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Research Article

The effects of moose and pine density on browsing damage in Swedish pine forests

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Moose *Alces alces* is a culturally and economically important game species in Sweden, but their browsing on regenerating Scots pine trees *Pinus sylvestris* often causes extensive damage to the production and quality of timber. Forest and wildlife managers are faced with the dilemma of how to reduce damage to timber trees while also supporting moose populations and hunting opportunities. The proportion of damaged trees can be reduced by decreasing the number of moose, but also by increasing the number of pines. However, the relative effectiveness of these two approaches is debated and has not been conclusively determined. Here, we addressed this question by analyzing the effects of moose and pine density on pine damage based on yearly data from almost all of Sweden's moose management areas (MMAs) over a 10-year period (2015–2024; 718 observations). We developed a mechanistic model to realistically represent the browsing process and used regression with mixed models to account for variable vulnerability (variation in damage risk at a fixed moose per pine ratio) among MMAs in the statistical analysis. The model explained 53% of the variation in the proportion of damaged trees and showed that, on average, the relative damage reduction effect of a decreased moose population was ~ 1.5× larger (25%) than the effect of increased pine density (17%). Vulnerability to browsing varied substantially among MMAs and between years within each MMA, especially in areas with low pine density. This variability prevents reliable predictions of management effects at the individual MMA level for most MMAs. Such local predictions may be improved in the future by incorporating longer time series of observations and additional variables, such as alternative forage sources, browsing by other deer species, and snow cover and duration.

Keywords: browsing, damage, forestry, model, moose, pine

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Introduction

Scots pine *Pinus sylvestris* (hereafter pine) is an important food plant for moose *Alces alces* in Sweden, especially in the winter when the availability of other food plants is limited (Cederlund et al. 1980, Månsson et al. 2007, Spitzer 2019, Felton et al. 2020). Browsing by moose damages young pine trees, causing mortality or reduced growth rates and lower future quality and economic value of the timber (Fig. 1; Pettersson et al. 2010, Bergqvist et al. 2013, 2014, Wallgren et al. 2013, 2014, Nilsson et al. 2016). These effects incur high costs to the forest industry, estimated at around EUR700 million in Sweden alone (Bergquist et al. 2019). At the same time, moose are a highly valued game species in Sweden, of high cultural and economic importance to society (Naturvårdsverket 2018). Management is therefore faced with the dilemma of how to reduce damage to timber trees to a level acceptable to forest owners, while at the same time supporting moose populations in the forests that provide adequate opportunities for hunting.

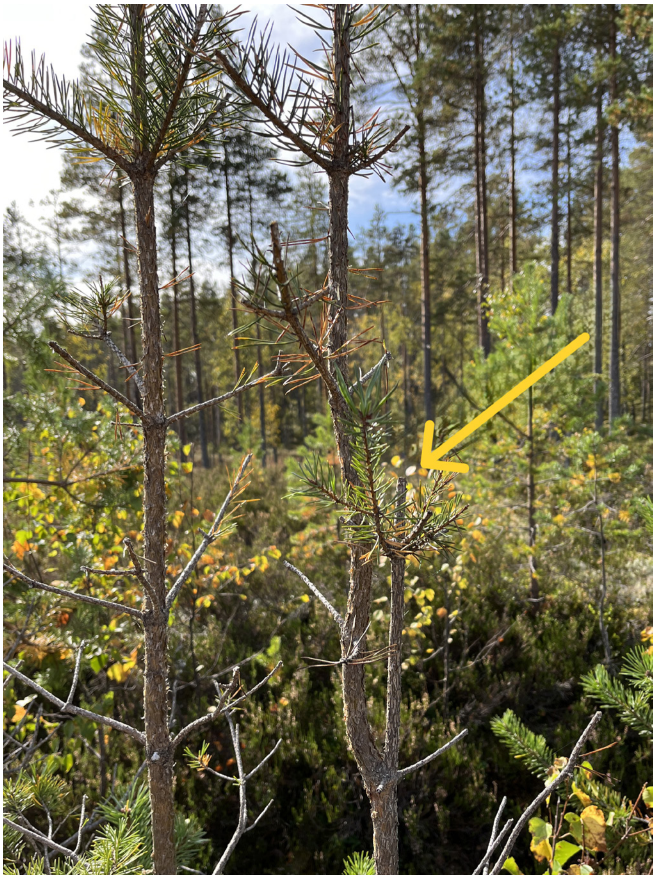

Figure 1. Browsing damaged pine to the right. The top shoot has been browsed (yellow arrow), which the pine has replaced by bending up a side shoot to form the new main stem. The resulting crooked stem reduces the future timber quality. The pine to the left has also been browsed, but only on the side shoots, which does not count as damage in the damage statistics used in our study.

Studies from Scandinavia have shown that moose browsing damage on pine stands is associated with both high moose population densities and low densities of pine trees within browsing height (Bergqvist et al. 2014, Felton et al. 2022, Pfeffer et al. 2022). This suggests that browsing damage, in terms of the proportion of damaged trees, can be remedied by either reducing the moose population density or by increasing the number of pine trees. Importantly, increasing the number of pine trees may reduce the *proportion* of damaged trees although the *number* of damaged trees increases.

Some studies have tested, but not found, a significant relationship between moose densities and damage levels (Andren and Angelstam 1993, Pfeffer et al. 2021), and some studies have reported that the relative (statistical) effect of the number of pine trees on the damage level (% of stems damaged) is higher than the relative effect of moose density (Felton et al. 2022, Pfeffer et al. 2022). This has resulted in a debate among managers and decision makers about which is the best/most efficient way to limit the damage risk – to increase the number of pine trees or decrease the number of moose? Recently, the opinion that increasing pine density is more effective than reducing moose density has gained more traction in moose management. There are also other factors associated with lower damage levels on young pines, such as a high availability of forage of other palatable plant species in the landscape (Felton et al. 2022), a low population density of smaller deer species that compete with the moose for forage (pine is a relatively small part of the diet of these deer species in Sweden, but there is a general overlap in diet composition; Spitzer et al. 2025), or few winter days with deep snow (Pfeffer et al. 2021). Often, however, the discussion in management focuses on the two main actors only, pine and moose, because they are monitored nationally and can be directly managed.

Scientific assessments of the factors driving pine damage levels in Sweden have so far been conducted mainly on small spatial or temporal scales, which limits the generality of the results and their relevance for moose management nationally. Further, we note that the studies differ both in how the effectiveness of methods to mitigate browsing damage was quantified statistically and how the results were interpreted in common language, which may have caused confusion in the debate. In Bergqvist et al. (2014), pine density explained most of the variation in browsing damage, while the effect (slope) was higher for moose density than for pine density. Despite these results, the authors concluded that this indicated that increasing the number of pine trees per ha may be a more efficient way of reducing damage proportions compared to reducing the moose population. Since then, data on browsing damage, pine density, and moose density have been collected (or estimated based on observations) in a consistent manner in all of Sweden's moose management areas (MMAs). We therefore now have a better empirical basis for a comprehensive analysis to elucidate the factors driving variation in browsing damage and the management possibilities at the national scale.

In this study, we investigated the relationships between browsing damage, moose and pine densities based on data from the national moose browsing damage inventory (Äbin; see 'Material and methods') for Sweden's MMAs from 2015 to 2024, with spatially matched estimates of moose densities. Acknowledging that there are other factors influencing variation in damage, as described above, we focus here on the two main actors only – pine and moose. We use an ecological model of the browsing process and its dependence on moose density, pine density, and a general vulnerability parameter. The model was evaluated statistically with different assumptions regarding the spatial and temporal variation of parameters in order to find the model that best explains the damage across all MMAs in Sweden over the years. Because managers are interested in the local effects of changes in moose and pine density within MMAs, we conducted a separate analysis of the effects of temporal variation within MMAs. We aimed to explain the effects of moose density, pine density, and a general browsing vulnerability on browsing damage across Sweden.

Material and methods

Data

Since 2000, the Swedish Forest Agency (SFA, Skogsstyrelsen) has conducted annual assessments of browsing damage in young forest stands, known as the Moose Browsing Inventory (Älgbetesinventering Äbin, www.skogsstyrelsen.se/abin). The inventory focuses on browsing that affects wood quality, particularly damage to the main stem. Lateral shoot browsing is not recorded. Three types of stem damage are registered: browsed apical leader (top shoot), bark stripping, and stem breakage – each of which reduces timber quality, especially of the butt log (Liberg et al. 2010). A stem is considered 'browsed' if it shows any of these damage types, with top shoot browsing being the most frequent (Bergqvist et al. 2001, Roberge et al. 2012). Although the inventory is designed to primarily target browsing damage by moose, damage from other ungulates, such as red deer, cannot be ruled out based on visual signs alone (Nichols et al. 2012). Consequently, we refer to the data as a 'browsing damage inventory' rather than exclusively 'moose browsing'. Since 2015, countrywide inventories have been conducted annually after snowmelt and before bud burst – typically in April in southern Sweden and June in the north. In the two northernmost counties, all moose management areas (MMAs; Fig. 2) are surveyed yearly, while in other counties, about half are sampled each year. The size of MMAs in Sweden vary a lot, but they are thought to support more or less distinct moose populations due to barriers such as fenced highways and major water bodies (Sandström 2011). The inventory targets young forest stands with a mean tree height of 1–4 m and a minimum area of 0.5 ha (see the Supporting information for the selection criteria). Up to 15 circular plots

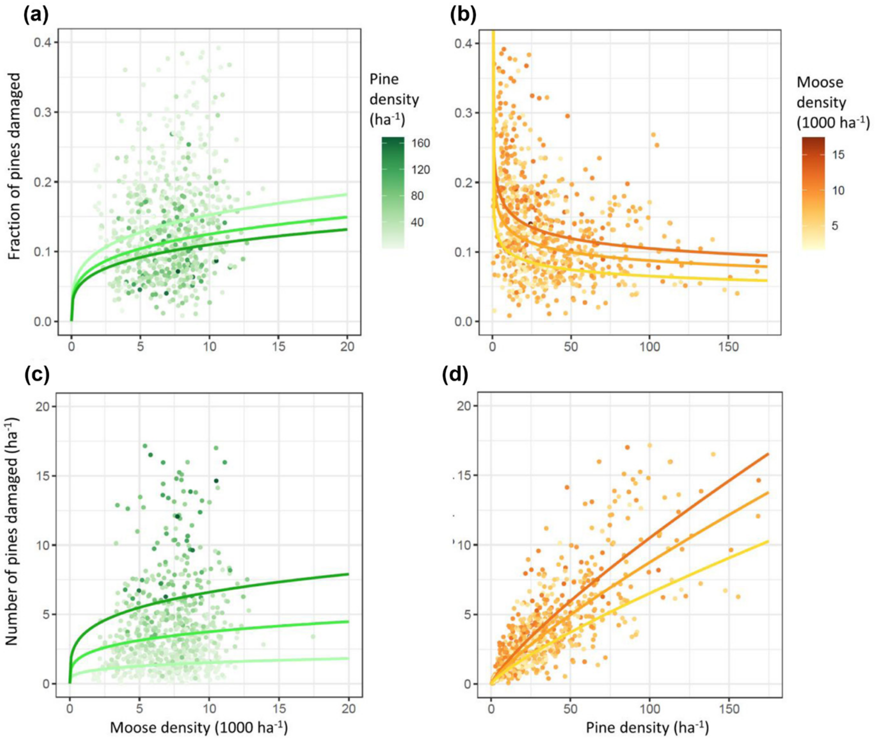

Figure 2. Moose browsing damage as a function of moose density and pine density. Observations (dots) and example model predictions (lines) for an average MMA. In panels (a) and (c), moose density was varied at three levels of constant pine density. In panels (b) and (d), pine density was varied at three levels of constant moose density.

(38.5 m^2, radius = 3.5 m) are assessed per stand. Within each plot, browsing damage from the previous growing season and the following winter is recorded. Damage is registered only on conifer stems above 0.3 m and taller than half the height of the two tallest conifers in the plot, excluding suppressed individuals from previous generations that are unlikely to contribute to future timber production. As a response variable, we used the annual proportion of browsed Scots pine stems. This is a key indicator in Swedish moose and forest management, where a target of $\leq$ 5% annually browsed pine stems is set by the Swedish Environmental Protection Agency (SEPA) and SFA to define acceptable browsing damage levels and inform moose harvest quotas (Naturvårdsverket 2018). In low-productive areas, such as parts of northern Sweden, the target is lower than 5%, even as low as 2%, because of the long period of time the slowly growing trees will be within browsing height.

Our study system included 131 MMAs in Sweden (55.6–68.0°N). Data on browsing damage and the number of pines originated from the National Browsing Inventory (Äbin), provided by the Swedish Forest Agency. The moose density estimates for each moose management area were derived from the Swedish Environmental Protection Agency (SEPA) and were based on the simulation model LST–Moose (unpubl.). For data extractions, we used the boundaries of the MMAs that were in place during 2024. Fifteen MMAs lacked either sufficient data on browsing damage or an estimate of the moose density, while 117 MMAs had sufficient data between the years 2015–2024. In total, our dataset contained 718 observations of browsing damage from the national moose browsing inventory for most of Sweden's MMAs in 2015–2024, with spatially matched estimates of moose densities.

Ecological model

Previously, linear models have often been used to analyze browsing damage related to moose and pine density (Andren and Angelstam 1993, Bergqvist et al. 2014, Pfeffer et al. 2021, Widemo et al. 2022). While easy to analyze statistically, a linear model is not always realistic because it predicts damage even at zero moose density (if the intercept is positive) and it eventually predicts damage greater than 100% as moose density increases. To avoid these pitfalls, we developed a mechanistic mathematical model grounded in fundamental principles of moose browsing behavior. This approach enables a tractable analysis of the interacting effects of moose and pine density on damage, and it allows more realistic predictions for conditions beyond the range of the observed data than a purely statistical regression model.

We assume that the higher the number of moose (M) per pine (P) in an area, i.e. the higher the ratio M/P, the larger the probability (p_{browse}) that a pine is browsed. We use the exponents a and b to account for non-linearity in the effects of M and P, e.g. due to interaction among moose or limited browsing capacity of each moose. We use a parameter c to account for the general damage risk (vulnerability), which can vary among areas due to site fertility (nutritional quality of the pine forage), habitat properties, weather, availability of alternative food, densities of deer, and other factors not explicitly included in the model. This results in Eq. (1) for the probability that a pine tree is damaged over a time interval dt, which is sufficiently small so that $p_{\text{browse}} < 1$.

$$p_{\text{browse}} = c\frac{M^a}{P^b} \tag{1}$$

The more pines that have already been damaged (P_d), the fewer remain undamaged ($P - P_d$). If the moose select pines at random, the rate of increase in damaged pines $\left(\frac{dP_d}{dt}\right)$ is equal to the damage probability times the number of undamaged pines (Eq. 2).

$$\frac{dP_d}{dt} = p_{\text{browse}}\left(P - P_d\right) = c\frac{M^a}{P^b}\left(P - P_d\right) \tag{2}$$

The solution to the differential equation Eq. 2 gives the development of the number and the proportion (F) of damaged pines over time (Eq. 3–4).

$$P_d = P\left(1 - e^{-tc\frac{M^a}{P^b}}\right) \tag{3}$$

$$F = \frac{P_d}{P} = \left(1 - e^{-tc\frac{M^a}{P^b}}\right) \tag{4}$$

Statistical evaluation

Variation among all MMAs and years

To enable the use of linear regression for estimation of model parameters we rearrange Eq. 4 as $\frac{1}{1-F} = e^{-tc\frac{M^a}{P^b}}$ and take the logarithm twice. Because we always evaluate damage over the same amount of time (yearly) we eliminate t by subsuming it in c. These transformations result in the linear Eq. 5.

$$\ln\left(\ln\left(\frac{1}{1-F}\right)\right) = \ln(c) + a\ln(M) - b\ln(P) \tag{5}$$

Linear regressions were used to estimate the parameters a, b, and c, based on the dataset described above. Scaled (z-transformed) values of M and P were used in the regression evaluation and the results re-transformed. We also adjusted model predictions for the bias in predicted mean damage caused by the log-transformation (Eq. 5).

Sweden is a large country covering a wide range of climate conditions, landscape and forest types, and we expect model parameters to vary among counties and MMAs. To account for this variation, we used mixed models. Because we did not know a priori how this variation is best represented, we tested all reasonable and converging model variants (with different random effects) and selected the variant with the lowest Aikake information criterion (AIC). The final model was used to calculate the mean relative sensitivity of browsing damage (proportion of damaged pine) to moose and pine density. Residuals were analyzed to identify model biases and limitations.

Variation within MMAs

It was not possible to completely separate temporal variation within MMAs from other variation components using a mixed model on the whole dataset. Within-MMA effects are the most relevant effects for management, which occurs at the MMA level. However, with a maximum of only 10 datapoints for each MMA we do not expect many significant effects for individual MMAs. Thus, we evaluated the effects of moose and pine densities (slopes) on the damage separately for each MMA with a linear model (Eq. 6) and then calculated the mean effects over all MMAs. In these calculations, we used MMAs with at least five observations, and the resulting slopes for each MMA were weighted by the inverse of their standard errors when calculating the mean slopes. The standard error of the means (SE) was calculated with the *weighted_se* function in R (www.r-project.org).

$$F = \mathrm{c}_t + a_t M - b_t P \qquad (6)$$

This linear model describes the mean observed effects within MMAs but should not be used to predict damage (extrapolate) beyond the observed moose and pine densities in each MMA, as discussed above ('Ecological model'). To enable extrapolation for illustration purposes, we combined these effects with the ecological model and its constraints (no damage without pines or moose, and a maximum damage proportion of 100%). We translated the values of the parameters a_t and b_t in Eq. 6 to corresponding values for the parameters a and b in the ecological model (Eq. 4), based on the fact that a_t and b_t represent differentials of damage with respect to M and P (see derivation in the Supporting information). The resulting parameter values for a and b were used to model the mean within-MMA effects of moose and pine density on damage, as was done for the full spatio-temporal model.

Results

Variation among all MMAs and years

The best model (Table 1) explains 53% of the variation in browsing damage between the MMAs and between years. On average, moose density has a stronger effect on the proportion of damaged pine than pine density (Table 2, Fig. 2). For the number of damaged pines (not proportion), pine density is the most influential variable. However, both effects are non-linear, i.e. the pine effect becomes most important at low pine densities, and the moose density effect is most important at low moose densities (Fig. 2). The contribution of the different variables to the damage varies geographically, as illustrated by the maps (Fig. 3).

The most important random effect in the selected model (Table 1) is the variation in the general vulnerability parameter (intercept) among MMAs, while the random effects of year and county are much smaller (Table 3). The effect of pine density (b) varies slightly among MMAs, whereas such a variation in the moose effect was not part of the selected model.

The residual analysis shows that the model tends to underestimate high damage levels and overestimate low damage levels (Fig. 4a). Furthermore, the residual plots show that this model limitation is mainly linked to MMAs with the lowest pine densities, while there is no clear relationship between residuals and moose density (Fig. 4b–c).

Variation within MMAs

Results for all MMAs are shown in the Supporting information. The mean slopes of proportion damaged pine (F) versus pine and moose density, based on 60 observations, were

Table 1. Model variants ranked by Aikake information criterion (AIC) with columns showing the R *aictab* output (R documentation). All models are based on Eq. 5 but with different sets of random effects. *Selected model.

Random effects	K	AICc	Delta_AICc	AICcWt	Cum.Wt	LL
(1 | County) + (P | MMA) + (1 | Year)*	9	1143.08	0	0.53	0.53	−562.41
(P | MMA) + (1 | Year)	8	1144.89	1.8	0.22	0.75	−564.34
(1 | County) + (P | MMA) + (M | Year)	11	1146.6	3.51	0.09	0.84	−562.11
(M | County) + (P | MMA) + (1 | Year)	11	1147.14	4.05	0.07	0.91	−562.38
(P | MMA) + (M | Year)	10	1148.42	5.34	0.04	0.95	−564.05
(M | County) + (P | MMA) + (1 | MMA) + (1 | Year)	12	1149.21	6.12	0.02	0.98	−562.38
(M | County) + (P | MMA) + (M | Year)	13	1150.69	7.61	0.01	0.99	−562.09
(1 | MMA) + (1 | Year)	6	1150.95	7.87	0.01	1	−569.42
(P | County) + (1 | Year) + (1 | MMA)	9	1153.77	10.69	0	1	−567.76
(1 | MMA) + (1 | County | Year)	6	1162.97	19.89	0	1	−575.43
(1 | MMA)	5	1169.17	26.09	0	1	−579.54
(M | MMA) + (P | MMA)	10	1169.73	26.65	0	1	−574.71
(M | County) + (P | County) + (1 | Year)	11	1216.45	73.36	0	1	−597.04
(M | County) + (P | County) + (M | Year)	13	1220.01	76.93	0	1	−596.75
(1 | County)	5	1229.37	86.29	0	1	−609.65
No random effects	4	1248.7	105.62	0	1	−620.32

Table 2. Model results, R^2, and sensitivities for the selected model variant (first model in Table 1) and the within-MMA temporal model. *At mean densities for moose (7.14 per 1000 ha) and pine (33.4 per ha).

Dependent variable	Parameters	R^2	Relative sensitivity (%)*	
			Moose density	Pine density
Proportion damaged pine (*F*, Eq. 4, 5), Full spatio-temporal model	$a = 0.28$, $b = 0.20$, $c = 0.14$	0.53	+25	−17
No. of damaged pine (*P*, Eq. 3, 5), Full spatio-temporal model	$a = 0.28$, $b = 0.20$, $c = 0.14$	0.71	+25	+81
Proportion damaged pine (*F*, Eq. 4, 6), Within-MMA temporal model	$a = 0.26$, $b = 0.22$, $c = 0.16$	0.67	+25	−21

−0.00038 ± 0.00014 and 0.0035 ± 0.0035, respectively, where the ± values represent standard errors of the weighted means. We transformed these slopes to the corresponding parameters in the ecological model (Supporting information). The resulting relative effects of moose and pine density were very similar to the effects for the full spatio-temporal model (Table 2).

Discussion

Variation among all MMAs and years

Not surprisingly, our results show that both moose and pine density are important in controlling the level of browsing damage. Their relative importance varies geographically (Fig. 3), and the lower the density of either moose or pine, the stronger its effect on the damage (steepness of the slope; Fig. 2). In contrast to a common opinion in the public debate, we show that moose density has a stronger effect on the proportion damaged pines than pine density (Table 2), although the effect of pine density is more certain (lower p-value in Table 3). These relatively clear results contrast to the diverging conclusions from previous studies. Besides the obvious differences among previous studies in scope, variables analyzed, and the models used (Andren and Angelstam 1993, Bergqvist et al. 2014, Pfeffer et al. 2021, 2022, Felton et al. 2022), there are also differences in interpretations of effect size and importance. Sometimes importance was based on the amount of variation explained (Bergqvist et al. 2014) and sometimes on the slope or effect size (Pfeffer et al. 2021). Further, reported effects (slopes) have been based on standardized (centered and divided by the standard deviation) independent variables (Pfeffer et al. 2021, Felton et al. 2022), which leads to larger slopes for variables with higher standard deviation and, vice versa, for variable with smaller standard deviation. Therefore, when standardized variables were used in the regression model, we re-transformed the estimated slopes (effects) back to non-standardized slopes for an accurate interpretation of the effect.

Although our model explains the overall patterns of damage across Sweden well, the residual analysis shows that it does not predict as well at the extremes, i.e. it overestimates at very low damage and underestimates at high damage (Fig. 4).

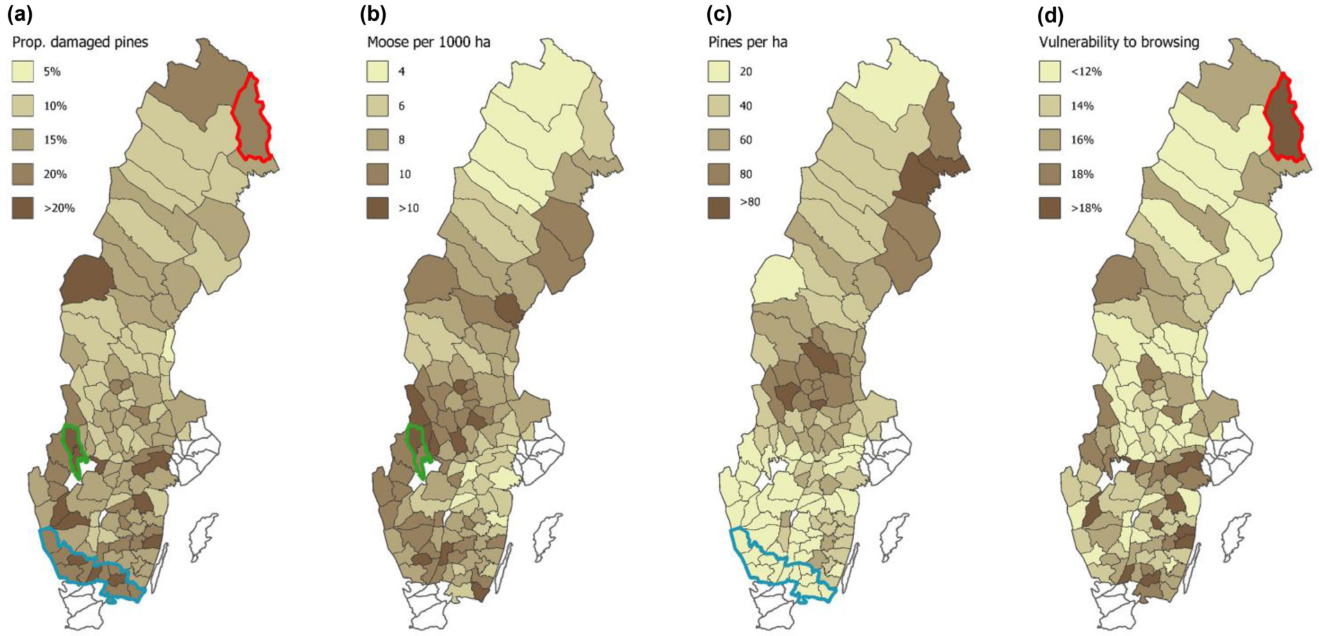

Figure 3. Maps of yearly browsing damage (a), moose density (b), pine density (c), and browsing vulnerability (d), i.e. predicted damage at common moose and pine densities (7.14 moose per 1000 ha and 33.4 pines per ha). The colored encirclings in panel (a) indicate areas with damage due to different underlying reasons: high moose density (green circle, b), low pine density (blue circle, c), and high vulnerability (red circle, d).

Table 3. Analysis of the selected model variant (first model in Table 1), showing output from R's *tab_model*. *Random slope-intercept correlation. #Intraclass correlation coefficient.

Predictors: model parameters	Estimates	CI	p-value
Fixed effects			
Intercept: ln(*c*)	−1.99	−2.40 to 1.58	< 0.001
Moose density, ln(*M*) : *a*	0.28	0.10 to 0.45	0.002
Pine density ln(*P*) : *b*	−0.20	−0.27 to −0.13	< 0.001
Random effects		**Variance**	
σ^2 (residual variance)		0.22	
MMA		0.46	
County		0.01	
Year		0.01	
ln(*P*) | MMA		0.02	
ρ_{01} MMA*		−0.96	
ICC#		0.36	
No. of groups			
N MMA		116	
N County		18	
N Year		10	
N Observations		718	
Marginal R^2/Conditional R^2		0.114/0.432	

This happens especially at the lowest pine densities (Fig. 4c), which could be related to small and yearly variable sample sizes of measured pine stands in these areas. Furthermore, because there are no MMAs with less than ca 2 moose per 1000 ha, the model predictions are not well constrained by observations at such low moose densities. Thus, the modelled slope of damage increases at low moose densities, i.e. the steep initial slopes in Fig. 2, should be interpreted with care and not be applied to guide moose management in individual MMAs (see 'Implications for management').

Variation within MMAs

The within-MMA analysis served to determine if the variation in moose and pine density over time within an MMA had different effects on damage than the spatial variation among MMAs included in the full spatio-temporal model. Because the analysis of variation in damage within MMAs is based on a maximum of 10 yearly observations for each MMA, the statistical power to quantify effects in each MMA is limited, resulting in very few significant effects. Among 60 MMAs, only 3 and 2 had significant pine or moose effects, respectively (Supporting information). However, the mean effects across all MMAs are significant for both moose and pine density, and they translate to very similar effects on the proportion of damaged pine compared to the effects including spatial variation (Table 2). This means that there is no relevant difference in the results of the two analyses. This is expected since the full spatio-temporal (mixed model) analysis includes MMA as a random factor, i.e. the mean damage is

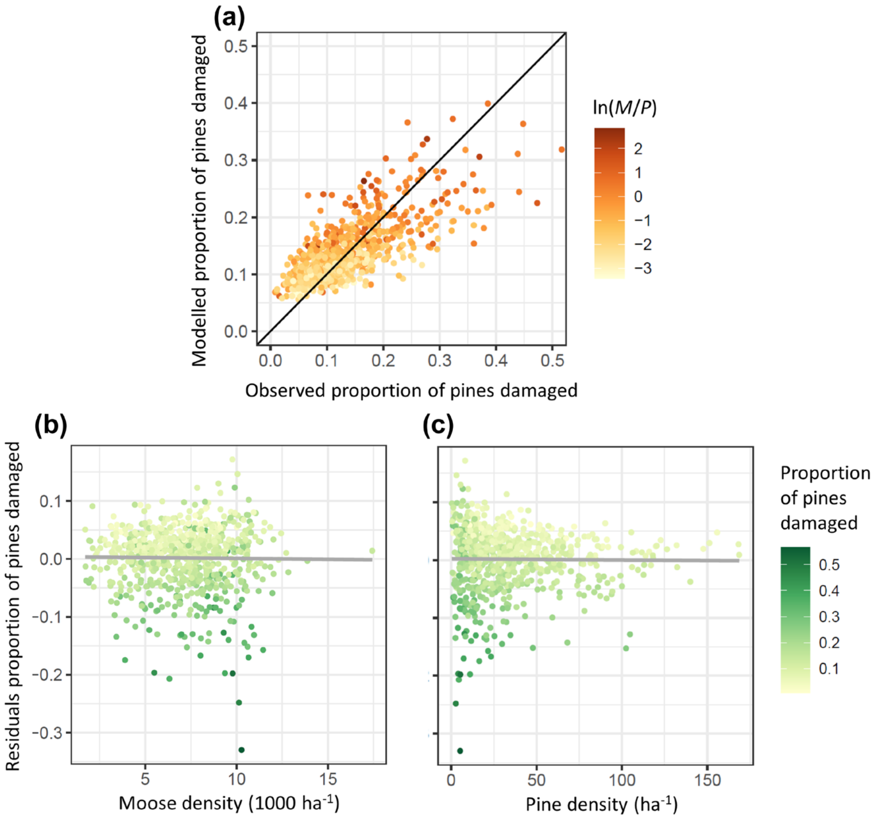

Figure 4. Residual plots. (a) Modelled versus observed damage, where the color indicates the logarithm of the ratio moose/pine density ln(*M*/*P*). (b, c) Residuals (modelled – observed damage).

estimated individually for each MMA, and the moose effect (parameter *a*) is common for all MMAs, roughly corresponding to the mean moose effect in the within-MMA model.

In contrast to the within-MMA model, the pine effect varies among MMAs in the full model (random effect (ln(P)|MMA) in Table 3), but this and the other random effects have minor influences, i.e. they account for a very small part of the total variance (Table 3). This means that we can expect mostly the same mechanisms with similar average effect sizes to operate on the scale within an average MMA over time as spatially across all MMAs, supporting a space-for-time substitution as done in grazing studies (Wang et al. 2022).

Implications for management and monitoring

Although our results show strong general effects and high importance of moose and pine densities for browsing damage, the highly variable and rarely significant effects within MMAs (Supporting information) imply that the general results have limited value for local management at the MMA level. Because the analysis excluding spatial variation produced only a somewhat larger R^2 but no difference in effects compared to the full model (Table 2), we conclude that the uncertain effects at the MMA level are mostly caused by the temporal variation in variables at the MMA level. This conclusion is further supported by comparing modelled and observed mean damage over time in each MMA (averaging out temporal and including only spatial variation), which resulted in an $R^2 = 0.95$, a strong reduction in uncertainty compared to the full spatio-temporal model with $R^2 = 0.53$. The reasons for relatively large year-to-year variation within MMAs are beyond the scope of our current analysis but a potentially important source is a large variation in both density and the number of damaged pines between years within the MMAs. This is likely explained by a combination of factors: the limited sample size, the use of random sampling instead of a fixed grid, and biological influences such as the number of days moose spend foraging in young forest stands, which in turn is affected by variation in snow cover (Pfeffer et al. 2022).

In addition to the uncertainties due to unknown random variation, moose management is likely to introduce a systematic bias. One important objective in moose management is to limit browsing damage on young pine within each MMA. National authorities state that the proportion of pines browsed annually should not exceed 5% (Naturvårdsverket 2018). When browsing pressure is considered too high, the moose population is reduced. Conversely, when browsing damage is below the acceptable threshold, managers may seek to increase moose density to achieve a higher annual yield (harvest rate). This bias may have a profound impact on observed patterns when studying damage levels across MMAs and years. For example, in areas and during years with high browsing vulnerability, moose populations will be regulated to lower densities than in areas and for years with lower vulnerability. Such management leads to a reduced frequency of high damage in vulnerable areas or following years with high vulnerability (e.g. due to snow conditions) at high moose density or low pine density, i.e. fewer points with high damage at high moose and pine density in Fig. 2 compared to a hypothetical scenario without management. This bias would flatten the modelled slope of the damage curves at high moose and pine densities, i.e. reducing the apparent relative effects of moose and pine density on damage estimated by the model (Table 2). This would mean that, in reality, lowering moose density or increasing pine density in high-damage areas would reduce browsing damage more than suggested by the model results. This moose management strategy also limits the ranges of variation of both browsing damage and moose populations, which in turn limits the possibility to calibrate and test the model under more extreme conditions.

Ways to improve management-relevant model predictions of moose and pine effects within MMAs in Sweden include using longer time series of data, more representative pine density and damage estimates, improved estimates of moose populations, and generating a wider range of observational data by allowing moose populations that are higher and lower than current moose populations in some MMAs. Furthermore, the yet unexplained geographical variation in modelled vulnerability to browsing at a common moose and pine density (Fig. 3d) suggests that additional drivers are at play. To deepen the understanding of factors driving variation in damage levels, future modelling could include estimates of other deer species, alternative food sources, and snow cover, the first two of which can be modified through either hunting or forest management. Even though the smaller deer (roe deer, red deer, and fallow deer) do not consume much pine per se (Spitzer et al. 2025), their browsing on other forage plants may still influence moose browsing intensity on pine via competition. For that reason, it may be good to include some kind of proxy for the densities of deer (e.g. harvesting statistics or dung pellet counts) in future models. Density estimates of hares may be relevant to include in regions with deep snow during the winter, as by sitting on top of the snow, hares can reach the top shoots of pine trees within the tree height range of the national pine damage inventory. Alternative food sources in the forest, such as broadleaved trees and ericaceous dwarf shrubs, are consumed in large amounts by both moose and the smaller deer. Inclusion of reliable estimates of the availability of these resources in browsing models may therefore improve model predictions (Felton et al. 2022). The availability of these forage plants varies among MMAs in Sweden due to natural gradients (e.g. in climate and soil conditions) and differences in forest management, where stand cleaning operations in young stands, and the tree species composition and density of production trees in older stands, have strong effects (Graf et al. 2025, Hedwall et al. 2025).

In conclusion, our analysis provides clear evidence and robust estimates for the mean effects of moose and pine density for browsing damage on young Scots pine across MMAs in Sweden. On average, the relative damage reduction effect of a decreased moose population was ~ 1.5× larger (25%) than the effect of increased pine density (17%). We also elucidate the geographical variation in the most important factors regulating damage across Sweden. The currently available data on browsing damage, pine and moose density are insufficient to make reliable predictions for the local impacts of moose and pine management in most individual MMAs. However, we believe that this may change if data quality improves, and observations of additional drivers, such as alternative food sources, become available and are incorporated in the model.

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Author contributions

Oskar Franklin: Conceptualization (equal); Formal analysis (lead); Investigation (equal); Methodology (equal); Writing – original draft (lead); Writing – review and editing (lead). **Christer Kalén**: Conceptualization (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Writing – original draft (equal); Writing – review and editing (equal). **Annika M. Felton**: Conceptualization (equal); Funding acquisition (equal); Investigation (equal); Methodology (equal); Project administration (equal); Writing – original draft (equal); Writing – review and editing (equal). **Märtha Wallgren**: Conceptualization (equal); Investigation (equal); Methodology (equal); Project administration (lead); Writing – original draft (equal); Writing – review and editing (equal).

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Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.x3ffbg81f (Franklin et al. 2026).

Supporting information

The Supporting information associated with this article is available with the online version.

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