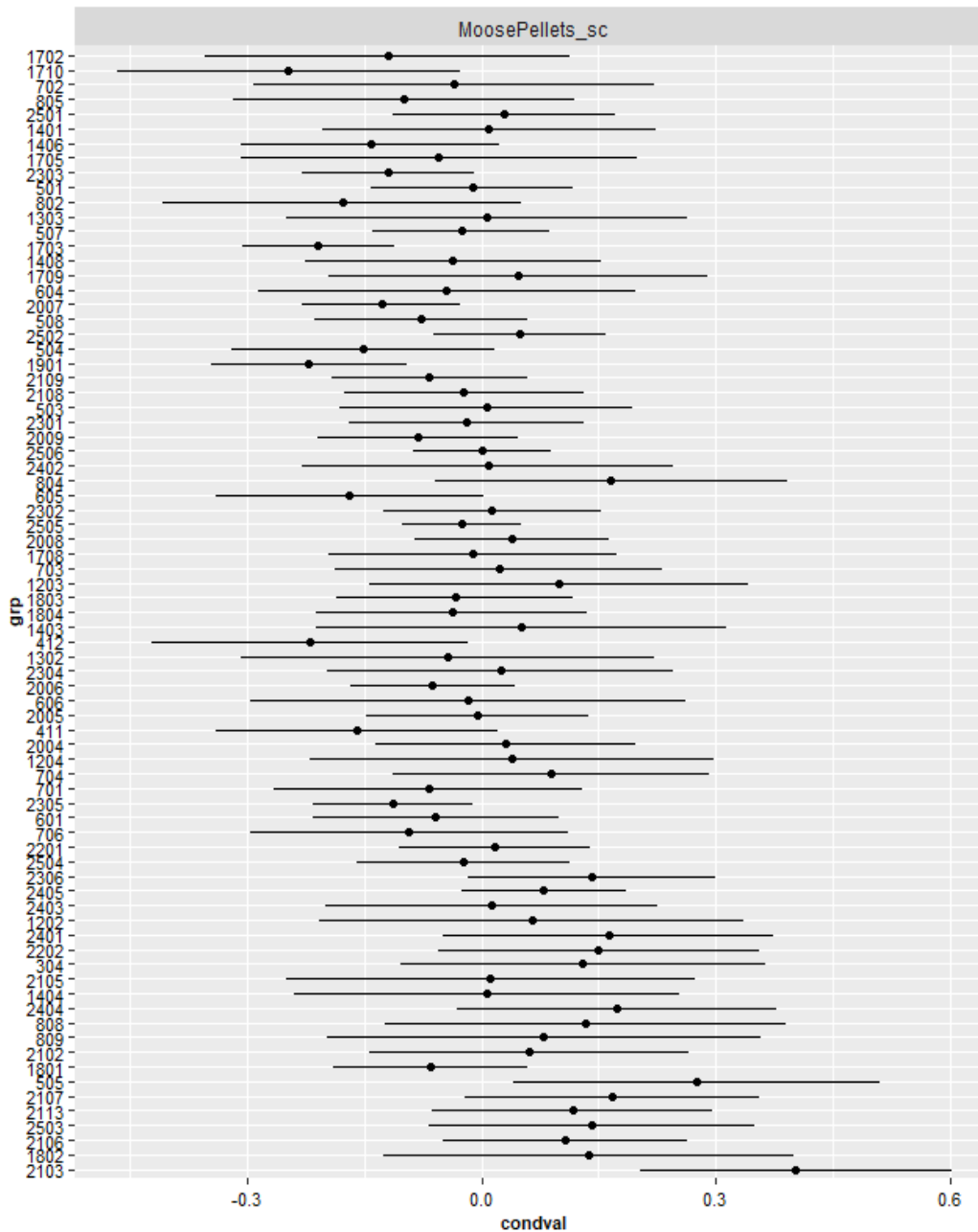
Figure A.2. To explore how browsing damage level changes in relation to moose density index. We plotted our final mode for Sweden including moose index as the random slope: (Moosepellets_sc | MMA/ Square). We extracted random slopes for each MMA with the ranef function in glmmTMB package (Brooks et al.,, 2017). This step was inconclusive as almost every MMA crosses the line of null- effect. There is not enough variation in moose density index values to detect any pattern. The only MMAs that did not cross the line of null-effect were: 2103, 505, 2305,412,1901, 2007 1710, 2303, 1703.

The Forest plot has the single slopes of the random effects for the final model of Sweden Each bar represent one MMA. On the y axis MMAs are identified by a univocal number ID (78 in totoal).

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