



Does recolonization of wolves affect moose browsing damage on young Scots pine?



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ABSTRACT

Ungulates frequently cause damage to human livelihoods, such as agriculture, livestock or forestry. In Sweden, forestry is the dominating land use and is a very important source of income. Moose (*Alces alces*) browsing commonly causes damage to young forest stands, mainly Scots pine (*Pinus sylvestris*). Factors known to affect the level of moose browsing damage are moose density, forage availability, site productivity, tree species composition, snow depth, and infrastructure. One hypothesis is that the recent recolonization of wolves (*Canis lupus*) in Sweden may lead to a decrease in browsing damage levels, through an effect of wolf predation on moose density or moose behaviour. We used data from annual moose browsing damage surveys, long-term wolf monitoring, moose harvest statistics, habitat composition, snow depth, and road network to investigate the effect of wolf recolonization on moose browsing damage on Scots pine. Contrary to predicted, wolf territory establishment and duration showed an increase in the level of moose damage on young Scots pine. But, the effect size was small and it is questionable if it can be considered as biologically relevant. Overall, other factors were more important than wolves in explaining browsing damage on pine by moose. Presence and cover of deciduous species increased the occurrence of moose browsing damage on pine but reduced the level of damage. Decreasing snow depth and increasing road density both resulted in a lower level of damage. We suggest that the strong human impact on all trophic levels on the Swedish forest ecosystem through harvest and intense forestry practices is likely to override wolves' effects on density and behaviour of moose, as well as their potential effects on preferred browsing species for moose.

1. Introduction

As other large herbivores, ungulates are keystone species as they often act as ecosystem engineers, modifying the structure and function of communities (Huntly, 1991; McShea & Rappole, 1992; Persson et al., 2000). Ungulates can have different effects on vegetation because of their foraging behaviours, e.g. grazing, browsing or bark-stripping, but also by other behaviours such as fraying, trampling and defecating (Persson et al., 2000). At high ungulate densities, browsing can hamper plant growth, reproduction and survival, sometimes leading to changes in species composition (Hobbs, 1996; Augustine & McNaughton, 1998; Côté et al., 2004; Skarpe & Hester, 2008). Browsing can also lead to significant financial losses for both agriculture and forestry due to decreased production of valuable plants and the need for preventive actions to reduce damage levels (Reimoser et al., 2011).

Ungulates also play an important role in food webs as a link

between plants and carnivores (Apollonio et al., 2010). A recent recovery of large carnivores, in large part of the world (Chapron et al., 2014; Ripple et al., 2014), may, have strong implications for ungulates but also for human interests. By regulating prey populations, large carnivores can have a major role in ecosystems that may result in cascading effects through the food web (McLaren & Peterson, 1994; Ripple & Larsen, 2000; Beschta & Ripple, 2009). For example, by reducing ungulate population density, predators may reduce their impact on vegetation (Bergerud et al., 1983; Ripple et al., 2001; White et al., 2003; Beschta & Ripple, 2009). Large carnivores can also modify the behaviour of prey, by changing their perception of predation risk according to the habitat characteristics, creating a "landscape of fear" (Laundré et al., 2001; Kuijper et al., 2013).

Sweden is one of the European countries with the largest areal of forested area, and silviculture constitutes a significant part of the Swedish economy (Forti, 2017). Ungulates, in particular moose (*Alces*

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alces), cause damage to forest by feeding on twigs and bark especially on Scots pine (*Pinus sylvestris*) during winter (Faber & Edenius, 1998; Bergqvist et al., 2001; Lav Sund et al., 2003). Scots pine is one of the major food sources for moose during winter, but diet also consists of birch (*Betula* spp.) and more selected, but less abundant species such as rowan (*Sorbus aucuparia*), willow (*Salix* spp.) and aspen (*Populus tremula*) (Cederlund et al., 1980; Månsson et al., 2007). Moose browsing on Scots pine in young forest stands can result in a significant reduction of timber production and quality (Gill, 1992) and cause an annual economic loss of hundreds of millions Euro for forest owners (Liberg et al., 2010).

The density of moose is one of several important factors affecting the browsing damage level in the forest landscape (Hörnberg, 2001; Månsson, 2009). However, in addition to moose density, several environmental and climatic factors may also be important. In particular, the availability of forage is known to affect moose damage levels (Månsson, 2009) with increased pine forage having a diluting effect, i.e. by adding trees at the landscape level a lower proportion of trees will be damaged for a given moose density. Moreover, the availability of selected deciduous species, like rowan, aspen or birch may also reduce browsing pressure on less selected, but commercially valuable tree species, such as Scots pine and Norway spruce (*Picea abies*) (Andrén & Angelstam, 1993). Climatic conditions can influence browsing damage such that increased snow depth will decrease the availability of the field layer that in turn may lead to increased consumption of twigs and bark on trees (Månsson, 2009). Also, human-related activities, such as traffic, may cause a redistribution of ungulates resulting in decreased damage levels near roads (Augustine & Decalesta, 2003; Neumann et al., 2011) or increased damage level if roads are fenced to avoid vehicle-wildlife collisions (Ball & Dahlgren, 2002).

Wolves started to recolonize central Scandinavia in the early 1980s after a long period of absence (greater than 100 years; Haglund, 1968; Wabakken et al., 2001). The return of wolves in this area has resulted in an increased risk of predation for their main prey, the moose (Sand et al., 2005; Wikenros et al., 2015), that may affect both moose density and behaviour, e.g. foraging pattern and spatial distribution.

In this study, we aim to improve our understanding of the interactions between wolves, moose and important forage species to moose. In particular, we examine how the pattern of browsing damage on Scots pine may be affected by the presence of wolves. We predict that the presence and level of moose damage on Scots pine will be lower; (1) inside wolf territories and decrease with time since territory establishment; (2) with increased presence of deciduous species (rowan, aspen, willow and oak (*Quercus robur*)) and at increased pine and birch proportions. Conversely, we predict higher damage level; (3) with increased moose density.

2. Materials & methods

2.1. Study area

The study was conducted in south-central Sweden in 5 different counties (Dalarna, Gävleborg, Värmland, Örebro and Västmanland) which represents a total area of 78 240 km². The landscape in the study area consists mostly of sub-boreal forest (69%), agricultural land (11%), mire (10%), urban area (3%) and other habitat types covering < 1% each (7%) (Nilsson & Cory, 2017). The sub-boreal forests are dominated by Norway spruce (43%) and Scots pine (40%) that have been managed intensively for timber and pulp. Mature stands are harvested by clear-cutting and then reforested by planting or natural regeneration, resulting in even-aged coniferous forest stands mixed with birch (*Betula* spp., 11%). Human density averaged 33.5 humans per km² in the study area (average for 6 counties included in the study area, Statistics Sweden, 2018). The intensive silviculture has led to an extensive forest road network, which with other roads, such as national, regional and highways, had a mean road density of 2.0 km per km² in the study area

(National Roads DataBase NVDB, nvdb.se). The mean snow depth (October–April 2014–2017) ranged between 5 and 12 cm in different regions of the study area (Swedish Meteorological and Hydrological Institute, <https://opendata-download-metobs.smhi.se/explore/>).

The moose population size has been fluctuating in Sweden for centuries (Liberg et al., 2010). Moose hunting was historically reserved to the ruling class, but this restriction was abolished in 1789 causing a moose population decrease. Intensive hunting but also overexploitation of forests, competition with cattle and sheep, and expansion of agricultural lands (Côté et al., 2004; Liberg et al., 2010) almost led to the extinction of moose in Sweden during the 19th century (Bergman & Åkerberg, 2006). However, during 1950–1980 due to regulated harvest, changed forestry (clear-cuts providing food), and a series of mild winters the moose population increased rapidly (Cederlund & Markgren, 1987; Lav Sund & Sandegren, 1989; Hörnberg, 2001; Lav Sund et al., 2003; Liberg et al., 2010).

Wolves were declared functionally extinct in Scandinavia in the 1960 s. In the 1980 s, two wolves from the Finnish-Russian population reproduced in a territory at the border between Sweden and Norway, thereby founded the current Scandinavian population (Wabakken et al., 2001; Liberg et al., 2005). Since then, the wolf population continued to increase in numbers and breeding range and in the winter of 2016–2017, the population in Sweden was composed of 56 territories and estimated to 355 (95% CI = 281–461) individuals (Svensson et al., 2017). Wolf density within the study area was approximately 3–6 wolves per 1000 km². Wolves are the main non-human predator of moose, which constitute more than 95% of their diet (Sand et al., 2005, 2008). Approximately 70% of moose killed by wolves are calves during winter and 90% during summer (Sand et al., 2005, 2008).

2.2. Moose browsing damage survey

The national moose browsing damage survey (“Äbin”) takes place each year during spring (April–June; Skogsstyrelsen, 2019). The main objective is to estimate the proportion of moose damage on Scots pine with a height between 1 and 4 m. Three types of damage are recorded; browsing of the apical shoot, stem breakage and bark-stripping. In this study, plot sampling data from a total of 4086 squares of 1 × 1 km (hereafter squares), randomly distributed in the study area and surveyed over the course of 3 years (2015 to 2017), were used. For the analyses, only squares with the presence of Scots pine in young forest stands were included (n = 3284). Within each stand, 1 to 15 sample plots (stand size dependent) were distributed according to an 80 m grid. All sample plots had a 3.5 m radius. For the analyses, the following measurements were used: number of damaged and undamaged stems of Scots pine, number of stems of birch, presence of highly selected tree species which include rowan, aspen, willow and oak (hereafter RAWO), and the presence of deciduous trees that were competitive with pine, i.e. at least the same height as pine. To obtain the total number of damaged and undamaged pine stems at the square level, upscaling estimation was made from the plot to the stand level, and then from the stand to the square level. Using the same method as Bergqvist et al. (2014), the proportion of browsed Scots pine with recent browsing damage (made during the preceding winter) was calculated for each square. The proportion of tree species available in each square was calculated by dividing the number of trees for each species by the total number of trees. Moreover, the proportion of plots containing RAWO was calculated by dividing the number of plots with the presence of RAWO by the total number of plots in each square (hereafter RAWO proportion).

Only sampled squares dominated with forest habitats were used for the analyses (2537 out of 3284). We classified each square according to their main land cover type (i.e. ≥ 50%) by using Corine Land Cover (CLC) 2012 version 18.5.1 (<https://www.eea.europa.eu/data-and-maps/data/clc-2012-raster>).

Table 1
 Highest ranked candidate models (within $\Delta AIC \leq 2$, shaded grey) and intercept model relating the presence of moose damage on Scots pine to wolf presence (M: Mean wolf territory, O: Observed wolf territory), wolf duration (time since territory establishment), moose index, RAWO proportion, pine and birch proportion, snow depth, and the length of small, medium and large roads. Year of survey and ID of local moose management units were used as random factors to account for temporal and spatial autocorrelation as well as repeated measurements of squares. For each candidate model, degrees of freedom (df), AIC, the difference in AIC relative to the highest-ranked model (ΔAIC), AIC weight (wi), and marginal and conditional R^2 are shown. For each variable, full model-averaged estimates (β) with standard error (SE), Relative Variable Importance (RVI), and partial r -squared (Partial R^2) are shown. Moose browsing damage on Scots pine was surveyed in south-central Sweden from 2015 to 2017. (Wolf territory presence: n = 2537, 512 models; Wolf duration: n = 1336, 512 models).

| | Intercept | Wolf index | Moose index | RAWO proportion | Pine | Birch | Snow depth | Small | Roads Medium | Large | df | AIC | ΔAIC | wi | Marginal R^2 | Conditional R^2 |
|---------------------------|-------------|-----------------|-------------|-----------------|-------------|-------------|-------------|--------------|--------------|--------------|----|---------|--------------|-------|----------------|-------------------|
| Wolf presence | X | X | X | X | X | X | X | X | X | X | 11 | 24450.4 | 0.48 | 0.025 | 0.63 | |
| | X | X | X | X | X | X | X | X | X | X | 12 | 24451.0 | 0.68 | 0.34 | | |
| | X | X | X | X | X | X | X | X | X | X | 12 | 24452.3 | 1.93 | 0.18 | | |
| Standardised β (SE) | 0.99 (0.22) | M = 0.07 (0.06) | 0.16 (0.04) | -0.01 (0.02) | 0.4 (0.03) | 0.40 (0.03) | 0.27 (0.05) | -0.18 (0.02) | -0.06 (0.02) | 0.001 (0.01) | | | | | | |
| RVI | 1 | 1 | 1 | 0.34 | 1 | 1 | 1 | 1 | 1 | 0.18 | | | | | | |
| Partial R^2 | 0.003 | 0.004 | 0.004 | 0.000 | 0.004 | 0.006 | 0.008 | 0.004 | 0.003 | 0.000 | | | | | | |
| Intercept model | X | | | | | | | | | | 1 | 24850.4 | | | | |
| Wolf duration | X | X | X | X | X | X | X | X | X | X | 11 | 12367.0 | 0.34 | 0.041 | 0.71 | |
| | X | X | X | X | X | X | X | X | X | X | 10 | 12367.6 | 0.68 | 0.24 | | |
| | X | X | X | X | X | X | X | X | X | X | 12 | 12367.8 | 0.82 | 0.22 | | |
| | X | X | X | X | X | X | X | X | X | X | 11 | 12368.1 | 1.13 | 0.19 | | |
| Standardised β (SE) | 1.31 (0.37) | 0.03 (0.01) | 0.29 (0.06) | -0.11 (0.04) | 0.54 (0.04) | 0.39 (0.04) | 0.46 (0.07) | -0.01 (0.02) | -0.16 (0.03) | -0.05 (0.06) | | | | | | |
| RVI | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0.41 | 1 | 0.66 | | | | | | |
| Partial R^2 | 0.001 | 0.003 | 0.003 | 0.000 | 0.012 | 0.010 | 0.020 | 0.000 | 0.005 | 0.000 | | | | | | |
| Intercept model | X | | | | | | | | | | 1 | 12625.8 | | | | |

2.3. Explanatory variables

2.3.1. Moose index

The number of moose harvested per km² during the hunting season (autumn/winter) preceding the moose browsing survey was used as a proxy for moose density (hereafter moose index). Moose harvest data were compiled on the level of local moose management units (“Älgjaktområden”, n = 3284, each unit covering in average 428 km², range 1–4276 km²). Data were retrieved from the website Älgdata (<http://www.algdata.se>).

2.3.2. Location of wolf territory and duration since establishment

The Scandinavian wolf population has been monitored since 1978, using foremost snow tracking, DNA analyses and radio-telemetry of collared wolves. The main objective of the monitoring is to confirm territory establishment and breeding status of all territorial wolves (Wabakken et al., 2001; Liberg et al., 2012; Svensson et al., 2017). Wolf territory polygons were calculated by using 100% Minimum Convex Polygon, according to presence indicators obtained from the monitoring (Svensson et al., 2017). The centroid of each polygon was determined using ArcGIS 10.5 (ESRI, 2017). Based on these centroids, a buffer of 18 km radius representing the average wolf territory size (1017 km²) was created (Mattisson et al., 2013; Wikenros et al., 2017).

As the complete wolf territory distribution was not known (except for GPS-collared territorial wolves), two different wolf indices were created. First, all squares with available moose browsing data were categorized as 1) outside the average wolf territory buffer (hereafter outside wolf territory), 2) inside the average wolf territory buffer (hereafter inside mean wolf territory) but outside the wolf territory polygon, or 3) inside the wolf territory polygon (hereafter inside observed wolf territory). Second, time since wolf establishment (hereafter wolf duration) was determined by counting the total number of years each square had been inside observed wolf territories. Of the total 2537 squares that were surveyed in forest habitats, 417 were located inside an observed wolf territory, 956 were inside a mean wolf territory, and 1164 were outside both observed and mean wolf territories.

2.3.3. Snow depth

Snow depth data was obtained from the Swedish Meteorological and Hydrological Institute (SMHI, <https://opendata-download-metobs.smhi.se/explore/>). Data were compiled from 121 weather stations across the six counties October to April 2014–2017. To estimate the snow cover (cm) across the six counties, the interpolation tool (Inverse Distance Weighted or IDW) from spatial analyst tools box in ArcGIS 10.5 was used (ESRI, 2017). The mean snow depth was obtained for each square according to the actual year of the survey.

2.3.4. Road densities

Three road categories could be distinguished according to the National Roads DataBase (NVDB, Trafikverket, 2006). Large roads correspond to highways and national roads (classes 0–2), medium is primary to tertiary roads (classes 3–6), and small represents local forest’s or exploitation roads (classes 7–9). We calculate the length of each road categories in km for each square.

2.3.5. Statistical analyses

We used two approaches to include the dependent variable (browsing damage) in the models, 1) binomial (i.e. presence and absence of damage) and 2) continuous (proportion of damaged trees, 0 < x < 1). To analyse the probability of having damage within included squares (n = 2537), we used General Linear Mixed Models (GLMM), and the “lme4” package (Bates, 2018), with a binomial distribution. For the analysis of damage level (proportion), all squares classified as having a damage level of either 0 and 1 (i.e. 0 or 100%) were deleted to enable the use of a GLMM with a beta distribution reducing the dataset to 1480 squares, applying the “glmmTMB”

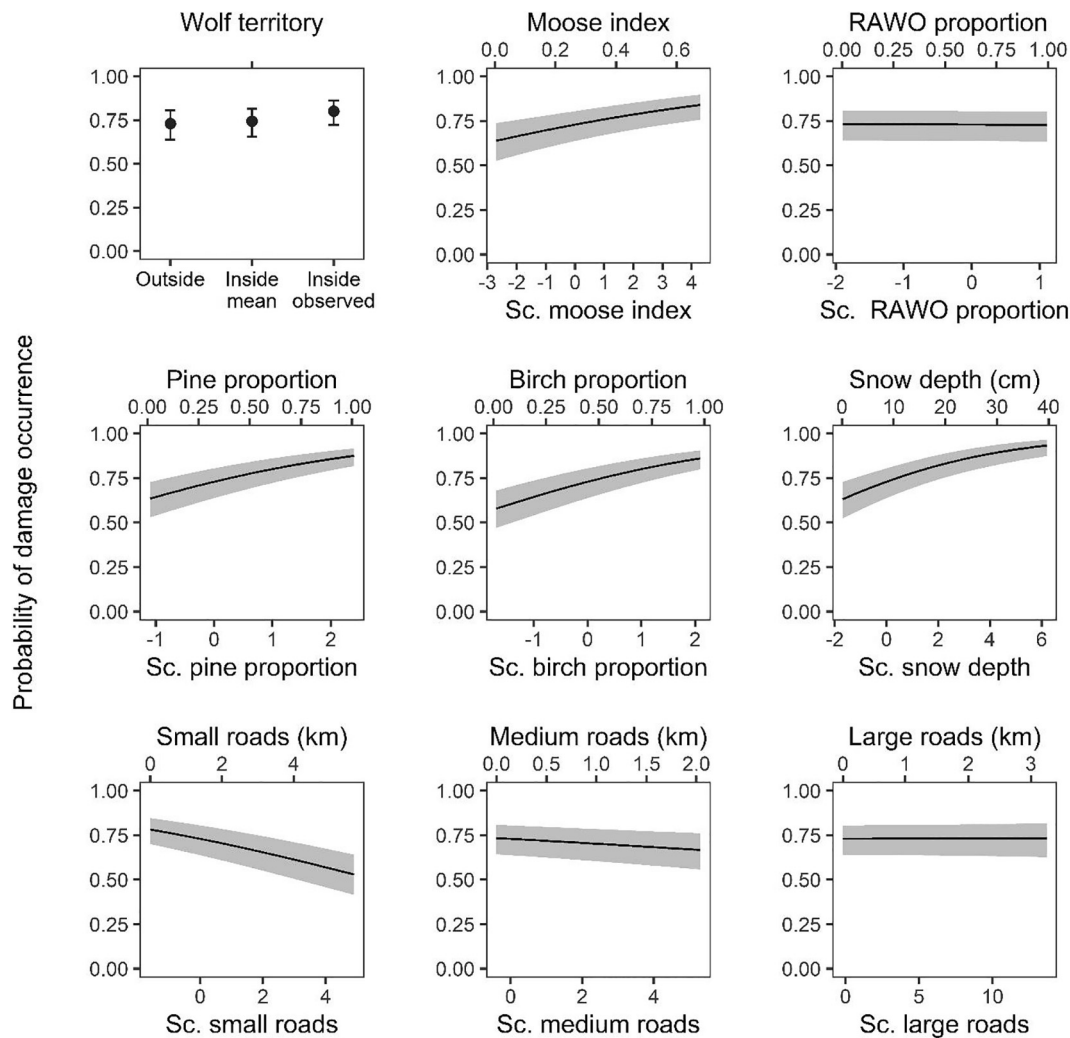


Fig. 1. Occurrence of browsing damage on Scots pine in relation to different predictors at the square level ($n = 2537$) of south-central Sweden from 2015 to 2017 for models including wolf territory as one of the factors. The dots and lines indicate the fitted values, with associated 95% CI, from the full model-averaged estimates (Table 1), with other variables held constant at average (Wolf territory is set to Outside and other scaled variables are set to 0). ‘Sc.’ stands for scaled.

package (Magnusson et al., 2017). All the statistical analyses were conducted using R version 3.6.1 (R Core Team, 2019). Models assumptions were verified.

In each model, the following explanatory variables were used: one of the wolf indices wolf territory presence (3-level category), and wolf duration (continuous variable, range between 1 and 15), moose index (continuous variable, range 0–0.81), RAWO proportion (proportion of squares, range 0–1), proportion of pine and birch trees (range 0.01–1, and 0–0.98, respectively), snow depth (continuous, range 0–40 cm), and small, medium and large roads length (continuous, range 0–6.24, 0–2.28, and 0–3.26, respectively). For all analyses, moose index, RAWO, pine and birch proportions, snow depth and road lengths were all standardised by using the scale function. When including the variable wolf duration, we also had to restrict the number of squares due to zero-inflation. Only squares that were inside mean or observed wolf territories were used, resulting in a sample size of $n = 1480$ for the damage occurrence; and a sample size of $n = 828$ for the damage level.

To account for repeatedly surveyed squares and spatial autocorrelation, the ID of the local moose management unit and year of the survey were included as random factors. The number of surveyed sample plots within each square was used to weight all analyses in relation to sample effort.

For all analyses, models of all combination of variables were compared using the Akaike Information Criterion (AIC) and AIC weights

(wi) from the “MuMIn” package (Barton, 2018). Models with $\Delta AIC \leq 2$ were used to generate full model-averaged parameter estimates (Burnham & Anderson, 2002). AIC weights on model set with $\Delta AIC \leq 2$ were used to generate Relative Variable Importance (RVI) weights for each explanatory variable. Partial R^2 was calculated for each variable, as well as the marginal and conditional total R^2 for the best models.

3. Results

Out of the 2537 squares, occurrence of Scots pine damaged by moose was found in 1534 squares with the damage level (i.e. proportion of trees damaged) ranging from 0 to 1.

3.1. Occurrence of browsing damage on Scots pine

Wolf territory presence was included in all of the top-ranked models explaining the probability of having moose damage ($RVI_{\text{wolf}} = 1$; Table 1), but the difference between the three wolf categories (outside wolf territory, inside mean wolf territory, inside observed wolf territory) was very small (Fig. 1; Table 1). The occurrence of moose damage was higher inside observed wolf territories (0.80 ± 0.04 SE) as compared to inside mean wolf territories (0.74 ± 0.04 SE) and outside wolf territories (0.73 ± 0.04 SE).

For models including wolf territory presence, all explanatory

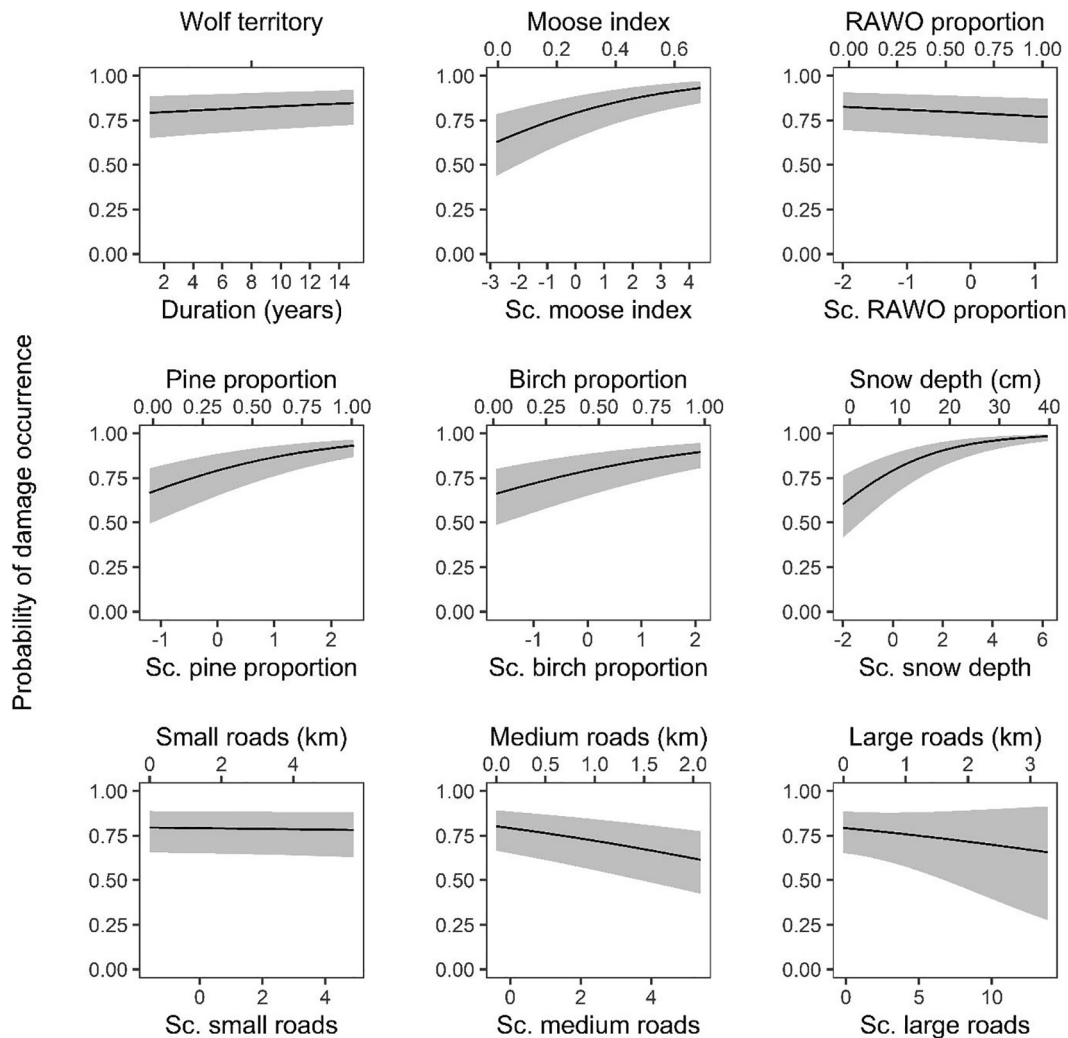


Fig. 2. Occurrence of browsing damage on Scots pine in relation to different predictors at the square level ($n = 1336$) of south-central Sweden from 2015 to 2017 for models including wolf duration (time since territory establishment) as one of the factors. The dots and lines indicate the fitted values, with associated 95% CI, from the full model-averaged estimates (Table 1), with other variables held constant at average (Wolf duration is set to 1 and other scaled variables are set to 0). ‘Sc.’ stands for scaled.

variables except the presence of RAWO and length of large roads were included in the best models (Table 1). RAWO proportion and length of large roads were only included in one of the three top-ranked models and with relatively low Relative Variable Importance weights (RVI; Table 1). Moose index, pine and birch proportion, and snow depth all increased the presence of moose damage whereas RAWO proportion decreased it (Fig. 1; Table 1). In contrast to large road length, small and medium-sized roads lengths decreased the presence of moose damage (Fig. 1; Table 1).

Standardized regression coefficients (β) showed that the proportion of pine and birch was the two most important variables explaining the occurrence of moose damages on pine among squares followed by snow depth, length of small roads, and moose index (Table 1).

Exchanging wolf territory presence with the duration of wolf resulted in that all variables showed the highest relative variable importance ($RVI_{\text{wolf}} = 1$), except for the length of small and large roads (Table 1). Similar to the effect of wolf territory presence, wolf duration increased moose damage (Fig. 2; Table 1), as well as moose index and snow depth, showing a similar relationship as in the models with wolf territory. However, contrary to the wolf territory presence models, large road length decreased moose damage in wolf duration models (Table 1). Standardized regression coefficients showed that the proportion of pine, and snow depth were the two most important variables

followed by the proportion of birch and moose density index for explaining variation in the occurrence of damage on pine among squares (Table 1).

3.2. Browsing damage level on Scots pine

For models on the level of moose damage on Scots pine, all environmental variables were included in all the best models, except for wolf territory and length of large roads (Fig. 3; Table 2). For models that included wolf territory, the level of moose damage was not significantly different inside observed and mean wolf territories, and outside wolf territories (0.15 ± 0.02 SE). Similar to the occurrence of damage, the damage level also increased with the moose density index. In contrast, RAWO proportion, pine and birch proportion, and snow depth all decreased the level of damage, as were the length of small and medium roads (Table 2).

Standardized regression coefficients showed that the proportion of pine was 3.3 times more important in explaining variation in moose damage levels on pine among squares than the effect of birch, which was the second most important variable (Table 2).

Replacing wolf territory presence with duration of wolf resulted in that this variable was present in all top-ranked models ($RVI_{\text{wolf}} = 1$; Table 2), with damage levels being slightly higher in areas with a longer

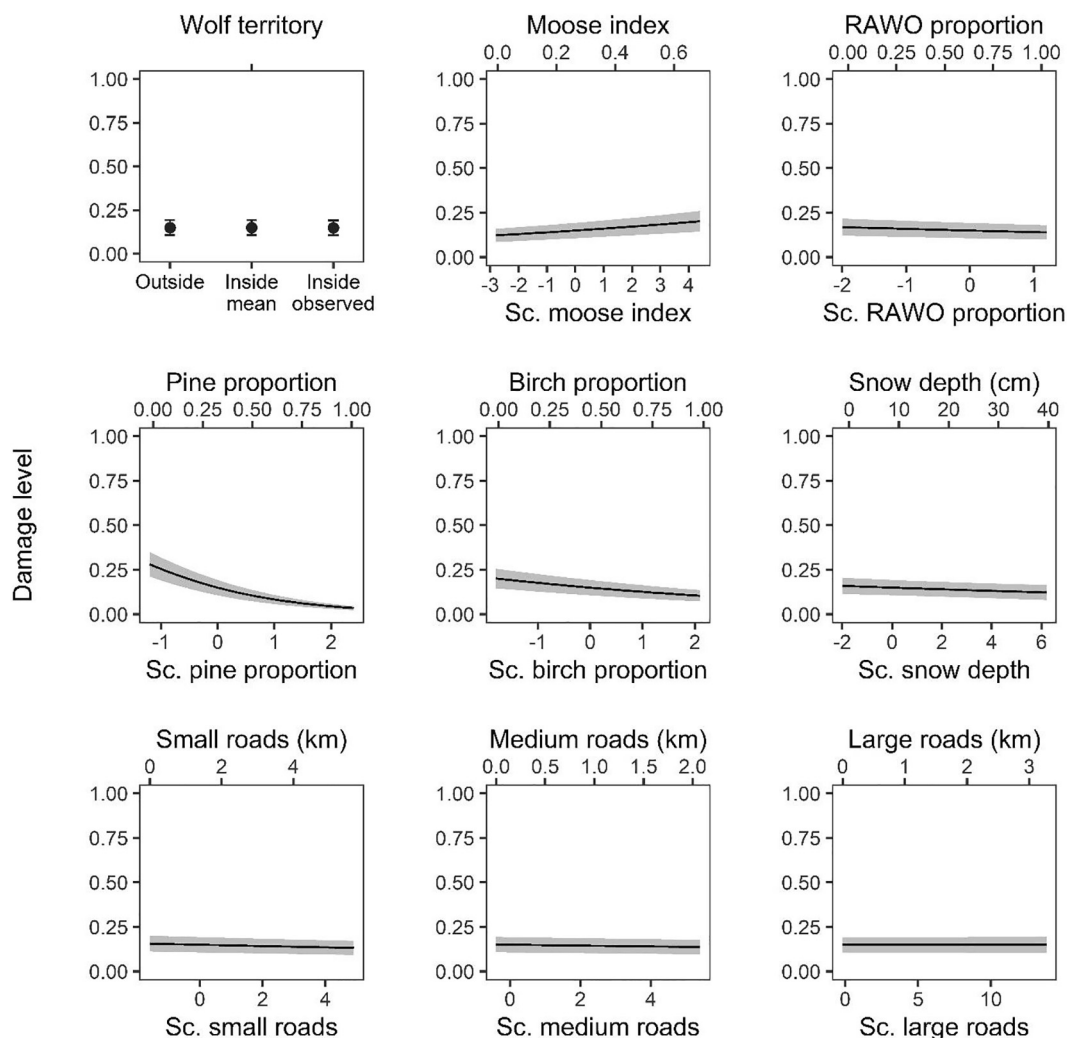


Fig. 3. Browsing damage level on Scots pine in relation to different predictors at the square level ($n = 1480$) of south-central Sweden from 2015 to 2017 for models using wolf territory presence as one of the factors. The dots and lines indicate the fitted values, with associated 95% CI, from the full model-averaged estimates (Table 2), with other variables held constant at average (Wolf territory is set to Outside and other scaled variables are set to 0). ‘Sc.’ stands for scaled.

duration of wolf territory establishment (0.02 ± 0.004 SE; Fig. 4). Also, all the top-ranked models included all environmental variables, except snow depth, and the length of medium sized roads, with these having the same type of effect (+/-) as the models including wolf territory presence (Table 2).

Standardized regression coefficients showed that the proportion of pine and the presence of RAWO was both equally important, and was 2.4 and 5.5 times more important than the proportion of birch, and moose density index, respectively (Table 2).

4. Discussion

The recent return of large carnivores in areas where they once were extirpated has raised attention towards their effects on prey species and ecosystems. For example, predators can have a major impact on prey density and behaviour that may lead to a chain of changes in different trophic levels i.e. cascading events (McLaren & Peterson, 1994; Ripple & Larsen, 2000; Beschta & Ripple, 2009). In this study, we investigated whether the recolonization of wolves in south-central Sweden have resulted in such an effect by altering moose browsing on young Scots pine. The results provide no evidence that the return of wolves has reduced damage levels on young plants of Scots pine. Instead, the analyses revealed that there was statistical support for that moose browsing damage on Scots pine was higher within observed wolf

territories and that the level of damage even increased with time since wolf territory establishment. However, even though the effect was statistically significant the effect of wolf territory presence was very small and it is highly questionable if it can be considered as biologically relevant. Instead, several other variables included in the models were more important explaining the spatial variation in moose browsing damage among forest stands.

Our results contrast to many North American studies and are more in line with recent studies showing that the return of wolves to the Scandinavian ecosystem have not resulted in a major effect on the density and behaviour of their main prey (Sand et al., 2006; Wikenros et al., 2009, 2016; Eriksen et al., 2011; Gervasi et al., 2013; Nicholson et al., 2014; Månsson et al., 2017), and that other environmental variables are actually more important (Ball & Dahlgren, 2002; Månsson et al., 2007; Månsson, 2009; Bergqvist et al., 2014, 2018; Mathisen et al., 2018). For example, the level of damage on Scots pine was more affected by the proportion of pine and birch and by moose density than by the presence of wolves. Increased moose density resulted in an increased risk of damage and a higher level of damage on Scots pine, a result in line with several other studies that have shown a positive relationship between ungulate population density and damage level (Hörnberg, 2001; Côté et al., 2004; Bergqvist et al., 2014).

Although some of the variables used in this study were included in the best models and were more important than the effect of wolves,

Table 2

Highest ranked candidate models (within $\Delta AIC \leq 2$, shaded grey) and intercept model relating the moose damage level on Scots pine to wolf presence (M: Mean wolf territory, O: Observed wolf territory), wolf duration (time since territory establishment), moose index, RAWO proportion, pine and birch proportion, snow depth, and the length of small, medium and large roads. Year of survey and ID of moose management units were used as random factors to account for year effects and repeated measure and spatial autocorrelation of squares. For each candidate model, degrees of freedom (df), AIC, the difference in AIC relative to the highest-ranked model (ΔAIC), AIC weight (wi), and marginal and conditional R^2 are shown. For each variable, full model-averaged estimates (β) with standard error (SE), Relative Variable Importance (RVI), and partial r squared (Partial R^2) are shown. Moose browsing damage on Scots pine was surveyed in south-central Sweden from 2015 to 2017. (Wolf territory presence: n = 1480, 512 models; Wolf duration: n = 828, 512 models).

| | Intercept | Wolf index | Moose index | RAWO proportion | Pine | Birch | Snow depth | Small | Medium | Large | df | AIC | ΔAIC | wi | Marginal R^2 | Conditional R^2 |
|---------------------------|--------------|------------------|-------------|-----------------|--------------|--------------|--------------|--------------|---------------|-----------------|----|----------|--------------|------|----------------|-------------------|
| Wolf presence | X | | X | X | X | X | X | X | X | | 11 | -4001.42 | | 0.54 | 0.25 | 0.77 |
| | X | X | X | X | X | X | X | X | X | | 13 | -4001.28 | 1.44 | 0.26 | | |
| | X | | X | X | X | X | X | X | X | X | 12 | -4001.22 | 1.99 | 0.20 | | |
| Standardised β (SE) | -1.74 (0.17) | M = 0.004 (0.01) | 0.08 (0.02) | -0.07 (0.01) | -0.66 (0.01) | -0.20 (0.01) | -0.04 (0.02) | -0.03 (0.02) | -0.02 (0.01) | -0.0002 (0.004) | | | | | | |
| RVI | | 0.26 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0.20 | | | | | | |
| Partial R^2 | | -0.3e-4 | 0.01 | -0.002 | 0.14 | 0.01 | 0.007 | 0.001 | -0.0001 | -0.2e-4 | | | | | | |
| Intercept model | X | | | | | | | | | | 1 | -36635.5 | | | | |
| Wolf duration | X | X | X | X | X | X | X | X | X | X | 12 | -23204.4 | | 0.38 | 0.24 | 0.79 |
| | X | X | X | X | X | X | X | X | X | X | 13 | -23203.6 | 0.78 | 0.26 | | |
| | X | X | X | X | X | X | X | X | X | X | 11 | -23203.2 | 1.17 | 0.21 | | |
| Standardised β (SE) | -1.84 (0.2) | 0.02 (0.004) | 0.13 (0.02) | -0.06 (0.02) | -0.71 (0.02) | -0.30 (0.02) | -0.02 (0.02) | -0.03 (0.01) | -0.005 (0.01) | -0.05 (0.02) | | | | | | |
| RVI | | 1 | 1 | 1 | 1 | 1 | 0.64 | 1 | 0.51 | 1 | | | | | | |
| Partial R^2 | | -0.002 | 0.02 | -0.002 | 0.16 | 0.02 | 0.008 | -0.001 | -0.0002 | -0.0004 | | | | | | |
| Intercept model | X | | | | | | | | | | 1 | -20985.8 | | | | |

several of them showed either low effect size (β , pseudo R^2) (wolves, RAWO proportion), or a divergent effect (birch proportion, snow depth) or both (length of large roads) depending on the type of dependent variable (occurrence of damage, level of damage) and dataset used. The reason for this is likely a combination of the high statistical power as received from the relatively large sample size (low effect size) and the fact that we used different subsets of the total dataset (divergent effect) for the different analyses (range of sample size: n = 828 – 2537, Table 1 and 2). This finding limits our ability to generalize the effect of different factors on moose damage on Scots pine, however, more importantly it also shows that results may be strongly dependent on the type of dataset and analyses used.

Nevertheless, some of the variables included produced interesting contrasting effects. For example, the risk of having (any) moose damage on Scots pine showed a relatively strong increase as the proportion of both pine increased from 0 to 100% whereas the level of damage showed an even stronger decrease with a similar change in pine proportion. One explanation to the divergent results may be that moose are attracted to areas dominated by pine or birch and therefore the risk of having pine damaged in these areas is also relatively high (Table 1). In our analyses on the level of damage (Table 2) we excluded (for analytical reasons) all squares with 0 and 100% damage on pine trees, which means that only squares with some level of moose damage to Scots pine were included. In this analysis, the level of damage decreased as the proportion of pine increased which may be similar to a density-dependent process (i.e. a dilution effect) where the high availability of pine reduces the proportion (level) of pine damaged by moose.

Similar to an earlier study (Jarnemo et al., 2014), our results showed damage level to be negatively related to the availability of alternative forage (e.g. proportion of RAWO). However, although the relationship between the alternative forage and the risk and level of damage made by moose were consistently negative, it was also weak meaning that a change in RAWO proportion changed the risk or level of damage on Scots pine only with a few percent (6% variation on average). This is also supported by several other studies that have found divergent effects of alternative forage such as RAWO on moose damage (Månsson et al., 2007; Månsson, 2009; Bergqvist et al., 2014). Possibly, the low abundance of RAWO is not enough to change the main foraging strategy by moose. Also, the length of roads of different size showed a relatively consistent effect on the risk and level of moose damage but the effect sizes were also small (5% variation on average) suggesting that this factor lacks biological relevance for the current question.

The fact that moose damage tended to be slightly higher inside wolf territories as compared to outside is an interesting observation. This outcome is supported by other types of data from three earlier studies in Scandinavia on how wolf might alter moose density or behaviours (Karlsson et al., 2007; Wikenros et al., 2015; van Beeck Calkoen et al., 2018), and it may have several mutually exclusive explanations. First, wolves may actively select for areas with a relatively higher density of prey (Wikenros et al., 2016). However, from an international perspective moose densities within wolf territories in Scandinavia are likely to be considered high or very high (Sand et al., 2012; Mattisson et al., 2013). It is therefore questionable if wolves would be able to perceive these relatively small differences between areas, and that this would lead to the active selection for areas with relatively higher moose density for the establishment of territories. Second, an alternative explanation is that the active management (reduced harvest) of moose within wolf territories is responsible for the current result. An earlier study showed that the establishment of wolf territories resulted in an almost instant response by moose hunters within the territory so as to reduce harvest on moose in order to buffer against the increased mortality by wolves (Wikenros et al., 2015). If the reduction in harvest is larger than the increased mortality caused by wolves this may within a few years result in higher moose densities within as compared to outside wolf territories. If true, this also means that the assumed positive relationship between moose density and harvest size would be violated

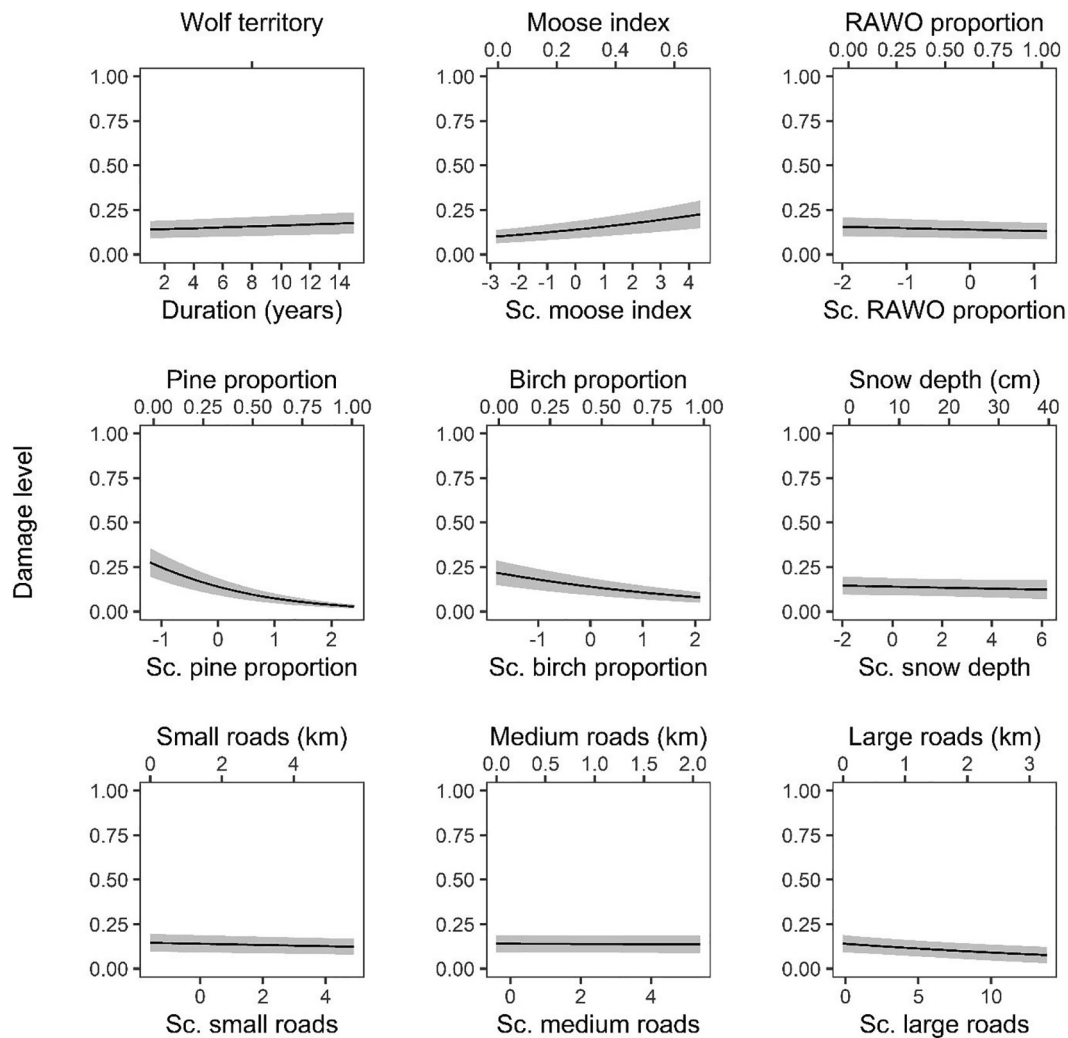


Fig. 4. Browsing damage level on Scots pine in relation to different predictors at the square level ($n = 828$) of south-central Sweden from 2015 to 2017 for models using wolf duration (time since territory establishment) as one of the factors. The dots and lines indicate the fitted values, with associated 95% CI, from the full model-averaged estimates (Table 2), with other variables held constant at average (Wolf duration is set to 1 and other scaled variables are set to 0). ‘Sc.’ stands for scaled.

by the presence of wolves. Third, the higher risk and levels of damage on pine within wolf territories may come from some other factors linked to habitat composition or land productivity that was not available in the current dataset. For example, the density of young plants of Scots pine has shown to be important for the occurrence of moose damage to pine (Månsson, 2009; Wallgren et al., 2013).

Our results are in contrast to several other studies of large carnivore effects on prey and vegetation, especially from North America (Bergerud et al., 1983; McLaren & Peterson, 1994; Ripple & Larsen, 2000; Ripple et al., 2001; Ripple & Beschta, 2004; Beschta & Ripple, 2009). However, one fundamental difference between the current and the other studies listed above is that the Swedish landscape is strongly influenced by human presence and management, which is likely to reduce the potential for effects of predation on other trophic levels (Kuijper et al., 2016). There are at least three important reasons why this may be the case. First, even if the wolf population in Scandinavia has quadrupled in size during the last 15 years (Chapron et al., 2016), it is still limited by both legal and illegal hunting (Liberg et al., 2011, 2012) to levels far below saturation (Mattisson et al. 2013). Even if this study limited the comparison of moose damage to inside and outside observed wolf territories the relatively low overall population density likely allowed wolves to have larger territories than in saturated populations (Mattisson et al., 2013; Zimmermann et al., 2015). Second, in

Sweden hunting is a very important factor affecting the moose population, as it represents approximately > 90% of the mortality on moose in areas with few or no predators (Ericsson & Wallin, 2001; Broman et al., 2002; Rönnegård et al., 2008), and more than 50% of the mortality in areas where wolves have established (Sand et al. 2012; Zimmermann et al. 2019; Wikenros et al. 2015). Thus, the management (harvest size and composition of harvest) of the local moose population will have an overriding effect compared to wolf predation in most areas (Gervasi et al., 2012; Jonzén et al., 2013). Third, the intensive land management in Scandinavia results in human actions that strongly improve both forage quantity and quality for ungulates through intensive forest practices such as clear-cutting and fertilization (Wam et al., 2016; Bergqvist et al., 2018). The increased land productivity and regulated hunting have resulted in a high density and one of the most productive moose populations in the world (Lavsund et al., 2003; Milner et al., 2013). Since the potential for trophic cascades is dependent on land productivity and is highest in low-productivity areas (Fretwell & Barach, 1977; Melis et al., 2009) this is likely to further reduce the likelihood for such an effect either alone or in combination with current management regime on wolf and moose populations in Scandinavia.

5. Conclusion

According to this and other recent studies, wolf recolonization does not seem to have a major impact on either moose density or moose behaviour in Scandinavia (Sand et al., 2006; Wikenros et al., 2009, 2016; Eriksen et al., 2011; Gervasi et al., 2013; Nicholson et al., 2014; Månsson et al., 2017; van Beeck Calkoen et al., 2018). Moose population density, as well as other environmental factors such as forage availability, road densities, and snow depth, affect moose browsing patterns and damage levels more than both direct and risk effects from wolves. Because the Scandinavian landscape is highly influenced by human activities such as forestry and hunting there is a reduced potential for a trophic cascade effect caused by large carnivores such as wolves. In Scandinavia, as in many areas of the world, hunting is still the main cause of mortality for the wolves' main prey, moose, and silvicultural practices strongly affects tree species composition and age structure in the forested landscape.

CRedit authorship contribution statement

Morgane Gicquel: Formal analysis, Writing - original draft, Visualization. **Håkan Sand:** Conceptualization, Writing - review & editing, Supervision, Funding acquisition. **Johan Månsson:** Conceptualization, Writing - review & editing, Supervision, Funding acquisition. **Märtha Wallgren:** Writing - review & editing. **Camilla Wikenros:** Conceptualization, Writing - review & editing, Project administration, Supervision, Funding acquisition.

Declaration of Competing Interest

The authors declared that there is no conflict of interest.

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