Recolonization of wolves in Sweden - does it affect moose browsing damage on Scots Pine?

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Master thesis

Recolonization of wolves in Sweden
- __does it affect moose browsing damage on Scots Pine?__

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Browsing damage types on Scots pine (*Pinus sylvestris*) caused by deer. The first image shows a "top shoot" injury; the second shows both fresh and old damage on the same pine tree, whereas the third one shows another type of damage called "bark stripping". Photo credit: The Swedish Forest Agency (Skogsstyrelsen).

Abstract

The recent recolonization by wolves (*Canis lupus*) of Sweden has provided a unique opportunity to study their importance within terrestrial ecosystems, in particular to investigate the impact that recolonizing large predators may have on ecosystems with strong anthropogenic influence. I used data from the Swedish Forest Agency to investigate the presence and abundance of moose (*Alces alces*), as well as presence and intensity of browsing by moose on Scots pine in relation to wolf occurrence in Sweden. Data from the Swedish wolf-monitoring system was used to study the effect of wolf presence/absence and time since wolf territory establishment on moose presence and abundance and on moose browsing presence and intensity. The probability of moose presence was higher inside wolf territories compared to outside, whereas moose abundance was not significantly affected by wolf presence. There was no effect of time since wolf territory establishment on moose presence and abundance. The probability of browsing presence was not affected by wolf presence, whereas browsing intensity was higher within wolf territories than outside. Time since wolf territory establishment was positively correlated to the probability of moose browsing, but had no effect on browsing intensity. It might be possible that wolves in Scandinavia actively decide to establish a territory in areas with a higher probability of prey encounter, i.e. moose presence, and such pattern could also explain the higher browsing intensity found within wolf territories compared to outside. This study highlights that the return of large apex predators to landscapes with strong anthropogenic influence may not result in the same top-down effects described in many studies located in national parks in North America.

Acknowledgment

1. Introduction

Trophic cascades are described as "reciprocal predator–prey effects that alter the abundance, biomass and/or productivity of a population community across more than one link in a food web" (Pace et al., 1999). The removal, as well as the return, of so-called *keystone species* (e.g. apex predators), which exert strong top-down dominance, can trigger a series of changes in an ecosystem (Strong, 1992). Predators can influence ecosystems either through direct lethal or indirect, non-lethal effects on prey (Paine, 1969). The former are observed when predation leads to a *direct* reduction in numbers of herbivores which in turn affects vegetation, whereby prey respond numerically to the mere presence of the predator (Lima and Dill, 1990; Schmitz et al., 1997; Creel and Christianson, 2008; Terborgh and Estes, 2010). Indirect non-lethal effects are mediated through increased predation risk, which in turn elicits a series of *behavioural* adaptations in the prey species (e.g. changes in foraging behaviour, habitat selection and distribution) (Lima and Dill, 1990; Schmitz et al., 1997; Creel and Christianson, 2008; Terborgh and Estes, 2010). For instance, the reintroduction of wolves (*Canis lupus*) into Yellowstone National Park has been claimed to facilitate aspen (*Populus tremuloides*) recruitment not only through the reduction in elk (*Cervus canadensis*) numbers, but also through changes in elk foraging behaviour and movement patterns (e.g. avoidance of certain areas of the park in response to an increased risk of predation) (Ripple and Larsen, 2000; but see Kauffman et al., 2010 for contrasting findings). Such top-down forces appear to be rather strong in systems where wolves are present, since herbivore densities are substantially lower compared to wolf-free guilds (Ripple and Beschta, 2012). Similarly to the case of Yellowstone National Park, studies on trophic cascades involving apex predators are commonly situated in national parks and other locations where there is little or no anthropogenic activity, and where indeed the potential to shape the dynamics and functions of an ecosystem is considerable (Mech, 1966; McLaren and Peterson, 1994; Berger et al., 2001, Terborgh and Estes, 2010, Mech, 2013). It is now also known that the alleged effects triggered by apex predators on ecosystems are context-dependent, i.e. other factors are also likely to be involved and they should always be considered (Ritchie et al., 2012). For instance, the recolonization of large predators in Europe is occurring in landscapes with strong human influence, such as forestry and game hunting. Such a structural difference in landscapes between Europe and some national parks in North America (location of most studies on trophic cascades) urges the need for further research into the impact that recolonizing large predators may have on ecosystems with anthropogenic influence (Sergio et al., 2008; Kuijper et al., 2016).

Interactions between humans and wildlife, in particular large predators, have existed since prehistorical times (Lee-Thorp et al., 2000) but the rapid increase of the human population and associated activities has led to an escalation in their severity and frequency in recent decades (Woodroffe, 2000; Conover, 2002; Graham et al., 2005). Land use transformation (Distefano, 2003; Nyamasyo and Kihima, 2014), habitat

loss, degradation and fragmentation (Kumar, 2012), increasing livestock population and competitive exclusion of wild herbivores (Mishra, 1997; Distefano, 2003; Mishra et al., 2003) as well as abundance and distribution of wild prey (Meriggi and Lovari, 1996; Polisar et al., 2003) have been identified as main driving forces of this trend (Woodroffe, 2000; Conover, 2002). Conflicts between human and large predators are the product of socio-economic and political aspects intertwining over a landscape (Thirgood et al., 2000; Sillero and Laurenson, 2001; Graham et al., 2005). They become especially controversial in circumstances where the predator is legally protected and competition with humans occurs over an ecomically valuable, limited and shared resource (Thirgood et al., 2000; Sillero and Laurenson, 2001; Graham et al., 2005). One of the most frequent causes of conflict between humans and large predators is competition for game species (Caro and Fitzgibbon, 1992; Fritts et al., 2003; Thirgood et al., 2000; Thirgood et al., 2005). Game hunting has a great socio-economic value in many countries (Graham et al., 2005), functioning as a source of employment and leisure activity as well as generating income (Graham et al., 2005). The recent recolonization of historical ranges by large predators has been opposed by hunters in many countries, who perceive predators as a threat to wild game population and hunting dogs (Fritts et al., 2003).

The recolonization of Scandinavia by wolves has provided a unique opportunity to study the importance of large predators within terrestrial ecosystems outside of national parks and with anthropogenic influence (Sand et al., 2006; Wikenros et al., 2015). Human density across the distribution of the Scandinavian wolf population is low (many regions < 1 person per km^2) (Swedish National Atlas, 1991; Statistics Norway, 2003), but nonetheless humans exploit the landscape through many activities. For instance, the population of moose (*Alces alces*) in Fennoscandia (Sweden, Norway and Finland) is one of the largest and most productive in the world, with estimates of winter population size and density in 2003 reaching 500,000 and 5-6 km^{-2}, respectively (Lavsund et al., 2003). Moose represent the most important game species in Sweden, and approximately 100,000 moose are harvested each year by a large number of hunters (Gundersen, 2003). At the same time, moose also represents the main prey species of wolves during both winter and summer (Olsson et al., 1997; Sand et al., 2005; 2008). In order to avoid a further decline in moose numbers as a consequence of the additive combination of wolf predation and human harvest to natural mortality (Sand et al., 2012), hunters in within wolf territories of Sweden reduced the harvest size as well as the proportion of hunted females (Wikenros et al., 2015). This situation is further exacerbated by the fact that the interests of Swedish hunters are frequently in contrast with those of forest companies for the management of the moose population (Sandström et al., 2011; Ezebilo et al., 2012). The former (hunters) expect the moose population to be sufficiently large to have a profitable harvest, whereas the latter (land owners) prefer a smaller moose population to limit browsing damages to commercially valuable tree species (Bergman and Åkerberg, 2006; Mattsson, 2008). Forest companies own approximately 42% of forests in Sweden (Karlsson, 2004), and browsing by moose is perceived as a large problem

since commercially valuable trees, like Scots pine (*Pinus sylvestris*), are vital contributors to the Swedish economy (Bergman and Åkerberg, 2006). Moose can exert strong browsing pressure on forest in young successional stages (Angelstam et al. 2000) and severe browsing damage on commercially important trees can result in reduced technical quality of timber, suppressed volume growth and impaired development of trees (Lavsund, 1987; Heikkilä and Härkönen, 1993; Bergqvist et al., 2001, 2014), all of which translate into economic losses for the land owner. Angelstam et al. (2000) found damages on average at 57% of all individual trees of Scots pine in pine-dominated stands in Sweden. Such an intensity of moose browsing have the potential to also hinder the development of deciduous trees like aspen (*Populus tremula*), rowan (*Sorbus aucuparia*) and willows (*Salix* spp.) (Angelstam et al., 2000; Ericsson et al., 2001), affecting the overall biodiversity since these trees are important species for many forest-living organisms. Several studies have indicated that multiple factors influence the amount of food browsed by moose and the resulting forest damage levels in winter, including forage availability (Cederlund et al., 1980; Månsson et al., 2007), diversity of forage species (Månsson et al., 2007) and moose density (Broman and Wallin, 2003). Mathisen et al. (2017) showed that moose display a preference for previously browsed trees, most likely as a result of greater relative availability of shoots within browsing height and potentially also increased palatability. Snow cover is also known to influence both moose density and consequently browsing damage (Månsson, 2009), since it can affect food availability and energy costs of movements, as well as hinder movements of moose (Safford, 2004; Doerr et al., 2005; Dussault et al., 2005; Poole and Mowat, 2005; Visscher et al., 2005). The risk of spending more energy moving across deep snow to feed than what is actually assimiliated through ingested food is thought to result in a strong selective pressure on moose (Lundmark and Ball, 2008). Therefore, moose presence and abundance is expected to be negatively correlated with snow depth. Linear features such as roads and rivers may possibly function as corridors for movement (Brown et al., 2006; Latham et al., 2011; Zimmermann et al., 2014), but can also be barriers (Vistnes et al., 2004; Epps et al., 2005; Laurian et al., 2008) for movements (Bartzke et al., 2015). Previous research suggested that moose avoid highway and forest roads, but sometimes select for habitats adjacent to highway sides in proportion to the availability of food and mineral salts, and possibly also to lower the risk of predation for females (Laurian et al., 2012). Heikkilä (1990) found that browsing intensity increased with increasing distance from roads, whereas Ball and Dahlgren (2002) observed the opposite pattern with proximity to highways.

The goal of this thesis was to test whether the presence of wolves will affect presence and intensity of moose browsing damage on Scots pine in young forest stands. More specifically, wolf presence and/or time since wolf establishment is predicted to be negatively correlated to moose presence and abundance, and such predator-induced reduction in moose numbers may in turn elicit parallel changes in browsing intensity to forest plants of commercial value. Furthermore, the effect of additional variables, known to affect damage levels, such as moose density, forage availability, forest

management status, previous browsing, snow cover and distance to roads were also investigated. The findings of this study will increase our understanding of the effect of wolf predation on lower trophic levels in the Scandinavian ecosystem.

2. Materials and Methods

2.1. Study area

The study was conducted between 2003 and 2016 across the geographical breeding range of wolves in south-central Sweden, including the counties of Dalarna, Gävleborg, Värmland, Västmanland, Västra Götaland, and Örebro (56°50' - 63°N, 11°50' - 17°E, approximately 102 916 km^2; Figure 1). The landscape is dominated by boreal forests, approximately 81%, 89%, 83%, 64%, 75% and 58% of land cover for Dalarna, Gävleborg, Värmland, Västmanland, Västra Götaland, and Örebro, respectively (Swedish Statistical Yearbook of Forestry, SSFY, 2014). All counties are subjected to intensive forestry practices, and the predominant tree species are Scots pine*, Norway spruce (*Picea abies*) and birch (SSFY, 2014). The extensive commercial logging and intensive forestry practices have also resulted in the creation of a vast network of gravel roads within the study area. The number of days with snow varies from approximately 50/year in the southernmost counties to over 200/year in the north, and average precipitation ranges around 600-900 mm/year (Swedish Meteorological and Hydrological Institute, SMHI, 2017).

During the study period the wolf population increased from 22 to 54 family groups and territorial pairs (Wabakken et al., 2004; 2016). The study area is also home to other large and medium-sized carnivores, such as brown bear (*Ursus arctos),* lynx (*Lynx lynx)* and wolverine (*Gulo gulo*) (Zimmermann, 2014). The dominant prey species of wolves in Scandinavia is moose, as it represents over 90% of the food biomass of wolves in summer and winter (Olsson et al., 1997; Sand et al., 2005; 2008). Other potential prey species are roe deer (*Capreolus capreolus*), semi domestic reindeer (*Rangifer tarandus*), red deer (*Cervus elaphus*) and smaller species like beaver (*Castor fiber*), badger (*Meles meles*), mountain and European hare (*Lepus timidus*, and *L. europeus*) (Sand et al., 2008). Moose winter density within the study area averages approximately 1.3 per km^2 (Zimmermann, 2014). Moose preferably feed on rowan, aspen, and willows, but also browse on other species such as silver birch (*Betula pendula*), downy birch (*Betula pubescens*) and Scots pine (Månsson et al., 2007). Scots pine represents quantitatively the most important food source for moose during winter in Sweden, despite being less preferred to aspen, willows and rowan (Cederlund et al., 1980).
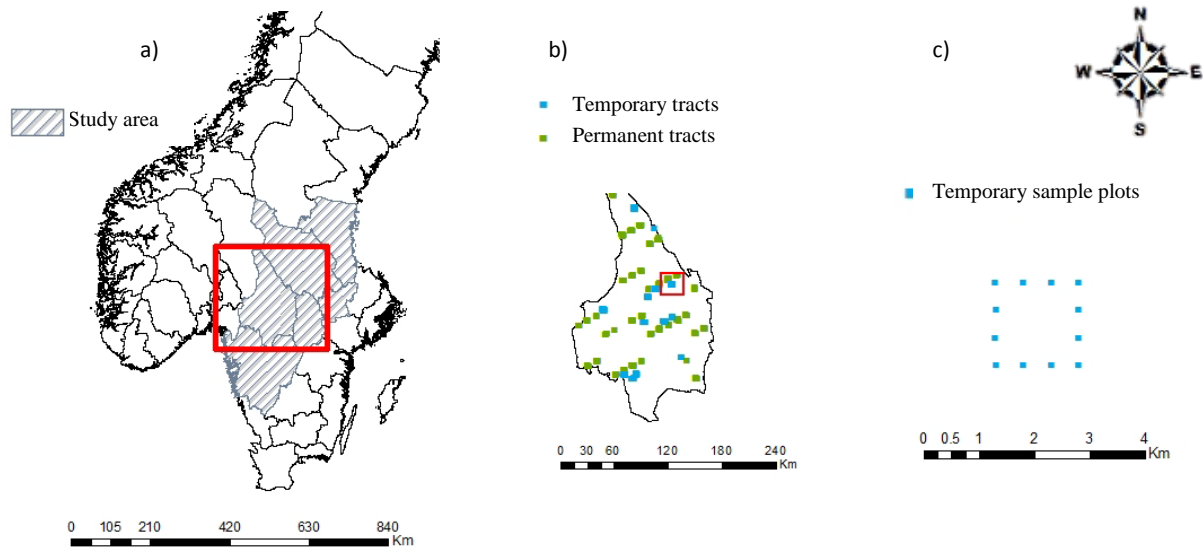
Figure 1: Location of the study area in south-central Sweden from 2003 until 2016: a) counties of Dalarna, GĀvleborg, Värmland, Västmanland, Västra Götaland and Örebro, where moose density and browsing damage were surveyed; b) Värmland county showing the permanent and temporary tracts sampled in 2010 (permanent tracts are revisited every 5th year, whereas temporary tracts are surveyed only once); and, c) within each tract, a number of plots ranging from 2 to 12 are surveyed. Maps created using ArcGIS 10.2.2 (http://support.esri.com/Products/Desktop/arcgis-desktop/arcmap/10-2-2)

2.2. Sampling design

The Swedish National Forest Inventory (SNFI) is based on the sampling of tracts that are systematically distributed over the whole country every year (Fridman et al., 2014). Tracts are clusters of sample plots where the plots are positioned alongside a rectangle or quadrat of variable lengths (usually ranging between 300 to 1800 m) depending on stratum and geographical location, i.e. tracts lie closer to each other in the south than in the north (Fridman et al., 2014; SNFI, 2004). The sample plots are usually circular and divided in sub-circles of different radius (Figure 2) (Tokola, 2006). Temporary plots have a radius of approximately 7 m and are surveyed only once. Permanent plots have a 10 m radius and are regularly re-surveyed, usually every 5th year, generating different times series where permanent plots have slightly different coordinates compared to the year before (Fridman et al., 2014). For instance, permanent plots visited in 2003 were revisited in 2008 and 2013, but permanent plots sampled in 2004 (and consequently in 2009 and 2014) had different locations than those in 2003. Therefore, during the study period (2003-2016), five different times series of permanent plots were included in the analysis: 2003-2008-2013, 2004-2009-2014, 2005-2010-2015, 2006-2011-2016, 2007-2012. Approximately 11000 sample plots are surveyed annually in Sweden between May and September (Wikman and Wessmark, 2017). The centre of each plot is selected randomly, and therefore sometimes the area of an individual plot extends over several forest stand types and/or different forest management status. When this happens, the plot is divided into smaller plots (1 or 2) as to ensure that each plots encompasses only one forest stand type and/or forest action (Wikman and Wessmark, 2017). In order to convey

information that is representative of larger areas SNFI has adopted a scaling factor, which is the factor that the plot area is multiplied with in order to obtain the area of the entire region that each individual plot represents (SNFI, 2004; Wikman and Wessmark, 2017). The scaling factor is dependent on the size of the plot, but also on its location, i.e. as a result of the smaller variation in the state of forests in northern Sweden, the network of plots is much sparser compared to central and southern Sweden, which entails that scaling factors for those plots are usually higher (Wikman and Wessmark, 2017). Scaling factors are applied to moose pellet counts and browsing on pine used in this study. Data from both permanent and temporary plots was used in this study, for a total of 17866 and 12523 surveyed plots, respectively. Moose pellet counts and browsing damage surveys are carried out within the smaller sub-circle of a plot (3.5 m radius, $\approx$38m^2) for both permanent and temporary plots. (Figure 3).
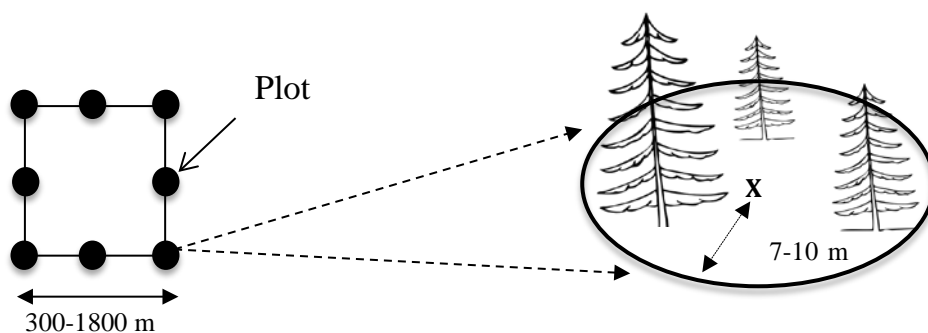
Figure 2: Design of the tracts and sample plots employed by the Swedish National Forest Inventory (SNFI) from 2003 to monitor the state of forest resources in Sweden. The center of the plot is marked with an *x*. Modified from: Tokola (2006).
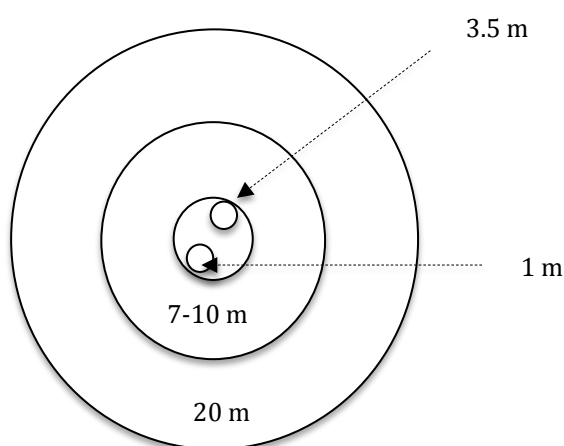
Figure 3: Design of the sample plots employed by the Swedish National Forest Inventory (SNFI) from 2003 to monitor the state of forest resources in Sweden. The numbers indicate the length of the radius for each subplot. Different parameters are measured in different subplots, e.g. ÄBIN and moose pellet counts in the 3,5m radius subplot. ÄBIN is a method used to survey forest damage locally and regionally. It produces an index of browsing pressure based on bark stripping, steam breakage and browsing on top shoots in Scots pine plantations (Bergman and Åkerberg, 2006). Modified from: Tokola (2006).

2.2.1. Moose pellet counts

The SNFI records moose pellet groups within each temporary and permanent plot, distributed over five different forest management status management: clear-cut, young forest, thinned forest, felled forest and selectively thinned forest. In order to be counted as a pile the number of pellets must be at least 20. The number of pellet groups per plot was used as a proxy for moose density, in order to investigate whether wolf presence and time since territory establishment had elicited a spatial and temporal response to increased predation in moose. Moose is known to concentrate near young forest stands (Gundersen et al., 2004), so in this study all different management statuses were used from 2003 onward as an explanatory variable for moose presence and abundance.

2.2.2. Moose browsing damage

The Swedish Forestry Agency implemented a nationwide moose browsing monitoring program in 2003 (ÄBIN) and during the same year the SNFI adopted ÄBIN as the only methodology to record moose browsing damage on pine trees, Scots pine and lodgepole pine (*Pinus contorta*) (hereafter pine), within both permanent and temporary plots. ÄBIN is used to survey forest damage locally and regionally and to produce data on moose browsing but also basic data to be used by decision−makers with regards to moose management (Kjellander, 2007; Reimoser and Putman, 2011). The monitoring program generates an index of browsing pressure based on bark stripping, steam breakage and browsing on top shoots in Scots pine plantations (Bergman and Åkerberg, 2006), which is aimed to allow for a relative estimate of moose population size in relation to the available forage within that area (Kjellander, 2007). The current ÄBIN survey is carried out in pine stands that fulfil the following criteria:

1. Young forest,
2. tree height between 1-4 m, and
3. main stems in the stand must constitute of at least 10% pine or birch.

In stands that fulfil these conditions, the SNFI records browsing damage in plots with a radius of 3.5 meters, and the surveyed stems of pine and birch need to be higher than half the mean height of the two tallest coniferous trees within the plot (SNFI, 2004; Kjellander, 2007). The obligatory variables to be registered for each plot are fresh (last winter) damage caused by moose (stem break and top shoot bites on both pine and birch, whereas bark stripping only on pine) (SNFI, 2004; Kjellander, 2007). Other non obligatory variables included in this study are old browsing damage, such as dead trees and stem breakage in the form of a ″bayonet″, i.e. loss of apical dominance of main stem, or other types of damage not caused by moose, as well as the number of pine trees without any damage (SNFI, 2004).

2.2.3. Tree coverage

Each plot is also surveyed to record the coverage (m^2) of available forage within a browsing height of 0.3-2.5 meters above the ground. Forage consists of both species of pine, birch, aspen, rowan, willow, common oak (*Quercus robur)*, common juniper (*Juniperus communis)*, and European ash (*Fraxinus excelsior)*. Between 1983 and 2003 pine coverage included both pine species (Scots pine and Lodgepole pine)*,* whereas from 2004 each species has been surveyed separately. In order to be able to compare pine coverage from 2003 until 2016, and hence study the potential long-term effects of pine coverage on browsing and moose density, the coverage data from Scots pine and lodgepole pine between 2004-2016 was aggregated together in order to obtain total pine cover for each individual plot, similarly to the measurement available for 2003. Pine coverage was further divided by the area of each plot to enable comparisons between plots of different sizes. Rowan, aspen, willow and oak are usually grouped under the name of RAWO (RASE in Swedish) species and coverage (m^2) of these species within each plot started to be registered with the onset of ÄBIN from 2003 onward. The coverage data for each RAWO species was aggregated together and subsequently divided by the area of each individual plot to also enable comparisons between plots of different sizes.

2.3. Snow depth

Data on snow depth was obtained for each year from all meteorological stations (n = 122, SMHI, 2017) within the study area (Figure 4). Snow depth was averaged among winter months (October, November, December, January, February, March and April) to match the timing of winter browsing and wolf monitoring (see below). Snow depth at each temporary and permanent plot was interpolated using Inverse Distance Weighting (IDW) in ArcGIS 10.2.2.
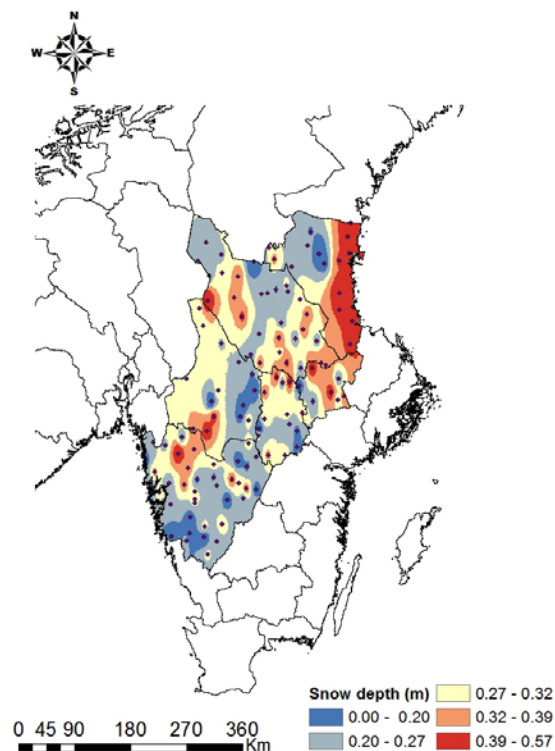
Figure 4: Snow depth over the study area in Sweden (counties of Dalarna, Gävleborg, Värmland, Västmanland, Västra Gotaland and Örebro) in 2016. Snow depth was tested as a potential factor affecting moose density and browsing damage between 2003 and 2016. The map displays snow depth (m) estimated from all the meteorological stations (SMHI) within the study area (n=22) by mean of Inverse Distance Weighing and averaged among winter months (October-April) for each year. Maps created with ArcGIS 10.2.2 (http://support.esri.com/Products/Desktop/arcgis-desktop/arcmap/10-2-2).

2.4. Wolf presence

Wolf presence was analysed using data available from the national wolf monitoring system conducted annually by the County Administrative Boards (Wabakken et al., 2004; Liberg et al., 2012). The territory size of wolves was calculated by using the 100% minimum convex polygon method (MCP; Mohr, 1947), which utilizes all the available locations obtained from snow tracking in combination with VHF or GPS position of tagged individuals per monitoring season. In order to give a full representation of wolf territory borders, a buffer was created around each territory based on the average wolf territory in Scandinavia (radius 18.0 km, average size = 1017 km^2; Mattisson et al., 2013). Wolf occurrence was classified for each temporary and permanent plot according to the following categories: (I) inside an observed wolf territory when the plot was located within the confirmed borders of a wolf territory according to monitoring data, (II) inside an average territory, if the plot was not located inside an observed wolf territory but within a distance corresponding to the average wolf territory radius from the nearest territory centre; or (III) outside of a wolf territory if the distance from the nearest territory centre was longer than the

radius used to classify an average territory (Figure 5; Wikenros et al., 2017). A plot thus belonged to only one category.
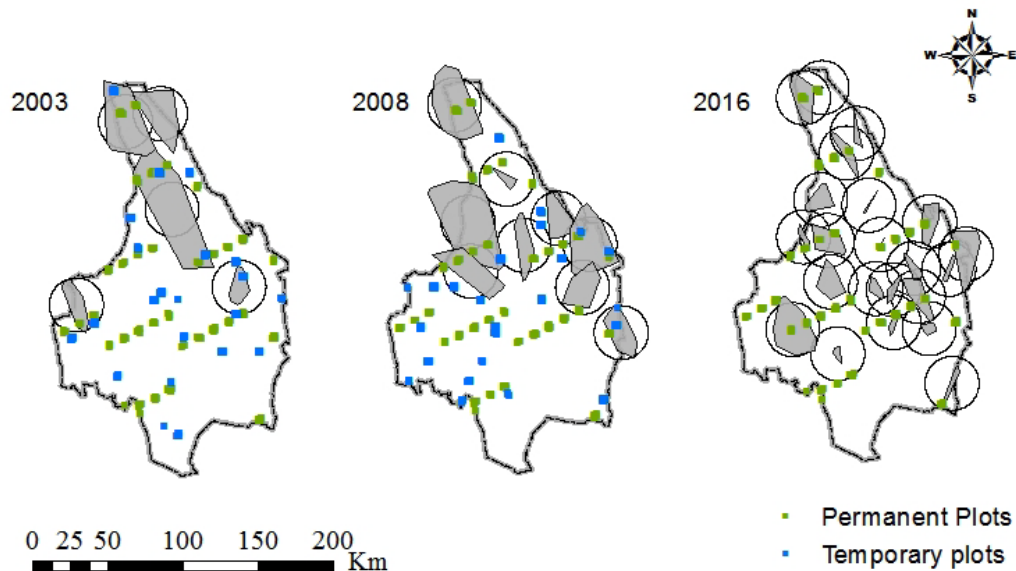
Figure 5: Locations of temporary and permanent tracts in the county of Värmland where moose browsing and pellet groups were surveyed from 2003-2016. Plots were classified according to a 3 level wolf category: (I) inside an observed territory (grey polygons according to monitoring data); (II) inside an average wolf territory (circles, according to Mattisson et al., 2013); or (III) outside a wolf territory (if not included in categories I and II). Maps created using ArcGIS 10.2.2 (http://support.esri.com/Products/Desktop/arcgis-desktop/arcmap/10-2-2).

In addition to the abovementioned criteria, two supplementary conditions were defined to classify a plot as *inside,* independently of which measurement was used to classify wolf occurrence (observed or average territory): 1) the plot was outside the year of the inventory, but had been inside for 70% or more of previous years since the first year the plot was located inside a wolf territory; and 2) the plot was outside the year of the inventory and not inside for 70% or more of years since first wolf establishment, but had been inside for ≥ 5 consecutive years prior the inventory year. Figure 6 shows three different cases to illustrate such criteria, and the final score (inside or outside) is shown under the column labelled "2007": a) plot 105 was surveyed in 2007, and since it was not located within a wolf territory in that particular year it would have normally been classified as outside. However, since wolves had established a territory in 1997 and the plots had been inside for 9 years, which is over 70% of total years since establishment (9 out of 11), plot 105 was classified as inside an observed territory; b) plot 305 was also classified as *inside* despite 1) being outside the year of the inventory (2007) and 2) not having the requirements to meet the first condition ($\geq 70\%$ years inside). This was because that plot met the second condition ($\geq$ 5 consecutive, previous years). Once determined whether a plot was inside an observed or average territory, the duration of wolf presence was calculated as the sum of years each plot had been located within the borders of an observed territory. This was done to get a quantitative estimate of time since territory establishment in order to test potential temporal effects of wolf presence on moose. The third plot (306) in figure 6 was added just to illustrate that the first condition was also applied to plots

that was classified as *inside* the year of the inventory (2007). The duration of wolf presence for this particular plot would have been calculated as the sum of all years *inside* a territory, in total 5 (cells highlighted in orange), but due to the big temporal gap between 1999 and 2006 where the plot was *outside*, it had not been *inside* for $\geq$ 70% of total years since wolf territory establishment, and was therefore assigned the value of 1 years inside wolf territory.

Plot	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	Classification	Time since territory establishment
105	0	0	1	1	1	1	1	1	1	1	1	1	0	1	10
305	0	1	1	0	0	0	0	1	1	1	1	1	0	1	5
306	1	1	1	1	0	0	0	0	0	0	0	0	1	1	1

Figure 6: Example of classification of sample plots surveyed for moose pellet groups and browsing damage by the Swedish National Forest Inventory (SNFI) in 2007 (year highlighted in red). Each plot was classified as *inside* or *outside* an observed (according to annual wolf monitoring data) or average (according to average wolf territory size) territory using a binary coding (1 = inside, 0 = outside). These plots were in 2007 all classified as being *inside* a wolf territory despite being *outside* the year of the inventory, since they had been inside a territory for over 70% of the total years since wolf establishment (1997). Sample plots in this study were all located in south-central Sweden and surveyed between 2003 and 2016. Cells highlighted in orange indicate wolf presence (1).

2.5. Roads
Vector data of roads was obtained from the Swedish Transport Administration (STA). In order to test for different effects of road size, road data was divided according to the classification (0-9) used by the STA, where class 0 refers to the most important roads and class 9 to the least important roads to the overall national road network. Forest roads belong to classes 7-9 whereas national, regional and local roads (hereafter main roads) to classes 0-6. Distance (meters) between each temporary and permanent plot and the nearest main and forest road was calculated using the Line Density tool in ArcGIS.

2.6. Statistical analysis

2.6.1. Factors affecting moose density
Potential *direct effects* of wolf presence and time since territory establishment on moose presence and abundance were investigated using independent non-repeated measures (temporary plots). Generalized linear mixed models with a binomial distribution were used to test moose presence/absence as a function of wolf presence, time since territory establishment and other variables of interest (i.e. forest management status, forage cover, snow cover and distance to main and forest roads). An interaction term between forest management status and wolf presence was added to investigate potential effects of wolves in different forest types. Year of survey was added as a random effect to the model to control for variation in moose presence/absence across years. As a consequence of high multicollinearity between wolf presence and time since territory establishment, two separate analyses were conducted: one testing the potential effects of wolf presence/absence on moose presence/absence, and one excluding plots without wolf presence (category III) to investigate the effects of duration of wolf presence on moose presence/absence. The same other predictors were used in both analyses.

Variation in moose abundance was tested using the same dataset as presence/absence, but selecting solely presence-only data since as a result of the scaling factor moose abundance ranged from 0 to 8668590 pellet count groups with over 80% of zeros. In order to facilitate multivariate analysis and model convergence, the number of pellet groups found in each plot was standardized using this formula:

$$z = \frac{x - \mu}{\sigma}$$

where x is a raw score, μ is the mean of the population and σ is the standard deviation of the population. This formula converts each raw score in a distribution to a z score, and is used to indicate in standard deviation units how far above or below the mean a given score in the distribution is, allowing to understand where a particular score is in relation to other scores in the distribution. Generalized linear mixed models with a gamma distribution were then used to investigate potential effects of wolf presence and time since territory establishment on moose abundance (same procedure as described above for presence/absence data).

2.6.2. Temporal effects of wolf presence on moose density
In addition to the abovementioned analyses, the potential temporal effects of wolf presence on moose were tested using a second dataset (i.e. the permanent plots). The inclusion of this dataset in the analysis was primarily done to test the interaction between time period and wolf presence using a repeated-measures design, which provides greater power to detect any temporal effects of wolves compared to independent measures that are sampled only once. Five different time series, covering the study period (2003-2016) were pooled together and each year was classified according to the following criteria: a) *time period 1:* first year of survey; b) *time period 2*: second year of survey (5 years later than *time period 1*); and c) *time period 3:* third year of survey (10 years later than *time period 1*). Generalized linear mixed models with a binomial distribution were used to investigate whether the presence of wolves affected the probability of moose presence over time. Plot ID and year of survey were used as random factors, and an interaction term between *time period* and wolf presence was added as an explanatory variable in addition to all the other variables of interest (i.e. forest management status, snow depth, forage cover, distance to main and forest roads).

2.6.3. Factors affecting browsing damage by moose
Potential *indirect effects* of wolf presence and time since territory establishment on moose browsing behaviour were tested using all the independent measures (i.e. non-repeated plots) pooled from both the temporary and the permanent plots datasets. Similarly to moose pellet counts, fresh browsing also ranged from 0 to values as high as 13078034 due to the scaling factor. The proportion of total fresh browsing damage was calculated using this formula:

$$y = \frac{a + b}{(a + b + c + d + e)}$$

Where each letter represents the number of trees with: a) fresh damage, b) fresh and old damage, c) old damage, d) other types of damage, and e) no damage. The same procedure was used to obtain the proportion of total old browsing damage by moose in each plot, to test whether the overall presence and proportion of old damage within a plot could affect moose presence and abundance.

Generalized linear mixed models with a binomial distribution were then used to test browsing damage presence/absence as a function of wolf presence, time since territory establishment and other variables of interest (old browsing, forage cover, snow cover and distance to main and forest roads). Year of survey was included as a random factor to control for potential inter-annual variation in presence/absence of browsing damage. Two separate analyses were also conducted on this dataset (testing the effect of wolf presence and time since territory establishment), using the same procedure as applied to the moose density dataset.

In addition to browsing presence/absence, the potential effects of wolf presence on the intensity of browsing were also tested using the same dataset, but by selecting solely browsing presence-only data. The exclusion of absence data was based on the fact that one common distribution applied to proportional data is the beta distribution (Crawley, 2007), which can only take values within the (0:1). Therefore, not only all 0s but also all 1s were removed from further analyses. No model with time since territory establishment was performed as a consequence of the small sample size after the filtering for wolf presence-only data (n = 44).

All models were tested for multicollinearity using VIF values, and the tests revealed that no collinearity was present within the data once the wolf variables were separated, as all other variables had VIF values below 10, which is considered the threshold after which there is cause for concern (Bowerman and O´Connell, 1990; Myers, 1990). If the average VIF value is substantially larger than 1 there is reason to believe that the regression may be biased (Bowerman and O´Connell, 1990); all average VIFs of the following models were very close to 1, suggesting that none of the regression models was biased. To select the best model, the Akaike information criterion (AIC) and ΔAIC were estimated in a stepwise AIC model selection procedure. All models with a ΔAIC < 2 were retained as potential candidates, but only the model presenting the smallest AIC value was selected and average parameter estimates calculated, according to standard procedures (Burnham and Anderson, 2004).

3. Results

3.1. Factors affecting moose density

<u>Moose presence.</u> A total of 11248 temporary plots were analysed, with 1396 located inside an observed territory, 2295 inside an average territory and 7557 outside of wolf territories. There was no effect of snow cover and the interaction term between forest management status and wolf presence was not significant (Table 1&2). The probability of moose presence was higher in young forest stands (RVI = 1.0), and increased with increasing pine cover (RVI = 1.0), birch cover (RVI = 0.99) and distance from forest roads (RVI = 1.0) (Table 1 & 2, Figure 7). Probability of moose presence was also higher inside an observed and average wolf territory compared to *outside* (RVI = 1.0, Table 1 & 2), whereas duration of wolf presence had no effect (RVI = 0.11, Table 1 & 2). This was further corroborated by the fact that there was no support for models including the interaction between time period and wolf presence (Table 5 & 6). The probability of moose presence decreased with increasing RAWO cover (RVI = 0.88).
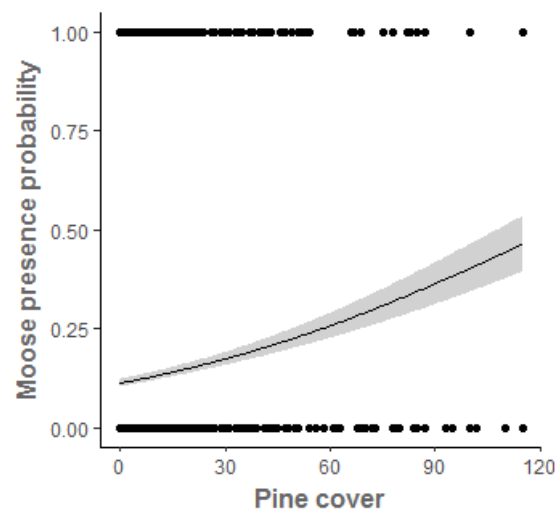
Figure 7: Probability of moose presence in relation to pine cover (proportion). Data on moose presence was recorded in six counties in Sweden (Dalarna, Gävleborg, Värmland, Västmanland, Västra Götaland and Örebro) between 2003 and 2016. The line indicates fitted values with associated standard errors from the model-averaged estimates. All other variables (birch cover, RAWO cover, snow depth and distance from big roads) were held constant at the mean value.

<u>Moose abundance.</u> Using only plots where moose were present resulted in 1266 plots, of which 200 and 275 were located inside an observed and average territory, respectively, and 791 outside of a wolf territory. Moose abundance was positively related to pine cover, distance from forest roads (both RVI = 1.0) and was higher in young forest (RVI = 1.0) (Table 3 & 4, Figure 8). Models including these variables

outperformed models including wolf occurrence (independent of the method used to classify wolf occurrence, Figure 8), snow, RAWO cover and birch cover (Table 3).
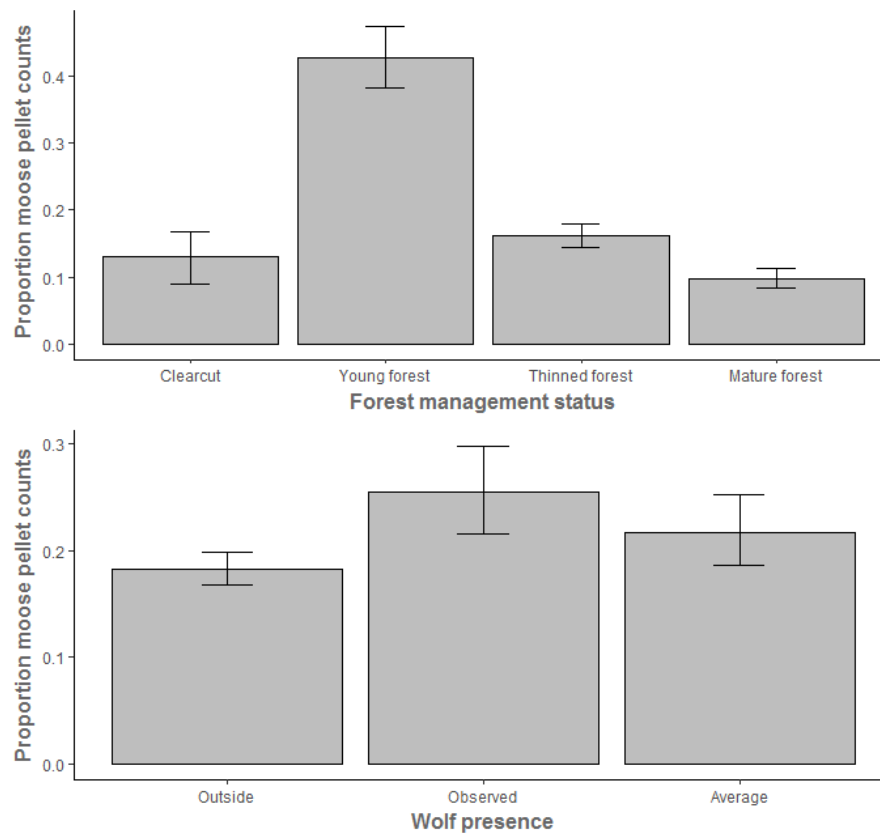
Figure 8: Proportion of moose pellet counts found in different forest management status (top) and in relation to wolf presence (bottom) in five counties (Dalarna, Gävleborg, Värmland, Västmanland, Västra Götaland and Örebro) during the time period 2003-2016. Pellet counts were recorded in each plot (3.5m radius) by the Swedish National Forest Inventory. Wolf presence is divided in three categories, indicating whether a plot was located inside an observed wolf territory, or inside an average territory or outside of a wolf territory. Forest management status refers to the successional stage of the forest each plot was situated in.

3.2. Factors affecting browsing by moose

Browsing presence. ÄBIN was recorded in 1401 plots, of which 177 and 294 were inside an observed and average territory, respectively, and 930 outside. The probability of browsing damage increased with increasing number of years since territory establishment, moose abundance, pine and birch cover, snow cover and old browsing (all RVI = 1.0, Figure 9, Table 7 & 8). Models including these variables outperformed models including wolf presence and RAWO cover.
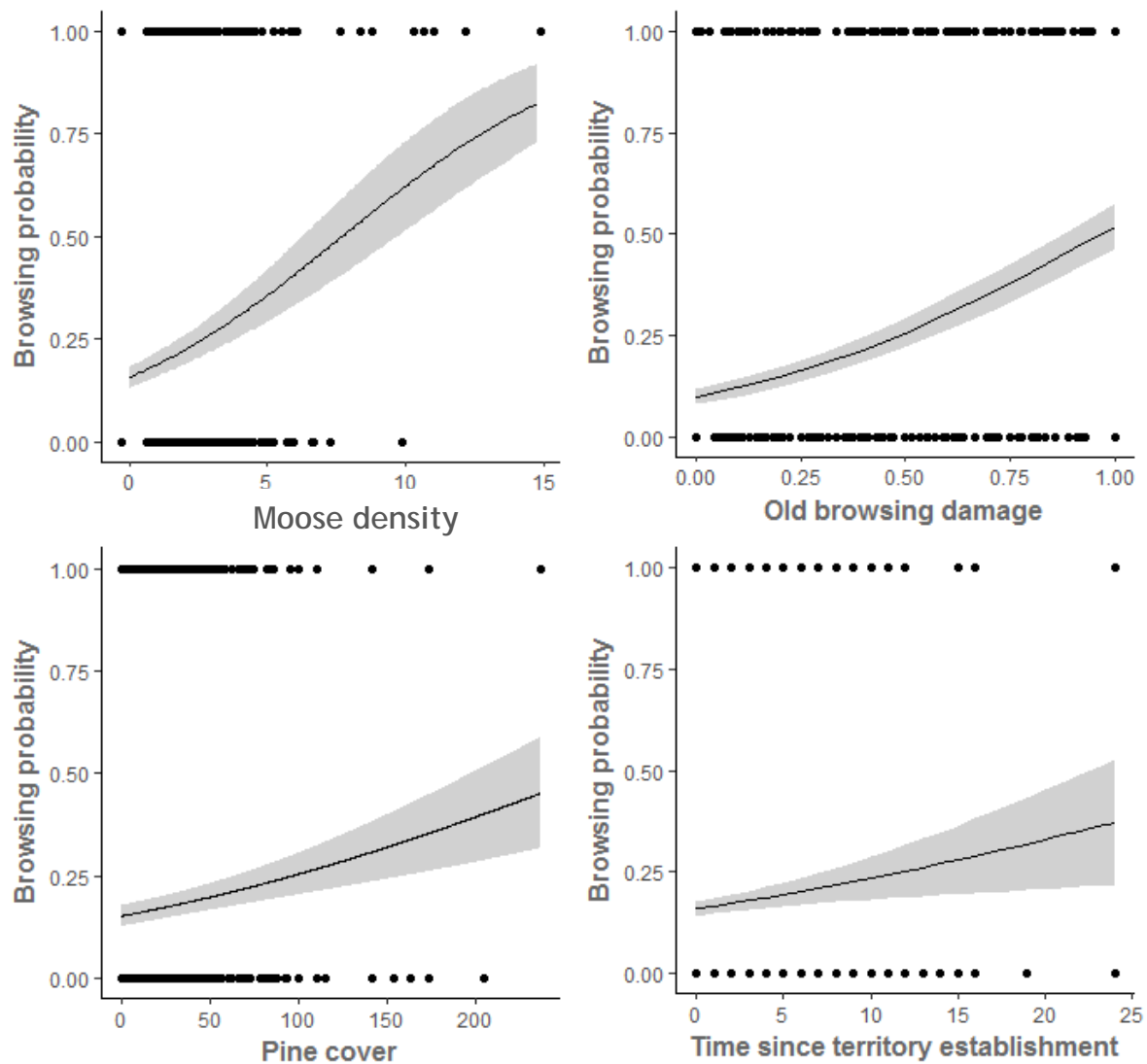
Figure 9: Probability of browsing presence in relation to moose density (measured as pellet counts), old browsing damage, pine cover and time since wolf territory establishment. Data on moose presence was recorded in five counties within Sweden (Dalarna, Gävleborg, Värmland, Västmanland, Västra Götaland and Örebro) between 2003 and 2016. The line indicates the fitted values with associated standard errors from the model-averaged estimates. All variables except for the predictor variable displayed in each logistic curve were held constant at the mean value (pine cover, birch cover, moose abundance, snow depth, time since territory establishment and old browsing damage).

Browsing intensity. Browsing intensity was recorded in 233 plots, of which 34 and 59 were situated inside an observed and average territory, respectively, and 140 outside of a wolf territory. Browsing intensity was negatively related to increasing pine cover (RVI = 1.0) and positively to old browsing damage (RVI = 1.0) (Table 9&10). A greater browsing intensity was found inside an observed territory than in an average and outside a territory (Figure 10; Table 9 & 10).
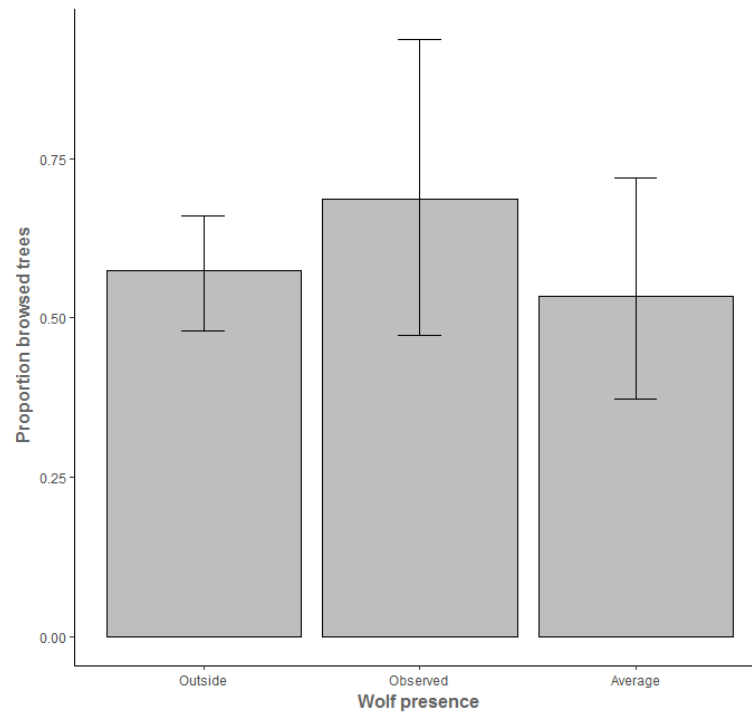
Figure 10: Proportion of browsed trees in relation to wolf presence in five counties (Dalarna, Gävleborg, Värmland, Västmanland, Västra Götaland and Örebro) during the time period 2003-2016. Browsing damage was recorded using ÄBIN, a method that produces an index of browsing pressure based on bark stripping, steam breakage and browsing on top shoots in Scots pine plantations (Bergman and Åkerberg, 2006)

Table 1: Highest ranked candidate models (∆AIC < 2) relating **moose presence/absence** to wolf presence, forest management status (and the interaction term between these two variables), RAWO cover (m²), distance to small and main roads (km), pine cover (m²), birch cover (m²) and snow cover (m). Two separate models were tested according to wolf occurrence measurements: 1.) *Wolf category* (I: inside an observed territory; II: inside an average territory; III outside of a territory); 2.) *Time since territory establishment*. Year of survey was used as random factor to account for variation in moose presence/absence across years. For each model, degrees of freedom (df), difference in AIC relative to highest-ranked model (∆AIC) and AIC-weight (w_i) are shown. Only models with ∆AIC < 2 and intercept only are presented. Management is a four-category variable where the parameter estimate is the difference in moose presence/absence for young forest, thinned forest, felled forest and mature forest compared to clearcut (intercept). Wolf category is a three-category variable where the parameter estimate is the difference in moose presence/absence probability for inside an observed territory and inside an average territory compared to outside a wolf territory (intercept). Moose presence/absence was surveyed in non-repeated temporary plots in south-central Sweden between 2003 and 2016 (n = 11248, Swedish Forest Agency).

Wolf occurrence	Model parameters	df	∆AIC	w_i
Wolf presence				
Birch cover + Wolf category + Management + Pine cover + RAWO cover + Forest roads	11	0	0.34
Birch cover + Wolf category + Management + Pine cover + RAWO cover + Forest roads + Snow	12	0.31	0.29
Birch cover + Wolf category + Management + Pine cover + RAWO cover + Forest roads+ Main roads	12	0.92	0.22
Birch cover + Wolf category + Management + Pine cover + RAWO cover + Forest roads+ Snow + Main roads	13	1.60	0.15
Intercept	2	203.2x	0
Time since territory establishment				
Management + Pine cover	6	0	0.20
Management + Pine cover + Main roads + Birch cover	7	0.52	0.15
Management + Pine cover + Main roads + Snow	8	1.10	0.12
Management + Pine cover + Snow	7	1.22	0.11
Management + Pine cover + Birch cover	7	1.47	0.10
Management + Pine cover + Forest roads	7	1.65	0.09
Management + Pine cover + Time since territory establishment	7	1.66	0.09
Management + Pine cover + Main roads + Forest roads	8	1.94	0.08
Management + Pine cover + RAWO cover	7	1.97	0.07
Intercept	3	19.35	0

Table 2**: Model averaged parameter estimates with standard error (SE) for each variable retained in the best models (∆AIC< 2) in Table 1.** Two different measurements of wolf occurrence (presence/absence and time since territory establishment) were used, as shown in **Table 1**.

Model parameters	Estimate	SE
Model 1: Wolf presence		
Intercept	-2.57	0.17
Birch	0.99	0.28
Young forest	0.75	0.17
Thinned forest	0.13	0.16
Mature forest	-0.31	0.17
Pine cover	0.02	0.002

RAWO cover	-2.43	1.12
Observed territory	0.25	0.11
Average territory	0.12	0.08
Snow	0.19	0.30
Main roads	0.004	0.01
Forest roads	0.48	0.11
Model 2: Time since territory establishment		
Intercept	-2.19	0.42
Birch	0.05	0.27
Young forest	0.77	0.43
Thinned forest	0.27	0.42
Mature forest	-0.25	0.44
Pine cover	0.018	0.01
RAWO cover	-0.06	1.21
Time since territory establishment	0.001	0.01
Snow	0.19	0.53
Main roads	-0.01	0.02
Forest roads	0.03	0.13

Table 3: **Highest ranked candidate models (**ΔAIC < 2) relating **moose abundance** to wolf occurrence, management status (and the interaction term between these two variables), RAWO cover (m²), distance to small and main roads (m), pine cover (m²), birch cover (m²) and snow cover (m). Two separate models were tested according to wolf occurrence measurements: 1.) *Wolf category* (I: inside an observed territory; II: inside an average territory; III outside of a territory); 2.) *Time since territory establishment* (years of territory establishment, ranging 1-25). Year of survey was used as random factor to account for year effects. For each model, degrees of freedom (df), difference in AIC relative to highest-ranked model (ΔAIC) and AIC-weight (w_i) are shown. Only models with ΔAIC < 2 are presented. Moose abundance was surveyed in non repeated temporary plots in south-central Sweden between 2003 and 2016 (n = 1266, Swedish Forest Agency).

Model parameters	df	ΔAIC	w_i
Model 1: Wolf presence			
Management + Pine cover + Forest roads	8	0	0.34
Management + Pine cover + Forest roads + RAWO cover	9	0.78	0.23
Management + Pine cover + Forest roads + Snow	9	1.56	0.16
Management + Pine cover + Forest roads + Main roads	9	1.81	0.14
Management + Pine cover + Forest roads + Birch	9	1.93	0.13
Intercept	3	79.20	0
Model 2: Time since territory establishment			
Birch + Pine cover + Time since establishment	6	0	0.30
Birch + Pine cover + Time since establishment + Forest roads	7	0.48	0.24
Birch + Pine cover + Forest roads	6	1.02	0.18
Birch + Pine cover	5	1.28	0.16
Birch + Pine cover + Time since establishment + Snow	7	1.94	0.12
Intercept	3	35.76	0

Table 4: Model averaged parameter estimates with standard error (SE) for each variable retained in the best models (ΔAIC <2) in **Table 3**. Two different measurements of wolf occurrence (presence/absence and time since territory establishment) were used, as shown in Table 1.

Model parameters	Estimate	SE
Model 1: Wolf presence		
Intercept	0.35	0.09
Birch	-0.01	0.06
Young forest	0.19	0.08
Thinned forest	0.02	0.08
Mature forest	-0.07	0.09
Pine cover	1.10	0.19
RAWO cover	-0.14	0.37
Forest roads	0.20	0.07
Main roads	-0.000	0.002
Snow	0.03	0.11
Model 2: Time since territory establishment		
Intercept	0.27	0.09
Birch	0.87	0.34
Pine cover	0.01	0.002
Forest roads	0.09	0.15
Snow	-0.03	0.18

Table 5: Highest ranked candidate models (ΔAIC < 2) relating **moose presence/absence** to **time period (1, 2 or 3)** and wolf category (with the interaction term between these two variables). Other variables such as big and forest roads (km), birch cover (m²), management status and pine cover (m²) were added to the model. Three separate measures of wolf category were tested: (I) inside an observed territory; (II) inside an average territory; (III) outside a territory. Plot identity and year of survey were used as random effects to account for repeated measures and year effects. For each model, degrees of freedom (df), difference in AIC relative to highest-ranked model (ΔAIC) and AIC-weight (w_i) are shown. Only models with ΔAIC < 2 are presented (n = 17866, Swedish Forest Agency)

Model parameters	df	ΔAIC	w_i
Main roads + Birch cover + Management + Pine cover + Wolf presence + RAWO cover + Snow	13	0	0.33
Main roads + Birch cover + Management + Pine cover + Wolf presence + RAWO cover + Snow + Time period	15	0.44	0.27
Main roads + Birch cover + Management + Pine cover + Wolf presence + RAWO cover + Snow + Forest roads	8	1.49	0.05
Main roads + Birch cover + Management + Pine cover + Wolf presence + RAWO cover + Snow + Forest roads + Time period	16	1.24	0.18
Intercept only	3	193	0

Table 6: Model averaged parameter estimates with standard error (SE) for each variable retained in the best models (ΔAIC < 2) in **Table 5**. Two different measurements of wolf occurrence (presence/absence and time since territory establishment) were used, as shown in Table 1.

Model parameters	Estimate	SE
Intercept	-3.73	0.19
Main roads	0.04	0.02
Forest roads	0.05	0.09
Young forest	4.87	0.36
Thinned forest	0.27	0.17
Mature forest	-0.05	0.17
Pine cover	0.01	0.00
RAWO cover	-2.85	1.23
Observed territory	0.29	0.09
Average territory	0.09	0.08
Birch	1.87	0.31
Period 2	-0.01	0.04
Period 3	0.05	0.09
Snow	0.83	0.35

Table 7: Highest ranked candidate models (ΔAIC < 2) relating **presence of browsing damage** to wolf occurrence, pine cover (m^2), birch cover (m^2), snow cover (m) and old browsing damage within a plot. Two separate models were tested according to wolf occurrence measurements: 1.) *Wolf category* (I: inside an observed territory; II: inside an average territory; III outside of a territory); 2.) *Time since territory establishment* (years of territory establishment, ranging 1-25). Year of survey was used as random factor to account for year effects. For each model, degrees of freedom (df), difference in AIC relative to highest-ranked model (ΔAIC) and AIC-weight (w_i) are shown. Only models with ΔAIC < 2 are presented. Browsing damage was surveyed in non-repeated temporary and permanent plots in south-central Sweden between 2003 and 2016 (n = 1401, Swedish Forest Agency).

Model parameters	df	ΔAIC	w_i
Model 1: Wolf presence			
Birch cover + Pine cover + Moose density + Old browsing + Snow	7	0	0.56
Pine cover + Moose density + Old browsing + Snow	6	1.70	0.24
Birch cover + Pine cover + Moose density + Old browsing	6	1.99	0.21
Intercept only	2	200.2	0
Time since territory establishment			
Birch cover + Pine cover + Moose density + Old browsing + Snow + Time since establishment	8	0	0.40
Birch cover + Pine cover + Moose density + Old browsing + Snow	7	0.71	0.28
Birch cover + Pine cover + Moose density + Old browsing + Time since establishment	7	1.85	0.16
Pine cover + Moose density + Old browsing + Snow + Time since establishment	7	1.86	0.16
Intercept only	2	200.2	0

Table 8: Model averaged parameter estimates with standard error (SE) for each variable retained in the best models (∆AIC<2) in **Table 7.** Two measurement of wolf occurrence (presence/absence and time since territory establishment) were used, as shown in Table 1.

Model parameters	Estimate	SE
Model 1: Wolf presence		
Intercept	-2.7	0.25
Moose density	0.22	0.04
Old browsing	2.30	0.20
Pine cover	0.006	0.002
Birch	0.61	0.50
Snow	1.36	1.05
Model 2: Time since territory establishment		
Intercept	-2.75	0.25
Birch	0.69	0.49
Pine cover	0.006	0.002
Moose density	0.22	0.04
Old browsing	2.29	0.20
Snow	1.44	1.02
Time since establishment	0.03	0.03

Table 9: **Highest ranked candidate models (**∆AIC < 2) relating **browsing intensity** to wolf occurrence, RASE cover (m²), pine cover (m²), birch cover (m²), snow cover (m) and old browsing damage within a plot. Two separate models were tested according to wolf occurrence measurements: 1.) _Wolf category_ (I: inside an observed territory; II: inside an average territory; III outside of a territory); 2.) _Time since territory establishment._ Year of survey was used as random factor to account for year effects. For each model, degrees of freedom (df), difference in AIC relative to highest-ranked model (∆AIC) and AIC-weight (w_i) are shown. Only models with ∆AIC < 2 are presented. Browsing damage was surveyed in non-repeated temporary and permanent plots in south-central Sweden between 2003 and 2016. Only first 10 models are shown (n = 233, Swedish Forest Agency)

Model parameters	df	∆AIC	w_i
Model 1: Wolf presence			
Pine cover + Old browsing + Wolf presence	7	0	0.12
Pine cover + Old browsing	5	0.37	0.10
Pine cover + Old browsing + Moose density	6	0.47	0.09
Pine cover + Old Browsing + Moose density + Wolf presence	8	0.49	0.09
Pine cover + Old browsing + Wolf presence + Snow	8	0.66	0.08
Pine cover + Old Browsing + Moose density + Wolf presence + Snow	9	1.22	0.06
Pine cover + Old browsing + Wolf presence + Birch cover	8	1.25	0.06
Pine cover + Old Browsing + Moose density + Wolf presence	9	1.60	0.05
Pine cover + Old browsing + Snow	6	1.65	0.05
Pine cover + Old browsing + Wolf presence + RAWO cover	8	1.66	0.05

Table 10: Model averaged parameter estimates with standard error (SE) for each variable retained in the best models (ΔAIC<2) in **Table 9**. Only one measurement of wolf occurrence (presence/absence) was used, as shown in Table 09..

Model parameters	Estimate	SE
Model 2: Wolf presence		
Intercept	-1.07	0.15
Pine cover	-0.01	0.001
Old browsing	0.91	0.17
Observed territory	0.13	0.16
Average territory	0.12	0.15
Moose density	0.01	0.02
Snow	0.14	0.35
Birch	-0.06	0.19
RAWO cover	-0.35	1.46

4. <u>Discussion</u>

Presence of wolves, forest management status, pine, birch and RAWO cover and distance from forest roads were all important factors explaining variation in moose density. In line with previous findings suggesting that moose tend to concentrate and feed in young forest stands (Bergström & Hjeljord, 1987; Hjeljord et al., 1990; Cederlund & Bergström, 1996; Gundersen et al., 2004), the highest number of moose pellet groups was found in young forest stands of pine trees. Pine cover, moose density and old browsing best explained browsing intensity by moose. The probability of moose presence was higher inside a wolf territory compared to outside, but wolf presence and time since territory establishment did not affect moose abundance. However, wolf presence was an important factor explaining the variation in browsing intensity, i.e. the proportion of browsed trees was higher inside wolf territories (both observed and average) compared to outside. Time since wolf territory establishment was positively related only to the probability of browsing presence, but not to browsing intensity, moose presence or moose abundance. The main other factors affecting moose presence and abundance were forest management status, pine and birch cover, distance from forest roads and RAWO cover. The main drivers of browsing presence and intensity on pine trees were moose abundance, pine cover and old browsing. The results did not support the hypotheses postulated in this study: that wolf presence and time since territory establishment would lead to a reduction in moose abundance, and that this would be reflected by parallel changes in browsing intensity and damage levels to forest plant of commercial value. The probability of moose presence was higher within wolf territories compared to outside and the proportion of browsing damage was also higher inside wolf territories, potentially suggesting that moose have not changed their feeding behaviour in response to wolf presence. Such a pattern may appear as surprising, but could suggest that wolves may establish territories based on local moose densities to increase the chances of prey encounter, a behaviour that would indeed explain the positive relationship between wolf and moose presence. According to Gervasi et al. (2013), wolves in Scandinavia try to maximise their hunting success by actively searching in areas of higher moose density, as well as patrolling certain areas where the encounter with a prey, and hence an attack, were more likely to occur and be successful. However, Ordiz et al. (2015) argued that wolves in Scandinavia are generally not constrained by moose densities,

as wolf pair establishment occurred in areas with varying moose densities. Nevertheless, as the authors themselves pointed out, most Scandinavian studies, including their own, have been based on data where moose density was recorded at larger scales than actual wolf territories (Ordiz et al., 2015). The scale used to compare moose densities in this study was indeed at the wolf territory, suggesting that although moose density might not play a role in territory establishment at larger scales, it could be a rather important factor at the intra-territorial use of habitats. An additional, but not mutually exclusive, reason as to why the probability of moose presence was higher within wolf territories might be linked to the response of moose hunters to the recent recolonization by wolves of the Scandinavia Peninsula. Wikenros et al. (2015) found that hunters responded to the establishment of wolves with adjustments in the total size of the harvest, but also by lowering the proportion of harvested females. The most severe reductions in harvest and hunting quotas were observed in the first year after wolf territory establishment, suggesting that hunters respond rather instantaneously to the presence of another predator (Wikenros et al., 2015). Hunter selection of moose differs from wolves, since the former is usually biased towards a higher proportion of adult males (Nilsen et al., 2005; 2006) whereas the latter are mostly selective in favour of calves and old females (Jonzén et al., 2013; Sand et al., 2008; 2012). Wolves also tend to target calves early in summer, which could relieve females from the costs associated with lactation (Swenson et al., 2007). It might therefore be plausible that the higher probability of moose presence within wolf territories observed in this study is a combination of two factors: 1) wolves select for areas with higher moose density to establish a territory, and 2) once they have established a territory, hunters within that area reduce the harvest of moose to compensate for the additive predation by wolves, resulting in an overall higher probability of moose presence.

Another finding of this study was that moose presence and abundance increased with increasing distance from forest roads. The avoidance of forest roads by moose has been associated to heavy equipment and logging trucks that act as disturbance (van Langevelde et al., 2009), but an additional reason might be that hunters and wolves are also known to use forest roads. The former use them during the hunting season (James and Stuart-Smith, 2000; Houle et al., 2009), and the latter often travels along man-made linear features (Whittington et al., 2005, 2011; Houle et al., 2010; Gurarie

et al., 2011; Zimmermann et al., 2014), especially minor roads where they have been found to travel nearly twice as fast as compared to off roads (Zimmermann et al., 2014). Therefore, the seasonal and year-round presence of hunters and wolves, respectively, coupled with the disturbance caused by forest machineries and vehicles, may outweigh the benefits of using forest roads and act as an additional deterrent for moose not to select for habitats nearby forest roads.

Moose in this study did not respond to an increased risk of predation by wolves, as found by other studies in North America (Ripple and Larsen, 2000; 2012). In Scandinavia large predators have been absent from the landscape for much longer periods of time (> 100 years) compared to North America, and human harvest has functionally replaced natural predation on moose by wolves and bears in the last century (Sand et al., 2006). Human harvest accounts for over 90% of moose mortality overall, and such hunting pressure has continued even after the return of wolves to Scandinavia, which, in comparison, account for much lower (< 5%) moose mortality (Sand et al., 2006). Under such conditions, where moose mortality from natural predators is almost negligible compared to hunting, anti-predator behaviours may take a longer time to be selected for, as hunting pressures from humans will lead to selection against such traits (Sand et al., 2006; Kuijper et al., 2016). The current best anti-predatory strategy for Scandinavian moose seems to be aimed at minimizing the risk of mortality from human hunting (the main source of mortality), even if this involves an increased risk of predation by wolves (Sand et al., 2006). Prey defences towards more than one predator can be synergistic or predator-specific and conflicting, and can influence both the *direct* and *indirect* effects of predators through changes in the predation rate and predator avoidance, respectively (Sih et al., 1998; Cresswell and Quinn, 2013). Moose in Scandinavia may be experiencing a situation where the costs of developing conflicting predator-specific responses (e.g. avoidance of certain areas) outweigh the benefits of doing so. Spatial avoidance is expected to become relatively unimportant with an increasing number of predators that effectively inhibit all the potential avoidance responses in prey (Cresswell and Quinn, 2013). In such a scenario, prey species may rely on improving their escape probability (Lima, 1992), and according to Wikenros et al. (2009) only a small proportion of moose in Sweden stood their ground when attacked by wolves compared to moose in North America.

Predator avoidance strategies might not be necessary if a prey species adopts successful predator-specific escape tactics (Wirsing et al., 2010), which in the case of Scandinavian moose would be to flee in all predator encounters, regardless if a hunter or a wolf. When more than one predator is considered, the gradients of predation risk within the landscape flattens out and the potential advantages of shifting habitat are not as strong, and therefore the optimal prey response becomes weaker (Lone et al., 2014). Consequently, weaker prey responses could elicit weaker non-lethal effects and ecosystem effects, and hence lower the potential for behaviourally mediated trophic cascades (Lone et al., 2014). Furthermore, wolf predation risk is rather unpredictable, whereas human-predation risk from hunting is relatively predictable both temporally and spatially, and such a difference in risk predictability is likely to affect the strength and magnitude of behavioural responses in prey species (Proffitt et al., 2008). Elk in Montana responded to both wolf and human predation risk in a similar manner, but responses aimed at minimizing human predation risk were stronger than the ones aimed at wolf predation risk (Proffitt et al., 2008). It could be possible that the recently resurfaced predation risk by wolves, coupled with the continuous hunting risk imposed by humans, have resulted in a rather homogenous landscape of fear, where predator-specific responses, such as predator avoidance, simply do not provide moose with sufficient advantages to be selected for.

Among the most important variables explaining browsing presence was moose abundance, pine cover and old browsing. These findings are in accordance with previous literature showing that browsing pressure on Scots pine increases with increasing moose density and pine cover (Månsson et al., 2007). In contrast, browsing intensity showed the opposite trend, i.e. browsing was less abundant with higher pine cover. Månsson et al. (2007) found that the overall browsing pressure, measured as the proportion of twigs removed, increased with increasing density of moose but declined with increasing forage availability of Scots pine. The similarities between this study and Månsson et al. (2017) are rather interesting, since the same negative correlation between browsing intensity and pine cover was found using two different measurements to quantify intensity and at two different spatial scales (tree vs. plot scale). Starvation is a constant risk to which large herbivores are continuously exposed to, especially during winter months (Lone et al., 2014), so perhaps in forest stands with a higher forage availability moose do not feel the need to feed as

voraciously as they would if less pine trees were available. Previous browsing has also been identified as an important predictor of fresh browsing pressure by moose (Bergqvist et al., 2003; Mathisen et al., 2017), and a positive correlation between old browsing and presence and abundance of fresh damage was found in this study. According to Mathisen et al. (2017), moose preference for previously browsed trees is the result of the rapid regrowth of new shoots (and therefore increased forage availability) within browsing height. This study analyzed old browsing damage at the sample plot scale, which is larger than the one used by Mathisen et al. (2017), who investigated fresh browsing in relation to old browsing at the tree level. Nevertheless, this study corroborates their findings by showing that old browsing damage significantly correlated with fresh browsing damage also at larger scales. Previously browsed tree stands, or stands with high intensity of old browsing damage, may bear higher forage availability (i.e. pine cover) compared to non-previously browsed stands and/or stands with only low levels of previous browsing, and hence attract moose.

This study found a significant temporal effect of wolf presence on browsing presence, but no such effect was then observed in browsing intensity. The small sample size used to test whether time since territory establishment had an effect on browsing presence could represent a potential limitation of this study, since it can result in a reduction in statistical power and consequent increase in the probability of a type II error. Further studies interested in investigating such dynamics should therefore aim to analyze a larger sample, in order to be able to detect a potential effect, if one truly exists. Another potentially biased result is the positive correlation between snow depth and moose presence and abundance, a trend that is in contrast with the predictions of this study. Snow depth was interpolated using Inverse Distance Weighing, where the interpolated values are in fact a function of the distance to surrounding locations, and the weight attenuates the influence of more distant points. Data about snow depth was obtained from 122 meteorological stations distributed across the study area, with a large variation in distance between them (closer to each other in the south, and further apart in the north). Therefore, such a large difference in distance between meteorological stations might have affected the individual values attributed to each sample plots in this study. This is further supported by the fact that the interpolated values of snow depth in the northern parts of the study area had much

larger error terms than those located in the south. Furthermore, this study only used longitude and latitude as covariates to interpolate snow depth, without the inclusion of altitude. According to Blanchet and Lehning (2010), IDW is the second best model to interpolate snow depth when longitude and latitude coupled with altitude were used as covariates. Further studies should therefore aim to include altitude as a covariate when interpolating snow depth data.

Conclusion

The results obtained did not find support for the hypotheses postulated by this study: that wolf presence and time since territory establishment would have a negative effect on moose density, and that this would reflect into parallel changes in browsing intensity and damage levels to forest plant of commercial value. Importantly, the positive correlations between a) moose presence and wolf presence; and b) browsing intensity and wolf presence, are to be further evaluated. Specifically, future research should aim at investigating whether such trends might be dictated by moose density at finer scales influencing the selection of suitable areas for wolf territory establishment, and/or by hunters within the same areas concomitantly lowering the number of harvested moose in response to wolves. These results should be taken into consideration within the ongoing debate between forest companies and Swedish hunters, as they could have important implications for the adaptive management of the Scandinavian moose population and related browsing damages.

APPENDIX

Factors affecting moose density

Appendix 1: Table showing response and predictor variables and corresponding level and direction of significance used in the analysis of temporary plots. The variables used in the model are highlighted in grey, and the significance of the model-average estimates for each variable is represented by different sizes of the + symbol (positive correlation) or the – symbol (negative correlation), i.e. larger +/- represent stronger significance.

Moose density	Predictor variables								
Response variables	**Wolf presence**	**Time since territory establishment**	**Forest management status**	**Pine cover**	**Birch cover**	**Distance from forest roads**	**Distance from main roads**	**Snow depth**	**RAWO cover**
Presence/absence	**+**		**+**	**+**	**+**	**+**			**-**
Moose abundance			**+**	**+**		**+**			

Moose density	Predictor variables								
Response variables	**Wolf presence**	**Time since territory establishment**	**Forest management status**	**Pine cover**	**Birch cover**	**Distance from forest roads**	**Distance from main roads**	**Snow depth**	**RAWO cover**
Presence/absence			**+**	**+**					
Moose abundance			**+**	**+**					

Effect of time and wolf presence on moose density

Appendix 3: Table showing response and predictor variables and corresponding level and direction of significance used in the analysis of the permanent plots. The variables used in the model are highlighted in grey, and the significance of the model-average estimates for each variable is represented by different sizes of the + symbol (positive correlation) or the – symbol (negative correlation).

Moose density	**Predictor variables**									
Response variables	**Wolf presence**	**Time since territory establishment**	**Forest management status**	**Pine cover**	**Birch cover**	**Distance from forest roads**	**Distance from main roads**	**Snow depth**	**RAWO cover**	**Time period**
Presence/absence	+		+	+	+		+	+	-	

Factors affecting browsing damage

Appendix 2: Table showing response and predictor variables and corresponding level and direction of significance used in the analysis of the pooled datasets (browsing damage). The variables used in the model are highlighted in grey, and the significance of the model-average estimates for each variable is represented by different sizes of the + symbol (positive correlation) or the – symbol (negative correlation).

Browsing by moose	Predictor variables								
Response variables	Wolf presence	Time since territory establishment	Moose density	Pine cover	Birch cover	Distance from forest roads	Distance from main roads	Snow depth	Old browsing
Presence/absence			**+**	**+**	**+**				**+**
Browsing intensity	**+**		**-**						**+**

Browsing by moose	Predictor variables								
Response variables	Wolf presence	Time since territory establishment	Moose density	Pine cover	Birch cover	Distance from forest roads	Distance from main roads	Snow depth	Old browsing
Presence/absence		**+**	**+**	**+**	**+**			**+**	**+**

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