



Forage availability, supplementary feed and ungulate density: Associations with ungulate damage in pine production forests

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ABSTRACT

Populations of large herbivores, including members of the deer family Cervidae, are expanding across and within many regions of the northern hemisphere. Because their browsing on trees can result in economic losses to forestry and strongly affect ecosystems, it is becoming increasingly important to understand how best to mitigate resultant damage. Previous research has highlighted the importance of regulating deer density and the availability of alternative forage to reduce browsing damage levels in conifer production stands. However, often only one or two proxies of forage availability have been used instead of applying a broad foodscape approach and more knowledge is needed to understand which types of alternative forage best mitigate damage. We conducted field inventories of damage that occurred during the previous fall/winter in 112 production stands in southern Sweden, while also measuring forage availability and cervid faecal pellets in the surrounding landscape (16 ha). Local landowners provided data on supplementary feeding. We found that variation in cervid (*Alces alces*, *Capreolus capreolus*, *Cervus elaphus* and *Dama dama*) browsing damage to top shoots or stems of young Scots pine trees (*Pinus sylvestris*, hereon pine), was better explained by the availability of alternative natural forage (using several indices and species of trees and shrubs) than by supplementary feeding. The proportion of damaged pine trees was higher in stands with a lower density of pine stems; in landscapes with a lower density of key broadleaf tree species (genera *Sorbus*, *Salix*, *Populus* and *Quercus*); and in landscapes with more open land (agricultural fields and paddocks). Damage was also higher in stands where relatively large amounts of moose faeces was found, while not related to the amount of faeces from other cervid species. The amount of supplementary feed (silage or other types such as root vegetables) did not explain variation in pine damage, but the result was possibly affected by relatively few study areas supplying sufficient data on supplementary feeding. The results from our inventory illustrate the efficacy of using naturally growing forage to mitigate browsing damage to young pine trees in managed landscapes. Creation of such forage is also recommended over supplementary feeding because of co-benefits to forest biodiversity and ecosystem services.

1. Introduction

Populations of large herbivores, primarily represented by members of the deer family Cervidae, have increased dramatically across extensive regions of the northern hemisphere over recent decades (Côté et al., 2004, Apollonio et al., 2017). These ruminant herbivores (hereafter

cervids) carefully select which plants to eat, affecting the growth and survival of many herb, shrub and tree species, and thereby modifying patterns of plant abundance and vegetation dynamics in response (Persson et al., 2000, Côté et al., 2004, Bernes et al., 2018). Cervid foraging can also result in economic losses to forestry and agriculture (Liberg et al., 2010, Reimoser and Putman, 2011), sometimes in ways

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that hinder the transition to more sustainable and resilient production systems (Felton et al., 2020a). Mitigating this damage by cervids using fencing or culling is not always possible due to economic, legal or cultural restrictions (Côté et al., 2004, Bergquist et al., 2009). Furthermore, limiting cervid movements or population sizes likewise reduces their valuable contributions to ecosystem services, via e.g. tourism, recreational hunting and meat provision (Schröter et al., 2014, Neumann et al., 2022). Also, previous studies have shown relationships between cervid densities and levels of damage on some timber tree species to be weaker as compared to relationships between forage availability and damage (e.g. Bergqvist et al., 2014, Pfeffer et al., 2021). When managing cervid populations and assessing the associated risks, it is therefore necessary to use a holistic approach (Apollonio et al., 2017). This requires management strategies that, under ideal conditions, align with the animals' foraging behaviour.

Several factors influence cervid foraging behaviour, and these factors operate at scales ranging from the region to the stand, and from the plant community to specific plant parts (Senft et al., 1987). Cervid food selection is highly dependent on the landscape configuration of vegetation cover and plant species composition; due to the protection that vegetation may provide against adverse weather (Herfindal et al., 2017), its influence on the animal's perceived vulnerability to predation (Creel et al., 2005), and direct relevance to food provision (Bergqvist et al., 2018). Within a forest, cervids select food items based in-part on tree species composition, forest age, plant age (time of season), weather and snow depth (Bo and Hjeljord, 1991, Ball and Dahlgren 2002, Månsson 2009, Wam and Hjeljord 2010). How a cervid species forages within forested landscapes, in-turn depends on its placement as a species on the gastro-intestinal continuum of dietary niches (Clauss et al., 2010). Of the northern cervid species, moose (*Alces alces*) consumes the highest proportion of woody material (Spitzer et al., 2020). Although the diets of European roe deer (*Capreolus capreolus*), red deer (*Cervus elaphus*) and fallow deer (*Dama dama*) also can contain substantial amounts of woody material, in general they contain far less than the moose diet (Mysterud 2000, Spitzer et al., 2020).

In Scandinavia, one of the two dominant timber production tree species of high economic importance is Scots pine (*Pinus sylvestris*, hereafter pine). This tree species also serves as a staple winter food for moose in several regions, while it is eaten by the other cervid species in smaller proportions of their diets (Cederlund et al., 1980, Spitzer, 2019). Extensive browsing by cervids on pine is regarded as a problem since it can negatively affect regeneration success, wood quality and volume growth, and thereby result in large economic losses to forest owners (Wam and Hofstad, 2007). The three most important local- or landscape-scale factors that are thought to affect damage levels on pine in Scandinavia are the density of the production tree species, population densities of cervids, and the availability of naturally growing forage alternatives to the production tree species (Bergqvist et al., 2014, Herfindal et al., 2015, Pfeffer et al., 2021). A recent study of national scale browsing damage data in Sweden reports that while the effect of cervid density on damage varies among the regions assessed, higher densities of pine within regenerating production stands (used as a proxy for forage biomass availability) is consistently associated with reduced browsing damage to this tree species in winter (Pfeffer et al., 2021). The same result was found in a study of twelve areas across southern Norway (Herfindal et al., 2015).

Forage availability is not always limited to just the vegetation cover in a landscape, as it can be augmented by supplementary feeding, which involves feed deliberately provided to wildlife by people. Supplementary feeding can therefore be part of the 'foodscape' (Searle et al., 2007), which we define as the combined forage value of a landscape for a species of large herbivore. There is a range of justifications for providing supplementary feed to wildlife. These include the desire to reduce crop and forest damage through diversion ("diversionary feeding", Milner et al., 2014), enhance an animal's reproductive success and winter survival (Schwartz and Hundertmark, 1993), increase hunting

opportunities and game viewing (Smith, 2001), or manipulate migration patterns (Gundersen et al., 2004). In Sweden, surveys have shown that the primary reason given by hunters and forest owners for supplementary feeding is to increase the survival of targeted species. However, supplementary feeding is also conducted to reduce damage to crops and forests, as evidenced by this often being the second reason given (Johansson, 2018; F. Widemo, unpublished data). Whatever the original intent, a range of unintended outcomes may occur due to supplementary feeding (Milner et al., 2014). For example, increased damage to local vegetation near supplementary feeding sites is often reported (Gundersen et al., 2004, Mathisen et al., 2014, Milner et al., 2014). In fact, merely ingesting energy rich food can make cervids increase their intake of browse (Doenier et al., 1997, Cooper et al., 2006, Timmons et al., 2010, Kamler and Homolka, 2016, Felton et al., 2017). However, due to the multitude of factors influencing the foraging choices of free ranging cervids, it is unknown whether such potential side-effects of supplementary feeding are detectable at levels relevant to forest managers.

Finally, whether alternative forage availability increases or decreases pine damage depends on the spatial scale. For example, a study conducted in southern Sweden showed that damage to pine was greater when the availability of birch in the stand was higher (Wallgren et al., 2013), while Herfindal et al., (2015) found that the more alternative forage available, the less pine damage occurred at landscape scales. Yet, at the plot level, the associated protection from alternative forage only applied when the densities of both pine and alternative forage were high. The relationships are therefore complex, and more studies are needed to understand which patterns prevail under different conditions. In this study we investigated whether variation in browsing damage on young pine trees can be explained by variation in the availability of naturally growing forage of several different types and at different scales, and/or the amount and type of supplementary feed used in an area. We also account for cervid density, which informs us about competition, and therefore per-capita forage availability. As such, we use a broad foodscape approach, highlighting that not only biomass estimates, but also specific assessments of a wide range of plant taxa must be included to capture the availability of forage resources for herbivores in landscapes (Searle et al., 2007). Based on previous findings we predict damage levels to be negatively related to the amount of forage growing in the local area but positively related to cervid density. We also hypothesize that there is a difference in the extent of damage between areas with smaller or larger amounts of supplementary feeding, and that these differences would vary depending on the type of feed used for supplementary feeding. We predict that lower damage levels in areas with a large amount of supplementary feeding indicate a diversionary effect, whereby the feed either acts to pull cervids spatially away from regenerating production stands (Borowski et al., 2019), or simply replace part of the cervids' food intake from pine. In contrast, higher damage levels to pine would indicate either a higher aggregation of individuals (Gundersen et al., 2004), and/or that the animals are trying to compensate for a nutritional imbalance induced by these energy-rich and fibre poor feeds (Felton et al., 2017).

2. Methods

2.1. Study area description

Sweden is divided into moose management areas (MMAs), which function as units for management planning and evaluation of resident moose populations. Moose management areas are in-turn divided into multiple moose management units (MMUs), within which the annual hunt is carried out. We collected data in six MMAs in the boreo-nemoral vegetation zone of southern Sweden (Fig. 1), each encompassing an area of 155 000 ha in average (88 529 ha SD, range 73 145–326 278 ha). While all six areas were located within the same climatic region, with similar snow depth and temperature during the winter, they differed in land use, forest type and structure, supplementary feeding intensity and

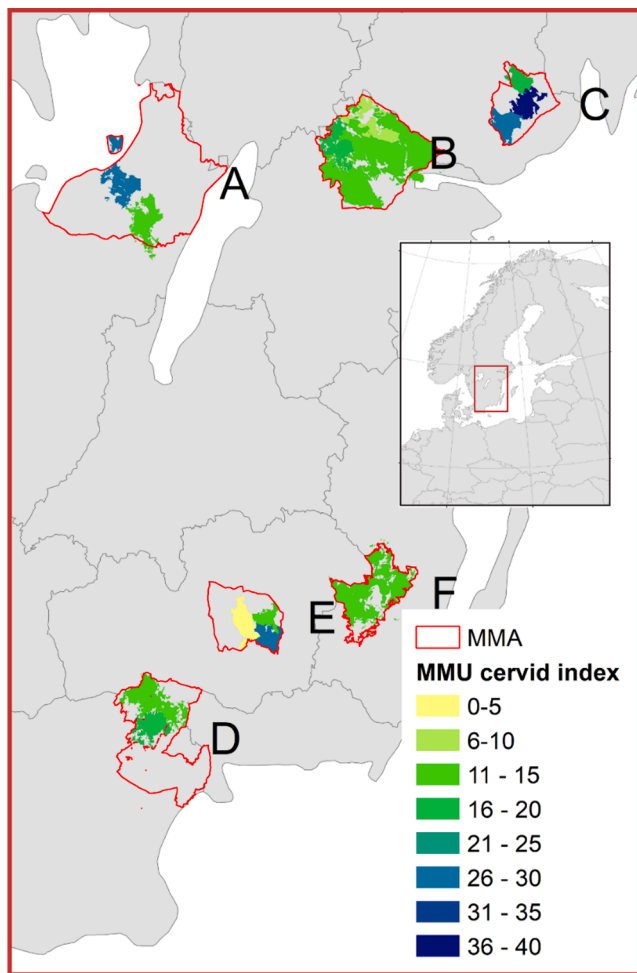


Fig. 1. The study region was located in southern Sweden (small inset). Six moose management areas (MMAs, red borders) were selected for data collection. Within each MMA, data was collected in three moose management units (MMUs). The relative density of cervids (moose and smaller deer species combined in one index) within MMUs is indicated in color, based on faecal pellet counts (number of piles/1000 m²) within inventory tracts (Fig. 2). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

population density of cervids. The mean annual precipitation in the region is 700 mm, with 25–100 days of annual snow cover. Of the region's terrestrial area, 63% is forested (SFA, 2014), and the vast majority (>80%) of the forest area is productive (approximately 5 M ha) and used for forestry (SLU, 2020). Planted Norway spruce (*Picea abies*, hereon spruce) or pine dominate production forests, and are to varying extents mixed with naturally regenerated broadleaves, primarily birch (silver birch *B. pendula* and downy birch *Betula pubescens*), rowan (*Sorbus aucuparia*), aspen (*Populus tremula*) and oak (*Quercus robur*). The use of herbicides is restricted on forest land (Löf et al., 2006), and the use of fertilization is limited (e.g. an average of 570 ha of the region's productive forest land was fertilized annually 2006–2020, SFA, 2021).

2.2. Study design

We collected data in three MMAs in the south-eastern and three in the north-eastern part of the region (Fig. 1). Within each of these two sub-regions, cervid composition and forest types are similar. The aim with the area selection was to include as much variation in supplementary feeding as possible, based on a government survey at the county level (SOU, 2014) and personal communication with local managers. In

Sweden, common supplementary feed includes silage (fermented grasses), grains and root vegetables. While grass silage may be a more or less nutritionally appropriate feed for some cervids (Renecker and Hudson, 1990), root vegetables have been cultivated for enhanced energy content, and have nutritional compositions that are highly inconsistent with the natural winter diet of most cervids (Felton et al., 2021). Nutritional imbalance after intake of such foods could therefore induce the cervids to forage more on tree material (Felton et al., 2017). Within both sub-regions, we selected three MMAs where we anticipated (based on the sources mentioned) distinctive patterns in the extent and type of supplementary feeding: One MMA where people reportedly provided almost no supplementary feeding; one MMA with relatively high amounts of root vegetables used as supplementary feed; and one MMA with relatively high amount of silage provided. In-turn, within each MMA we focused data collection in three MMUs. The selection of these smaller units was made to be consistent with the categorization of the larger unit (MMA). Note that this anticipated pattern of supplementary feeding was simply a guidance of study site selection, and should not be seen as a treatment description. In the analyses, actual data of supplementary feeding was used instead. Moose and roe deer were present in all 18 MMUs, while red deer and fallow deer were present in 10 and 15 MMUs respectively (Table A1).

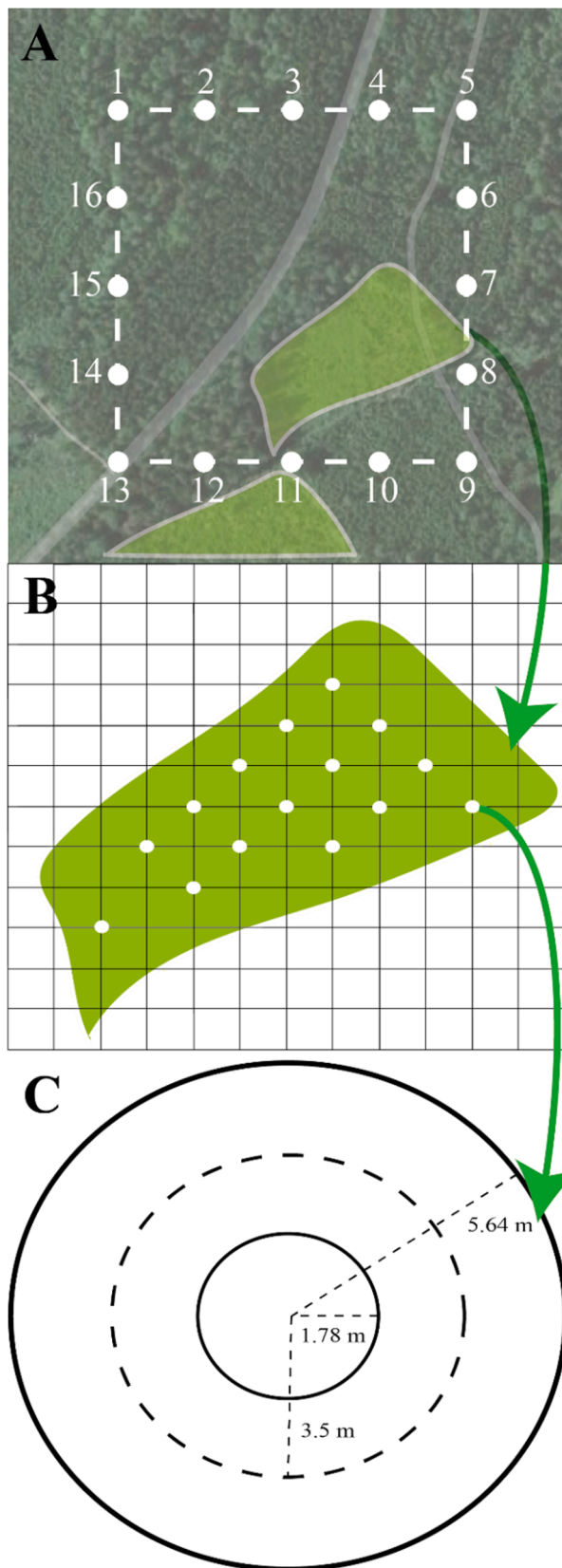
To enable an unbiased estimate of the average browsing pressure and forage availability, we randomly dispersed 10–15 inventory tracts (400 × 400 m) in each of the 18 MMUs (Table A1), with a minimum distance of 1 km between tracts (264 tracts in total, Table 1). Because a significant proportion of cervid forage can be found outside of forests in most landscapes (Hörnberg, 2001), we sampled all habitat types whether forested or not. However, randomly suggested tracts that resulted in allocation to waterbodies, roads or buildings were discarded, and a replacement tract was randomly assigned. Each tract had 16 circular sampling plots, placed at 100 m intervals along its outer edge (Fig. 2A). The radius of the plot differed depending on the type of inventory conducted (Fig. 2C).

Using the Swedish Forest Agency's online data (SFA, 2018a) we identified production forest stands (minimum 0.5 ha) that had been harvested and regenerated between 2007 and 2014 (3–10 years prior to the study), within a radius of 600 m from the tract centre (1.13 km²). These stands were used to collect data on browsing damage (and for faecal pellet counts additional to those conducted in tract plots). This phase of the forest rotation period is the most sensitive to browsing damage (Bergqvist et al., 2014) and it also represents the habitat type in

Table 1

Information about the various levels of sampling carried out in this study, and associated sample size as sums across the whole study. Moose management units (MMU) were nested within moose management areas (MMA). Inventory data was collected in up to 15 tracts per MMU, with up to 16 plots per tract. When present, one young production forest stand containing pine trees was inventoried per tract, by sampling up to 15 plots per stand. Telephone interviews to obtain data on supplementary feeding was carried out with people owning land in the majority of inventory tracts ("tracts with interview data"). In a subset of these tracts we obtained interview data that covered at least 25% of the total estate area. "Tracts used in SF Analysis" indicates the number of tracts which we could use for data analysis regarding the effect of supplementary feeding on pine damage. These tracts had to provide data on the pine damage situation in associated forest stands, interview data that covered at least 25% of the total estate area, as well as complete cervid dung pellet inventories in both stands and tracts. See Table A1 for breakdown of these numbers per MMU.

Sampling unit	Sample size sum
Moose management areas (MMA)	6
Moose management units (MMU)	18
Inventoried tracts	264
Young production forest stands with pine present	112
Tracts with interview data	230
Tracts with interview data with $\geq 25\%$ coverage	148
Tracts used in SF analysis	50



(caption on next column)

Fig. 2. A. An inventory tract (400 × 400 m) showing 16 sampling plots (white dots, referred to as tract plots), 100 m apart, along its outer edge, used to record forage availability and cervid faecal pellets, in southern Sweden 2017. If present, production forest stands < 10 yrs old (green) were identified within tracts, one of which was selected (see selection criteria in Methods) for detailed inventory of browsing damage. B. Outline of a forest stand and how plots (referred to as stand plots) were systematically placed in the nodes of a pre-determined, randomly placed, 20 × 20 m grid. Depending on the size of the stand, 8–15 plots were placed with 20, 40 or 60 m distance from each other. C. The inventory was conducted in circular plots. We used a plot radius of 5.64 m (100 m²) to count moose and red deer faecal pellet groups in both tract and stand plots. We used a plot radius of $r = 3.5$ m (38.5 m²) to record forage availability in tract plots, and browsing damage in the forest stands. We used the smallest plot size ($r = 1.78$ m) to count roe and fallow deer faecal pellet groups in both tract and stand plots. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

the region with the highest concentrations of tree browse within browsing height (Wam et al., 2010; Bergqvist et al., 2018). We performed an inventory in one of these stands per tract (if present). When selecting among several available stands, we prioritised stands that 1) had a suitable shape and size for fitting 15 plots (see below), 2) had a maximum mean height of 3 m as this includes the browsing height distribution for all four cervid species (Nichols et al., 2015); and 3) were located closer to the tract centre. In cases when criteria 1 and 2 were not fulfilled we accepted slightly smaller and/or taller stands, if they were not further than 600 m from the tract centre. Stands were included regardless of which production tree species was dominant. In this paper we present data from stands where pine trees were present in at least one stand plot. The spacing of plots (20, 40 or 60 m apart) depended on the size of the stand, and field personnel located the plots using a pre-designed systematic grid (Fig. 2) in a digital map tool. We refer to these plots as stand plots. The aim was to space the plots so they were evenly distributed within the whole stand, excluding a border of 20 m from the stand edge. Spacing decisions were made prior to starting the inventory. 84% of stands inventoried could fit 15 plots, and the lowest number of plots was 8 (2 stands, due to smaller size). All but 5 stands were within the predefined upper mean height limit of 3 m (the greatest mean height was 4.5 m). We found relevant forest stands in 112 of the 264 tracts (Table 1). Because of differences in land use among the six MMAs, the percentage of tracts per MMA with such forest stands present, ranged between 20 and 75% (Table A1).

2.3. Field inventory

Data were collected by five persons, between March 7th and May 11th 2017. Calibration exercises were done to minimise observer bias, and at least two persons worked in parallel in each MMU.

2.3.1. Data collection in tract plots (landscape scale)

In plots located along the edge of tracts (Fig. 2a) we classified the general habitat type and the dominant forest floor vegetation, and collected data on browse availability and the number of cervid faecal pellet groups (faeces were also counted in the stand plots, see below). We refer to this scale as “the landscape scale”.

2.3.1.1. Habitat type. Due to the importance of land cover habitat types in explaining cervid damage (Jarnemo et al., 2014; Spake et al., 2020) we categorised the general habitat type (within $r = 5.64$ m) as one of eight different classes: forest stands up to 10 yrs of age (using the same method of identification as described above); forest stands older than 10 yrs (all other forest stands); agricultural fields; edge zones with vegetation; waterbodies; roads; other open land (e.g. meadow or paddock); or other (areas free of vegetation e.g. building). We calculated the percentage of each tract’s plots that had each habitat type. For later analysis

we summed “agricultural field” and “other open land” into one category (“open land”).

2.3.1.2. Forest floor vegetation. As a significant part of the cervids’ forage is found in the forest floor vegetation, we categorised the dominant type of this strata (within $r = 3.5$ m) as one of five classes: No forest vascular floor vegetation (e.g. mostly stone, bare soil or mosses); dwarf shrubs (either one or a mix of cowberry *Vaccinium vitis-idaea*, bilberry *V. myrtillus*, and heather *Calluna vulgaris*); grass; forbs (including ferns and raspberry *Rubus idaeus*); or lichens. We calculated the proportion of plots per tract representing each category. To reduce the number of variables in later analysis, we only included the dwarf shrubs, as they are an important winter forage for the cervids concerned (Spitzer et al., 2021).

2.3.1.3. Availability of forage from trees. We assessed the availability of seven forage tree species, within browsing height (0.3–3 m): pine, silver birch, downy birch, rowan, aspen, willow (*Salix caprea* and closely related species), and oak (*Quercus robur* and *Q. petraea*). Hereafter, unless otherwise specified, when referring to any of these tree taxa, we are specifically referring to trees within browsing height. Within a radius of 3.5 m, we categorised each tree species as being represented in one of five density classes: 0) 0 stems, 1) 1–10 stems, 2) 11–50 stems, 3) 51–100 stems, 4) 100–200 stems. We summed the class notation (0–4) across all plots per species and tract, and divided that sum with the number of plots inventoried (i.e. if in 16 inventoried plots, pine had been noted in class 1 in 4 plots, and not at all in the other plots, the index would be $(4+(12*0))/16 = 0.25$). Hereafter we refer to this index as representing the relative availability of each tree species within browsing height per tract. Data for the two birch species were combined in our statistical analyses. The four remaining broadleaved tree species, rowan, aspen, willows and oak, are all highly preferred forage species by the cervids in this region (Månsson et al., 2007). Because these four tree species are relatively rare compared to birch and the two conifer species, we combined the four species into one index (as per Bergqvist et al., 2014), and we call this group AROW (for Aspen, Rowan, Oak and Willow).

2.3.1.4. Cervid density indices. To index cervid density, we conducted a faecal pellet count in each of the tract plots. The distribution of winter faecal pellet groups provides an estimate of the local habitat use by cervids during the winter (Ball and Dahlgren, 2002). We counted pellet groups produced by the two larger cervid species, moose and red deer, within a radius of 5.64 m (100 m²). For efficiency, pellet groups by the smaller roe deer and fallow deer were counted within a radius of 1.78 m (10 m²; Fig. 2c). For each fresh pellet group, we first counted the number of pellets and recorded the species based on visual inspection. In cases of suspected fallow deer or roe deer (two species with similar pellets), we noted the species identification based on a pellet-number threshold (fallow deer > 45 pellets; roe deer ≤ 45 pellets) as suggested by Edenius (2012). The centre of a pellet group had to fall within the plot boundaries to be included in the count. We only counted pellet groups that consisted of at least 20 individual pellets in the case of moose and red deer, and at least 10 pellets for roe and fallow deer, to not double-count pellets that may have been kicked up. To ensure that the pellet count largely represented the winter densities, we counted only pellet groups lying above the leaf litter and not heavily decomposed. Because we used a definition of pine damage designed to target damage caused primarily by moose (top shoot damage, see below), we used moose pellet count data separately (“moose index”, pellet groups / 1000 m²) from the three smaller deer species (where the three species’ pellet counts are combined into one “deer index” by summing pellet groups / 1000 m²) in our data analysis regarding pine damage. Both the moose and deer indices were used as continuous variables, for both stands and tracts. A combined cervid index (all four species) was also calculated.

2.3.2. Data collection in forest stands

2.3.2.1. Browsing damage and tree height. In stand plots ($r = 3.5$ m, Fig. 2b) we counted all stems of production tree species that had a height greater than half of the mean height of the two tallest stems in the plot (Kalén et al., 2019), excluding stems below 0.5 m. In this region, common production tree species include pine, spruce and birch. Following the same procedure as the national browsing damage monitoring scheme, each pine tree (belonging to the above described category) was noted as having recent damage or not, caused by cervids, and the damage was categorized as browsing on the top shoot, stem breakage (anywhere below the topmost whorl of shoots), or bark damage present on the stem above 0.3 m (Kalén et al., 2019). A tree could have more than one damage type. Recent browsing damage was defined by the colour of the bite surface. If the surface was green-yellow and pale it was assumed that the animal had taken the bite sometime during the previous five months, i.e. late fall and winter (Öhmark et al., 2015). If the surface of the bite was dark, grey and dry, it was assumed it was an older bite and was not included in the count. We only counted bites with a frayed appearance as this is the signature mark of a cervid, as opposed to the clean cut of a hare or rabbit (ibid). We calculated the density of pine per hectare. We also calculated the percentage of pine trees with recent damage per stand, pooling all three damage categories.

2.3.2.2. Cervid density indices. In stand plots (Fig. 2b) we also conducted the faecal pellet count as described above for tract plots.

2.4. Supplementary feeding – Interviews

We collected information regarding supplementary feeding by interviewing people owning properties within a radius of 600 m of each tract centre (113 ha). Excluding properties < 10 ha in size, we identified 1127 persons or organizations as possible respondents. Property owners were contacted by telephone during spring 2017 for a structured telephone survey (Supplementary Methods, Appendix) regarding any supplementary feeding taking place (amount, type) during the previous winter season. We did not reach all the relevant property owners in each tract (in total we reached 57%, and 20% of them declined to participate). To get a measure of data quality, we therefore calculated the total combined area of all estates identified as relevant for each tract (“total estate area”; range 188–4223 ha). We then divided the sum of property areas that were successfully included in the survey, with the total estate area, and used this proportion as an index of data quality. If this proportion was < 25% we did not include the tract’s data in statistical analyses of relationships with pine damage and browsing pressure. Data regarding the amount (kg/ha) of different supplementary feeding types were lumped together into two major categories: grass silage and “other”. “Other” supplementary feed included: beets (*Beta vulgaris*), carrots (*Daucus carota*), potato (*Solanum tuberosum*), oat (*Avena sativa*), wheat (*Triticum aestivum*), corn (*Zea mays*), pea (*Pisum sativum*), fruit or manufactured game pellets.

2.5. Statistical analyses

Statistical analyses were conducted in R version 4.0.2 (RCoreTeam, 2020).

2.5.1. Comparisons among moose management units

To assess variation in our measured variables at a large spatial scale, we first assessed whether there were differences among the 18 MMUs (Table A2). Due to the abundance of zeros in our response variables (e.g., many stands lacked damaged pine), we used beta regression for zero-inflated bounded proportion data to compare MMUs in terms of the likelihood of pine being damaged. This is a generalized logistic model, which allows us to mix two distribution functions for the same response

data (Ospina and Ferrari, 2010). In our case, we used a beta function for its proportional part (response $y > 0$), and an additive function for its binomial part (response $y = 0$; with logit- and log-link respectively). We used this approach in several assessments involving pine damage (further described below). We focused our interpretation on the proportional part while the binomial part is presented in the [supplementary information](#). These and all other statistical models described below, except those named GLM and GLMM, were performed using the `gamlss` function in the `gamlss` package (Rigby and Stasinopoulos, 2005).

Generalized Linear Models (GLM) were used (followed by an ANOVA test) to compare MMUs in terms of forage availability indices (pine, birch and AROW), cervid index and total amount of supplementary feed reported by respondents (each response modelled separately with MMU as a fixed explanatory variable). The responses forage availability, cervid index and amount of supplementary feed (kg/ha) were modelled with a Gaussian distribution with identity link and a dispersion function with a log-link that accounts for heteroscedasticity (i.e. different variance in the response across MMUs). Generalized Linear Mixed Models (GLMM) with tract ID as a random (intercept) effect, and Gaussian distribution with identity link, was used to test if there were differences between tracts and stands in the moose and deer indices. These GLMs and GLMMs were done using the `glmmTMB` function in the `glmmTMB` package (Brooks et al., 2017).

2.5.2. Factors accounting for variation in pine damage

Zero-inflated beta regression on the tract level, with MMU as a random effect (exploratory analyses showed that including MMAs had no significant bearing on the results), was used to assess which factors account for variation in recent damage to pine among stands. At first we did not include the aspect of supplementary feeding, but utilized the larger data set including all tracts from which we had data regarding pine trees in stand plots ($n = 112$ tracts, i.e. stands with pine present, both with and without damage). We included the density of pine per m^2 in the stand as an explanatory variable ("pine in stand"). As explanatory variables we also included the availability of pine, birch and AROW in the tract plots surrounding the stands (density of trees within browsing height as indicated by availability indices, see above), percentage of tract plots with forest < 10 yrs old or open land (habitat type), percentage of tract plots dominated by dwarf shrub cover (forest floor vegetation), the moose density index (stand level) and the deer density index (stand and tract level). We also included the interaction term "moose density index in stands \times availability of AROW". The animal density indices and the tree availability indices were log-transformed (natural logarithm) to reduce the effects of extreme values. All variables included in the model were standardized prior to modelling by subtracting the mean and dividing by the standard deviation (Z-transformation) to make the model coefficients comparable across explanatory variables. From the full model we performed a stepwise model selection based on AIC, whereby all variables are tested by removal and subsequent reintroduction to the model in iterative steps.

Similarly, zero-inflated beta regression, with MMU as a random effect, was used to assess the linkages between damage on pine and supplementary feeding at the landscape level. The number of tracts for which we obtained both interview data and stand inventory data was limited ($n = 50$ tracts, out of the pool of 112 stands with pine present), and to avoid over-parameterization, we were restricted in how many explanatory variables we could include. We first tested the relationship between the proportion of damaged pine stems in the stand and the natural logarithm of the total amount of supplementary feed (kg) per hectare, also including the density of pine per m^2 in the stand ("pine in stand") and the availability of AROW in tract, as these two variables were the strongest variables explaining variation in recent damage to pine in the above analysis. We tested the same model again but this time including an interaction term between the amount of supplementary feed and the availability of AROW in tract. Finally, we ran the same test again, but instead of the total amount of supplementary feed, we

included the logarithm of each of the two fractions silage and other supplementary feed (kg/ha). Due to weak distribution of data points and small sample size, we could not include more explanatory variables or interaction effects.

3. Results

3.1. General patterns from field inventory and supplementary feeding survey

Across tract plots in the 112 tracts with relevant stands, we found on average 1.29 ± 1.8 SD moose faecal pellet groups/1000 m^2 (range 0–11), and 15.6 ± 18.5 SD small deer faecal pellet groups/1000 m^2 (range 0–100). The equivalent density in stands was 3.2 ± 4.8 SD for moose (range 0–40) and 23.1 ± 26.3 SD for small deer (range 0–129). The GLMMs show that there were significantly more pellet groups in stands than in tracts, both regarding moose ($p < 0.001$) and smaller deer ($p < 0.01$). The most commonly found faecal pellet groups on a landscape scale were from moose and roe deer (observed in 61% and 59% of all inventoried tracts respectively), while we found pellet groups from fallow deer and red deer in 26% and 14% of the tracts respectively. There was a significant difference among MMUs in the density of cervid faecal pellet groups in tract plots ($p < 0.001$, Table A2).

The average height of the inventoried pine stems was 1.6 m (SD 0.77 m). We assessed 2435 pine trees, of which 10.4% displayed recent damage caused during the preceding fall/winter. In most cases (87%) the damage involved browsing on the top shoot, as opposed to breakage of stem or bark damage (no pine trees were encountered that had more than one type of recent damage). There were no significant differences among MMUs in the proportion of damaged pine trees ($p = 0.137$). However, the availability indices for forage trees within browsing height, as measured in tract plots, varied significantly among the 18 MMUs ($p < 0.001$ for all tree species assessed, Table A2). The four broadleaf tree species AROW lacked representation of stems within browsing height (0.3–3 m) in 34–64% of inventoried tracts depending on the species (aspen lacking in 53% of tracts, rowan 34%, oak 64%, willow 49%). Pine, spruce and birch were lacking in 24%, 10% and 17% of tracts respectively.

We obtained telephone survey data from 230 tracts. Of these 230 tracts, 148 (64%) were covered by the telephone survey in such a way that we obtained data from at least 25% of the combined area of all properties identified as relevant for each tract ("total estate area", see Methods). We call these 148 tracts "interviewed areas". The interviewed areas were well distributed across the six moose management areas (range 17–32 tracts per MMA, average 23 tracts/MMA). The variation in reported amount of supplementary feed ranged between 0 and 423 kg per km^2 (average $24 \text{ kg}/km^2 \pm 49.17$ SD for the whole season). About a fifth (19%) of the interviewed areas had only respondents who reported that they did not supply any feed at all during the season in question. The most common supplementary feed used (54% of study areas) was silage of some variety (average $45.5 \text{ kg}/km^2$ across the 96 study areas who used silage; average $22 \text{ kg}/km^2 \pm 47.5$ SD across all 148 areas (range 0–415 $kg}/km^2$)). Silage is normally placed out as round-bales, with the plastic cover partially opened or entirely removed to allow the game access to the fermented grass mixture. Respondents from 24 study areas (18%) reported the use of root vegetables, i.e. beets, carrots and potato. Root vegetables were used in relatively small amounts compared to silage (average $3.3 \text{ kg}/km^2$ across the 24 study areas who used root vegetables; average $0.6 \text{ kg}/km^2 \pm 2.39$ SD across all 148 areas (range 0 – 18 $kg}/km^2$)). As many as 64% of interviewed areas had respondents who reported the use of supplementary feed other than silage or root vegetables (i.e. oat, wheat, corn, pea, hay, fruit, or game pellets). These feeds were also used in relatively small amounts (average $1.7 \text{ kg}/km^2 \pm 4.02$ SD across all 148 areas (range 0 – 25 $kg}/km^2$)). Sixty-six areas reported supplying both silage and other types of food at the same time. There were significant differences among the 18 MMUs with

regard to the total amount of supplementary feed that managers reported they had placed out into the landscape the year of the study ($p < 0.001$, Table A2).

3.2. Factors explaining variation in recent damage on pine trees

With data from 112 tracts (supplementary feeding not included) we found that the proportion of damaged stems was significantly higher in the young forest stands that had a lower density of pine stems ($p < 0.001$). Damage levels were also higher in the stands within tracts where the AROW availability index ($p < 0.001$) was lower, the availability of open land ($p = 0.007$) was higher, and where the moose density index was relatively high in the stand ($p = 0.003$, Fig. 3; Final model in Table 2; Full model in Table A4). The interaction term was not included in the final model, indicating that the positive relationship between moose density and pine damage was not dependent on the availability of AROW in the landscape surrounding the stand. The deer index (moose not included) was not retained in the final model, neither with data collected in stand plots nor in tract plots.

The proportion of pine stems that were recently damaged by browsing was not associated with the overall amount of supplementary feed that people had placed within or near the tract during the winter (Table 2). In the model where the total amount of supplementary feed (regardless of type) was included, the % of damaged stems was lower in stands with a high density of pine ($p < 0.001$) and where the availability of AROW was high in the tract ($p = 0.021$). There was no significant interaction between the total amount of supplementary feed and the

availability of AROW ($p = 0.288$, Table A5). The outcome was similar when the type of supplementary feed was specified. While the density of pine in the stand was negatively related to pine damage levels ($p = 0.001$), neither silage nor “other” supplementary feed (root vegetables etc) were significant explanatory variables (Table 2). There was no correlation between the % of estate area covered by the interview per tract (our measure of data quality, see Methods) and the damage level on pine ($r = -0.075$).

4. Discussion

The key finding of our study was that variation in cervid browsing damage to young pine in production stands could be best explained by the availability of pine and broadleaf forage in the stand or the surrounding landscape (as defined by our inventory tract, 16 ha), while the presence of supplementary feed did not account for variation in damage (Table 2). We found that 10% of all inventoried pine had been damaged by cervids during the previous winter. For perspective, this is double the Swedish Forest Agency’s goal that not >5% of Scots pine stems are damaged by cervids in a given year (SFA, 2018b), but lower than in other recent assessments of the region (Pfeffer et al., 2021). Although this may be unacceptably high for commercial forestry, it is worth noting that at least the majority of damage we found was in the form of top shoot browsing (as in Bergqvist et al., 2001), rather than stem breakage, that has more serious repercussions for the trees (Heikkilä and Löyttyniemi, 1992). As expected, we found that pine damage was lower in stands with a lower density of moose faeces. This is in line with

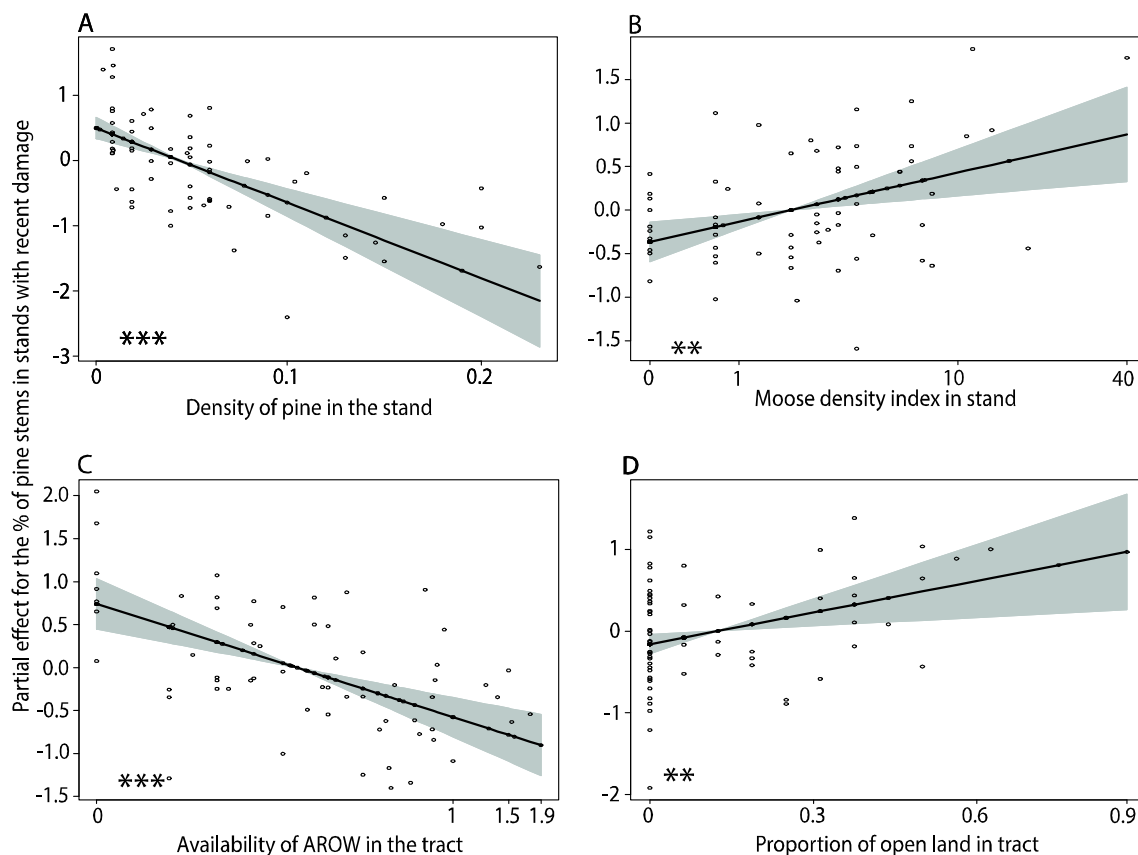


Fig. 3. Associations between forest stand and landscape scale variables and the proportion of pine stems in production stands ($n = 112$) that have been recently browsed by deer and moose (cervids) in southern Sweden 2017. The four variables depicted are those included in the final regression model^a, which excluded supplementary feed (Table 2). Panels illustrate the partial effect of each variable (controlling for the other variables in the model; solid line), the variation (\pm SE, grey field), and partial residuals (dots). Panel A) Density of pine in the stand (stems/m²); B) moose density index in the stand (number of pellet groups/ 1000 m²); C) Availability of aspen, rowan, oak and willow (AROW) in tract plots (index based on # stems/ha of trees 30–300 cm in height); D) Proportion of tract plots on open land. Level of significance is indicated with stars on each panel (corresponding to Table 2). ^aModelled with a beta regression, where a binomial part models the likelihood of 0 outcomes (no pine damage, see Table A4). The proportional part, which is shown here, models the outcomes where > 0 pines were damaged.

Table 2

Beta regression analyses^a of factors explaining variation in cervid damage on pine trees growing in production forest stands (up to 10 yrs old) in southern Sweden 2017. The response variable was the proportion of pine stems that were recently damaged by cervids (see Methods for definition). In the first analysis, we included all tracts from which we had data on pine trees in young production stands (n = 112), and several variables regarding forage availability (indices), % of plots in open land or in forest < 10 yr, and moose and deer density indices (T = tract level data); whereas supplementary feeding was excluded (see foot note). The second analysis was limited to 50 tracts, but included data on the total amount of supplementary feed (Tot SF) used by local landowners, along with density of pine in the stand (Pine in stand) and availability of AROW in tract (AROW avail). In the third analysis, the model included the amount of supplementary feed classified as either silage or other feed types. Stepwise model selection was performed for the first analysis in the table (here depicting the final model), but not for the second and third analyses (here depicting full models).^bIn this type of regression a binomial part models the likelihood of 0 outcomes (no pine damage, see Table A3). The proportional part, which is shown here, models the outcomes where > 0 pines were damaged.

Association between landscape scale factors and pine damage, excl. supplementary feeding; Final model ^b ; n = 112				
	Estimate	Std.Error	t value	Pr(> t)
Intercept	-1.71	0.09	-17.99	< 0.001
Moose in stand	0.27	0.09	3.11	0.003
AROW avail (T)	-0.44	0.09	-4.86	< 0.001
Open land (T)	0.24	0.09	2.74	0.007
Pine in stand	-0.57	0.11	-5.05	< 0.001

Association between supplementary feeding (Total) and pine damage ^b ; n = 50				
	Estimate	Std.Error	t value	Pr(> t)
Intercept	-1.65	0.12	-13.34	< 0.001
Tot SF	0.08	0.12	0.68	0.500
AROW avail (T)	-0.28	0.11	-2.55	0.015
Pine in stand	-0.75	0.17	-4.42	< 0.001

Association between two categories of supplementary feeding and pine damage; n = 50				
	Estimate	Std.Error	t value	Pr(> t)
Intercept	-1.51	0.16	-9.72	< 0.001
Silage (log)	0.12	0.14	0.83	0.412
Other SF (log)	-0.07	0.18	-0.38	0.71
Pine in stand	-0.68	0.20	-3.46	0.0014

^a More variables were included in the full model (see Table A4);

^b Model results including an interaction term are presented in Table A5.

several other studies of ungulate systems (e.g. Angelstam et al., 2000, Côté et al., 2004, Bergqvist et al., 2014), and indicates that there is a positive correlation between damage and the amount of time moose spend in a stand. The lack of a similar relationship between damage and our density estimates of other cervids was also expected, due to their different feeding physiology and -behaviour. It is important to note however, that although the other cervids may not damage pine to the same extent as moose, they can influence moose foraging via competition in their shared foodscape (Spitzer et al., 2021).

Our findings highlight the influence that natural forage availability has on cervid damage to pine, as likewise supported by a number of previous studies (e.g., in Sweden: Hörnberg 2001, Ball and Dahlgren 2002, Jarnemo et al., 2014, Gicquel et al., 2020). Importantly, damage was lower within production stands with a higher density of pine stems (Fig. 3, as in Bergqvist et al., 2014, Pfeffer et al., 2021). Even though a habitat rich in young pine may be attractive to moose and other deer (Nikula et al., 2004), the dilution effect of many pine stems results in a lower proportion of stems being damaged (as in Hörnberg, 2001, Ball and Dahlgren, 2002, Cassing et al., 2006). In our study, we cannot tell whether the low pine density found in those stands that were most affected by damage was the result of several years of high browsing pressure, or past forest management decisions. However, moose and

deer density indices at the landscape level were not strong explanatory factors in relation to damage in stands, suggesting that the stand pine density was not simply a result from the preceding winter's browsing pressure. In addition, browsing pressure on pine and broadleaved trees as measured in the tract plots was not significantly correlated with pine damage in the associated stand (A. Felton, unpublished data).

We also found that a relatively high availability of key broadleaf trees (AROW: aspen, rowan, oak and willow) in the surrounding landscape, was associated with lower levels of damage to pine (Table 2), and importantly, our measure of AROW availability was not correlated with moose or deer density indices. This negative relationship between AROW availability and pine damage is in accordance with a large-scale moose selection study showing that when AROW density at the municipality level (several thousand ha) is higher, moose selection for pine is lower (Wam and Hjeljord, 2010). The AROW species are known to be highly selected by cervids, likely due to their more beneficial nutritional composition (Hjeljord et al., 1982, Felton et al., 2021). In Scandinavia, where rotational, even-aged production forestry is the norm (Felton et al., 2020a), the availability of these four broadleaf tree species and other key food resources for moose, is strongly influenced by the amount of forest in young succession stages (Wam et al., 2010, Bergqvist et al., 2018). Therefore, we expected that a high proportion of forest < 10 yrs of age in the surrounding landscape would be associated with lower damage to pine in production stands. The variable 'forests < 10 yr of age' was significant in the full model but was not retained in the final model. Instead, we found that the less open land there was in the surrounding landscape, the lower the damage to pine (Fig. 3). Open land in this case is defined as agricultural fields, meadows, paddocks and similar. This indicates that the forage that is present in several habitats (e.g. forests of all ages, and edge zones with vegetation), in addition to young production forests, significantly lowers the browsing pressure on production trees (as in Jarnemo et al., 2014).

About 1% of Sweden's productive forest land is clear cut every year (SFA, 2021), and the estimated amounts of woody forage present in stands regenerating after clear cutting range between 0.2 and 3 tonnes ha⁻¹, up until this vegetation grows out of browsing height (Kalen and Bergquist, 2004, Månsson et al., 2015). In comparison, supplementary feed is provided at much lower amounts and is even more patchily distributed. Our survey revealed large geographical variation in the types of supplementary feed provided, and that it was available at amounts comparable to those recorded by other studies identifying a significant influence of supplementary feeding on cervid movements and foraging choices (Schmidt 1993, Guillet et al., 1996, Sahlsten et al., 2010, van Beest et al., 2010). The lack of a signal in our data suggests that even in regions where supplementary feeding is part of the foodscape, its effects are hard to predict due to many context-dependent factors.

Such context-dependant outcomes have been shown in other socio-ecological systems. For example, fallow deer browsing intensity on young Norway spruce in south western Sweden was strongly moderated by the relative availability of forest floor vegetation (*Vaccinium* spp. and *Calluna* spp.) and young deciduous trees (Garrido et al., 2014), despite close proximity to silage feeding sites. The availability of alternative, naturally growing, forage in the landscape likely takes the burden off production trees, both in terms of providing food for the elevated densities of game surrounding the feeding stations (Garrido et al., 2014), and via the provision of forage items that are nutritionally complementary to the supplementary feed (Timmons et al., 2010, Felton et al., 2020c). It is therefore reasonable to expect that an effect of supplementary feeding on pine damage may depend on how much alternative natural forage is available in the surrounding landscape. However, we did not find this interaction in our data (Table 2).

The lack of an effect of supplementary feeding on pine damage in our study may be due to several reasons. First, there was a mismatch in the response scales measured. We estimated forage availability within ca. 400 m of the stand, whereas the area covered by phone interviews was

larger (as a direct effect of different estate sizes; range 188 – 4223 ha). This meant that feeding stations were likely located at variable distances from where damage was measured, which is known to be an important determinant of outcomes (Gundersen et al., 2004, Garrido et al., 2014). Second, the effects of supplementary feeding on pine damage may cancel each other out if the cervid community is diverse in their dietary niches; as was the case in our study. The potential effects of a given type of food on browsing behaviour should depend on the species of consumer (Milner et al., 2014, Felton et al., 2017). For example, whereas grass silage supplementation may induce higher levels of pine damage by moose (Mathisen et al., 2014), it can reduce damage caused by red deer (Borowski et al., 2019) (but see Rajska et al., 2008). Third, the relative influence of supplementary feeding on surrounding vegetation will also depend on the local cervid populations' use of these feeding stations. During the winter of our study, snow fall was limited, which may have both increased the availability of alternative browse, and reduced cervid reliance on such stations (Guillet et al., 1996, Doenier et al., 1997). Finally, because supplementary feeding is controversial in Sweden, it is possible that our interview respondents understated their use of supplementary feed, or that respondents who declined to partake represented the more active providers of supplementary feed. Both outcomes would increase the noise and decrease the signal in our results. For these reasons, we caution against using our findings to conclude that the type and extent of supplementary feeding does not alter damage outcomes in timber production stands.

4.1. Implications for game and forest management

Our results support the efficacy of using naturally growing forage to mitigate cervid browsing damage to pine in managed forested landscapes. The availability of naturally growing forage can be increased in production-forest dominated landscapes by either limiting the removal of edible biomass, or by actively promoting its growth. Notably, within browsing height (0.3–3 m), willow, aspen and oak were missing in half or more (depending on the species) of the tracts in our study. The frequent absence of these trees may at least in part be due to a high browsing pressure on these preferred tree species over many years, and raises important questions about the prevalence of mature AROW individuals in the future (Angelstam et al., 2017). However, despite their limited and patchy occurrence, the current density of AROW in our study locations was never-the-less sufficient to apparently have an alleviating effect on pine damage, although controlled experiments are needed to verify this pattern. This is positive news, as it indicates the potential to which pine damage could be reduced in the region by actively promoting these broadleaf trees species during the cleaning and thinning of production stands, and in the management of hedge rows, edges and small forest roads. Additional contributions to the availability of alternative natural forage can be made by forest owners and managers when deciding which production tree species to regenerate after harvest. For a given level of timber production, the high needle area of spruce dominated forests leads to darker understories than pine forests, resulting in a poorer understory and forest floor vegetation layer (Pettersson et al., 2019). To efficiently create more forage during the whole rotation period, landowners could prioritize tree species other than spruce (e.g. broadleaf trees, pine), limit stem density, and increase the rotation time (Pettersson et al., 2019). Our results also indicate that landowners could help reduce forest damage by ensuring a sufficiently high overall density of regenerating pine in the landscape at any given time.

The management approaches mentioned here are particularly relevant to areas where browsing damage results in significant economic losses, and increased culling is not an acceptable option due to conflicts with other societal goals and cultural values. Increasing the prevalence of pine and broadleaf trees, as well as promoting the cover and diversity of understory vegetation, is likely to have a range of additional ecological and societal benefits, allowing for a potential win-win

solution for timber production, species conservation and ecosystem services (Felton et al., 2020b). In contrast, recent trends in Scandinavia involving land owners shifting timber production from pine to spruce, and shortening rotation times, runs counter to such recommendations, raising concerns as to the longer-term vulnerability of such landscapes to browsing and additional biotic and abiotic risks (Pettersson, 2019, Felton et al., 2020b).

4.2. Conclusion

A range of strategies is available to those trying to reduce the risk of cervid browsing damage in production forests, and thereby help sustain their delivery of vital ecosystem services. Our results suggest that the most effective strategy for reducing damage to pine will rely on the retention and creation of natural forage in the foodscape, while also regulating moose densities. The lack of a clear signal in our results linking supplementary feeding with browsing damage raises questions regarding the efficacy of this practice to reduce damage. Our results indicate that targeted controlled experiments are now needed to test the effect of supplementary feeding on pine damage at the landscape scale. The large number of biodiversity and ecosystem service co-benefits associated with retaining and creating sources of natural forage raises the promise of landscape scale solutions that successfully combine forestry with healthy cervid populations and additional societal values. As both pine production forests, and the four cervid species assessed are prevalent features of European and other northern hemisphere landscapes, our results have implications that extend well beyond Sweden's borders.

Other Information.

We handled the personal information of respondents according to SLU (EU) regulations.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Author contribution statement

AMF, AF, EL, JM, EH and HKW formulated the idea; AMF, AF, EL and EH developed methodology; AMF conducted field work; EL supervised interviews; POH and AMF performed data analyses; AMF, POH, AF, FW, MW, EH, EL, JM, RN and HKW interpreted results and wrote the manuscript.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2022.120187>.

References

- Angelstam, P., Pedersen, S., Manton, M., Garrido, P., Naumov, V., Elbakidze, M., 2017. Green infrastructure maintenance is more than land cover: Large herbivores limit recruitment of key-stone tree species in Sweden. *Landscape and Urban Planning* 167, 368–377. <https://doi.org/10.1016/j.landurbplan.2017.07.019>.
- Angelstam, P., Wikberg, P.E., Danilov, P., Faber, W.E., Nygren, K., 2000. Effects of moose density on timber quality and biodiversity restoration in Sweden, Finland and Russian Karelia. *Alces* 36, 133–145.
- Apollonio, M., Belkin, V.V., Borkowski, J., Borodin, O.I., Borowik, T., Cagnacci, F., Danilkin, A.A., Danilov, P.I., Faybich, A., Ferretti, F., Gaillard, J.M., Hayward, M., Heshtaut, P., Heurich, M., Hurynovich, A., Kashtalyan, A., Kerley, G.I.H., Kjellander, P., Kowalczyk, R., Kozorez, A., Matveytchuk, S., Milner, J.M., Mysterud, A., Ozoliņš, J., Panchenko, D.V., Peters, W., Podgórski, T., Pokorny, B., Rolandsen, C.M., Ruusila, V., Schmidt, K., Sipko, T.P., Veeroja, R., Velihurau, P., Yanuta, G., 2017. Challenges and science-based implications for modern management and conservation of European ungulate populations. *Mammal Res.* 62 (3), 209–217. <https://doi.org/10.1007/s13364-017-0321-5>.
- Ball, J.P., Dahlgren, J., 2002. Browsing damage on pine (*Pinus sylvestris* and *P. contorta*) by a migrating moose (*Alces alces*) population in winter: Relation to habitat composition and road barriers. *Scand. J. For. Res.* 17, 427–435.
- Bergquist, J., Löf, M., Örlander, G., 2009. Effects of roe deer browsing and site preparation on performance of planted broadleaved and conifer seedlings when using temporary fences. *Scand. J. For. Res.* 24 (4), 308–317. <https://doi.org/10.1080/02827580903117420>.
- Bergqvist, G., Bergström, R., Edenius, L., 2001. Patterns of stem damage by moose (*Alces alces*) in young *Pinus sylvestris* stands in Sweden. *Scand. J. For. Res.* 16 (4), 363–370.
- Bergqvist, G., Bergström, R., Wallgren, M., 2014. Recent browsing damage by moose on Scots pine, birch and aspen in young commercial forests - effects of forage availability, moose population density and site productivity. *Silva Fennica* 48:13. [10.14214/sf.1077](https://doi.org/10.14214/sf.1077).
- Bergqvist, G., Wallgren, M., Jernelid, H., Bergström, R., 2018. Forage availability and moose winter browsing in forest landscapes. *For. Ecol. Manage.* 419, 170–178. <https://doi.org/10.1016/j.foreco.2018.03.049>.
- Bernes, C., Macura, B., Jonsson, B.G., Junninen, K., Müller, J., Sandström, J., Löhm, A., Macdonald, E., 2018. Manipulating ungulate herbivory in temperate and boreal forests: effects on vegetation and invertebrates. A systematic review. *Environ. Evidence* 7, 13. <https://doi.org/10.1186/s13750-018-0125-3>.
- Bø, S., Hjeljord, O., 1991. Do continental moose ranges improve during cloudy summers? *Can. J. Zool.* 69 (7), 1875–1879. <https://doi.org/10.1139/z91-260>.
- Borowski, Z., Balazy, R., Ciesielski, M., Korzeniowski, K., 2019. Does winter supplementary feeding affect deer damage in a forest ecosystem? A field test in areas with different levels of deer pressure. *Pest Manag. Sci.* 75 (4), 893–899.
- Brooks, M.E., Kristensen, K., Van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J., Machler, M., Bolker, B.M., 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R J.* 9, 378–400.
- Cassing, G., Greenberg, L.A., Mikusiński, G., 2006. Moose (*Alces alces*) browsing in young forest stands in central Sweden: A multiscale perspective. *Scand. J. For. Res.* 21 (3), 221–230. <https://doi.org/10.1080/02827580600673535>.
- Cederlund, G., Ljungqvist, H., Markgren, G., Stålfelt, G., 1980. Foods of moose and roe-deer at Grimsö in central Sweden: results of rumen content analyses. *Swedish Wildlife Res.* 11, 171–247.
- Clauss, M., Hume, I.D., Hummel, J., 2010. Evolutionary adaptations of ruminants and their potential relevance for modern production systems. *Animal* 4 (7), 979–992.
- Cooper, S.M., Owens, M.K., Cooper, R.M., Ginnett, T.F., 2006. Effect of supplemental feeding on spatial distribution and browse utilization by white-tailed deer in semi-arid rangeland. *J. Arid Environ.* 66 (4), 716–726. <https://doi.org/10.1016/j.jaridenv.2005.11.015>.
- Côté, S.D., Rooney, T.P., Tremblay, J.-P., Dussault, C., Waller, D.M., 2004. Ecological impacts of deer overabundance. *Annu. Rev. Ecol. Evol. Syst.* 35 (1), 113–147.
- Creel, S., Winnie, J., Maxwell, B., Hamlin, K., Creel, M., 2005. Elk alter habitat selection as an antipredator response to wolves. *Ecology* 86 (12), 3387–3397.
- Doenier, P.B., DelGiudice, G.D., Riggs, M.R., 1997. Effects of winter supplemental feeding on browse consumption by white-tailed deer. *Wildl. Soc. Bull.* 25, 235–243.
- Edenius, L., 2012. Referensområden för klövviltförvaltning i södra Sverige: årsrapport 2012. Vilt, fisk och miljöö, SLU, Umeå.
- Felton, A., Löfroth, T., Angelstam, P., Gustafsson, L., Hjältén, J., Felton, A.M., Simonsson, P., Dahlberg, A., Lindblad, M., Svensson, J., Nilsson, U., Lodin, I., Hedwall, P.O., Sténs, A., Lämås, T., Brunet, J., Kalén, C., Kriström, B., Gemmel, P., Ranius, T., 2020a. Keeping pace with forestry: Multi-scale conservation in a changing production forest matrix. *Ambio* 49 (5), 1050–1064. <https://doi.org/10.1007/s13280-019-01248-0>.
- Felton, A., Petersson, L., Nilsson, O., Witzell, J., Cleary, M., Felton, A.M., Björkman, C., Sang, Å.O., Jonsell, M., Holmström, E., Nilsson, U., Rönnerberg, J., Kalén, C., Lindblad, M., 2020b. The tree species matters: Biodiversity and ecosystem service implications of replacing Scots pine production stands with Norway spruce. *Ambio* 1–15. 49 (5), 1035–1049.
- Felton, A.M., Felton, A., Crowsigt, J.P.G.M., Edenius, L., Malmsten, J., Wam, H.K., 2017. Interactions between ungulates, forests and supplementary feeding: the role of nutritional balancing in determining outcomes. *Mammal Res.* 62 (1), 1–7. <https://doi.org/10.1007/s13364-016-0301-1>.
- Felton, A.M., Holmström, E., Malmsten, J., Felton, A., Crowsigt, J.P., Edenius, L., Ericsson, G., Widemo, F., Wam, H.K., 2020c. Varied diets, including broadleaved forage, are important for a large herbivore species inhabiting highly modified landscapes. *Sci. Rep.* 10, 1–13. <https://doi.org/10.1038/s41598-020-58673-5>.
- Felton, A.M., Wam, H.K., Felton, A., Simpson, S.J., Stolter, C., Hedwall, P.-O., Malmsten, J., Eriksson, T., Tigabo, M., Raubenheimer, D., 2021. Macronutrient balancing in free-ranging populations of moose. *Ecol. Evol.* 11 (16), 11223–11240. <https://doi.org/10.1002/ece3.7909>.
- Garrido, P., Lindqvist, S., Kjellander, P., 2014. Natural forage composition decreases deer browsing on *Picea abies* around supplemental feeding sites. *Scand. J. For. Res.* 29, 234–242.
- Gicquel, M., Sand, H., Månsson, J., Wallgren, M., Wikenros, C., 2020. Does recolonization of wolves affect moose browsing damage on young Scots pine? *For. Ecol. Manage.* 473, 118298. <https://doi.org/10.1016/j.foreco.2020.118298>.
- Guillet, C., Bergström, R., Cederlund, G., 1996. Size of winter home range of roe deer *Capreolus capreolus* in two forest areas with artificial feeding in Sweden. *Wildlife Biol.* 2 (2), 107–111.
- Gundersen, H., Andreassen, H.P., Storaas, T.S., 2004. Supplemental feeding of migratory moose *Alces alces*: forest damage at two spatial scales. *Wildlife Biol.* 10 (3), 213–223.
- Heikkilä, R., Löytyniemi, K., 1992. Growth response of young Scots pines to artificial shoot breaking simulating moose damage.
- Herfingal, I., Lande, U.S., Solberg, E.J., Rolandsen, C.M., Roer, O., Wam, H.K., 2017. Weather affects temporal niche partitioning between moose and livestock. *Wildlife Biol.* 2017 (1), 1–12.
- Herfingal, I., Tremblay, J.-P., Hester, A.J., Lande, U.S., Wam, H.K., 2015. Associational relationships at multiple spatial scales affect forest damage by moose. *For. Ecol. Manage.* 348, 97–107. <https://doi.org/10.1016/j.foreco.2015.03.045>.
- Hjeljord, O., Sundstol, F., Haagenrud, H., 1982. The nutritional value of browse to moose. *J. Wildl. Manage.* 46, 333–343. <https://doi.org/10.2307/3808644>.
- Hörnberg, S., 2001. The relationship between moose (*Alces alces*) browsing utilisation and the occurrence of different forage species in Sweden. *For. Ecol. Manage.* 149 (1–3), 91–102.
- Jarnemo, A., Minderman, J., Bunnefeld, N., Zidar, J., Månsson, J., 2014. Managing landscapes for multiple objectives: alternative forage can reduce the conflict between deer and forestry. *Ecosphere* 5 (8), art97.
- Johansson, M., 2018. Supplementary feeding of game; an attitude survey of hunters, forest owners and farmers. Swedish university of agricultural sciences, Umeå.
- Kalén, C., Bergqvist, J., 2004. Forage availability for moose of young silver birch and Scots pine. *For. Ecol. Manage.* 187 (2–3), 149–158.
- Kalén, C., Bergqvist, J., Carlstedt, F., 2019. Åbin Fältinstruktion. Swedish Forest Agency.
- Kamler, J., Homolka, M., 2016. The importance of cultivated plants in the diet of red and roe deer and mouflon. *Acta Universitatis Agriculturae et Silviculturae Mendelianae Brunensis* 64 (3), 813–819.
- Liberg, O., Bergström, R., Kindberg, J., von Essen, H., 2010. Ungulates and their management in Sweden. Pages 37–70 in M. Apollonio, R. Andersen, and R. Putman, editors. *European Ungulates and Their Management in the 21st Century*. Cambridge University Press.
- Löf, M., Rydberg, D., Bolte, A., 2006. Mounding site preparation for forest restoration: Survival and short term growth response in *Quercus robur* L. seedlings. *For. Ecol. Manage.* 232 (1–3), 19–25. <https://doi.org/10.1016/j.foreco.2006.05.003>.
- Månsson, J., 2009. Environmental variation and moose *Alces alces* density as determinants of spatio-temporal heterogeneity in browsing. *Ecography* 32 (4), 601–612. <https://doi.org/10.1111/j.1600-0587.2009.05713.x>.
- Månsson, J., Kalén, C., Kjellander, P., Andrén, H., Smith, H., 2007. Quantitative estimates of tree species selectivity by moose (*Alces alces*) in a forest landscape. *Scand. J. For. Res.* 22 (5), 407–414. <https://doi.org/10.1080/02827580701515023>.
- Månsson, J., Roberge, J.-M., Edenius, L., Bergström, R., Nilsson, L., Lidberg, M., Komstedt, K., Ericsson, G., 2015. Food plots as a habitat management tool: forage production and ungulate browsing in adjacent forest. *Wildlife Biol.* 21 (5), 246–253. <https://doi.org/10.2981/wlb.00019>.
- Mathisen, K.M., Milner, J.M., van Beest, F.M., Skarpe, C., 2014. Long-term effects of supplementary feeding of moose on browsing impact at a landscape scale. *For. Ecol. Manage.* 314, 104–111. <https://doi.org/10.1016/j.foreco.2013.11.037>.
- Milner, J.M., Van Beest, F.M., Schmidt, K.T., Brook, R.K., Storaas, T., 2014. To feed or not to feed? Evidence of the intended and unintended effects of feeding wild ungulates. *J. Wildl. Manag.* 78 (8), 1322–1334. <https://doi.org/10.1002/jwmg.798>.
- Mysterud, A., 2000. Diet overlap among ruminants in Fennoscandia. *Oecologia* 124 (1), 130–137. <https://doi.org/10.1007/s004420050032>.
- Neumann, W., Levers, C., Widemo, F., Singh, N.J., Crowsigt, J.P.G.M., Kuemmerle, T., 2022. Hunting as land use: Understanding the spatial associations among hunting, agriculture, and forestry. *Ecol. Soc.* 27. <https://doi.org/10.5751/ES-12882-270102>.
- Nichols, R.V., Crowsigt, J.P.G.M., Spong, G., 2015. DNA left on browsed twigs uncovers bite-scale resource use patterns in European ungulates. *Oecologia* 178 (1), 275–284. <https://doi.org/10.1007/s00442-014-3196-z>.
- Nikula, A., Heikkinen, S., Helle, E., 2004. Habitat selection of adult moose *Alces alces* at two spatial scales in central Finland. *Wildlife Biol.* 10 (2), 121–135.
- Öhmark, S.M., Iason, G.R., Palo, R.T., 2015. Spatially segregated foraging patterns of moose (*Alces alces*) and mountain hare (*Lepus timidus*) in a subarctic landscape: different tables in the same restaurant? *Can. J. Zool.* 93 (5), 391–396.
- Ospina, R., Ferrari, S.L.P., 2010. Inflated beta distributions. *Stat. Pap.* 51 (1), 111–126. <https://doi.org/10.1007/s00362-008-0125-4>.
- Persson, I.L., Danell, K., Bergström, R., 2000. Disturbance by large herbivores in boreal forests with special reference to moose. *Ann. Zool. Fenn.* 37, 251–263.
- Petersson, L., 2019. Replacing Scots pine with Norway spruce: Implications for biodiversity in production forests. *Sveriges lantbruksuniversitet, Alnarp*.
- Petersson, L., Holmström, E., Lindblad, M., Felton, A., 2019. Tree species impact on understory vegetation: Vascular plant communities of Scots pine and Norway spruce managed stands in northern Europe. *For. Ecol. Manage.* 448, 330–345.

- Pfeffer, S.E., Singh, N.J., Crowsigt, J.P.G.M., Kalén, C., Widemo, F., 2021. Predictors of browsing damage on commercial forests – A study linking nationwide management data. *For. Ecol. Manage.* 479, 118597. <https://doi.org/10.1016/j.foreco.2020.118597>.
- Rajský, M., Vodňanský, M., Hell, P., Slamečka, J., Kropil, R., Rajský, D., 2008. Influence supplementary feeding on bark browsing by red deer (*Cervus elaphus*) under experimental conditions. *Eur. J. Wildl. Res.* 54 (4), 701–708. <https://doi.org/10.1007/s10344-008-0199-2>.
- RCoreTeam, 2020. R: A language and environment for statistical computing. *in* R. F. S. Computing, editor., Vienna, Austria.
- Reimoser, F., Putman, R., Putman, R., Apollonio, M., Andersen, R., 2011. Impacts of wild ungulates on vegetation: costs and benefits. In: Putman, R., Apollonio, M., Andersen, R. (Eds.), *Ungulate Management in Europe: Problems and Practices*. Cambridge University Press, Cambridge, pp. 144–191. <https://doi.org/10.1017/CBO9780511974137.007>.
- Renecker, L.A., Hudson, R.J., 1990. Digestive kinetics of moose (*Alces alces*), wapiti (*Cervus elaphus*) and cattle. *Anim. Sci.* 50 (1), 51–61.
- Rigby, R.A., Stasinopoulos, D.M., 2005. Generalized additive models for location, scale and shape. *J. Roy. Stat. Soc.: Ser. C (Appl. Stat.)* 54, 507–554.
- Sahlsten, J., Bunnefeld, N., Månsson, J., Ericsson, G., Bergström, R., Dettki, H., 2010. Can supplementary feeding be used to redistribute moose *Alces alces*? *Wildlife Biol.* 16 (1), 85–92. <https://doi.org/10.2981/08-085>.
- Schmidt, K., 1993. Winter ecology of nonmigratory Alpine red deer. *Oecologia* 95 (2), 226–233.
- Schröter, M., Barton, D.N., Remme, R.P., Hein, L., 2014. Accounting for capacity and flow of ecosystem services: A conceptual model and a case study for Telemark, Norway. *Ecol. Ind.* 36, 539–551. <https://doi.org/10.1016/j.ecolind.2013.09.018>.
- Schwartz, C.C., Hundertmark, K.J., 1993. Supplemental feeding of moose during winter: Can hay serve as an emergency ration. *Alces* 29, 135–147.
- Searle, K.R., Hobbs, N.T., Gordon, L.J., 2007. It's the "foodscape", not the landscape: using foraging behavior to make functional assessments of landscape condition. *Israel J. Ecol. Evol.* 53 (3-4), 297–316.
- Senft, R.L., Coughenour, M.B., Bailey, D.W., Rittenhouse, L.R., Sala, O.E., Swift, D.M., 1987. Large herbivore foraging and ecological hierarchies. *Bioscience* 37 (11), 789–799.
- Sfa, 2014. *Statistical yearbook of forestry 2014 (in Swedish) Skogsstatistisk årsbok 2014*. Swedish forest agency, Jönköping.
- SFA. 2018a. Skogsdataportalen, <http://skogsdataportalen.skogsstyrelsen.se/Skogsdataportalen/>. Swedish Forest Agency.
- SFA. 2018b. Viltskadepolicy. Swedish Forest Agency, <https://www.skogsstyrelsen.se/globalassets/bruka-skog/skogsskador/skogsstyrelsens-viltskadepolicy.pdf>.
- SFA. 2021. Statistikdatabas, <http://pxweb.skogsstyrelsen.se/pxweb/en/Skogsstyrelsens%20statistikdatabas/>. Swedish Forest Agency.
- Slu, 2020. Skogsdata 2020: Aktuella uppgifter om de svenska skogarna från Riksskogstaxeringen. Sveriges lantbruksuniversitet, Umeå.
- Smith, B.L., 2001. Winter feeding of elk in western North America. *J. Wildlife* 65 (2), 173. <https://doi.org/10.2307/3802896>.
- SOU. 2014. Bilaga 6 Utfodring och attityder till utfodring i Sverige. In: *Vildsvin och viltskador – om utfodring, kameraövervakning och arrendatorers jakträtt: delbetänkande*. ISBN: 978-91-38-24149-3. *in* S. Government, editor.
- Spake, R., Bellamy, C., Gill, R., Watts, K., Wilson, T., Ditchburn, B., Eigenbrod, F., Bennett, J., 2020. Forest damage by deer depends on cross-scale interactions between climate, deer density and landscape structure. *J. Appl. Ecol.* 57 (7), 1376–1390.
- Spitzer, R., 2019. *Trophic resource use and partitioning in multispecies ungulate communities*. Swedish University of Agricultural Sciences. Umeå. PhD thesis.
- Spitzer, R., Coissac, E., Felton, A., Fohringer, C., Juvany, L., Landman, M., Singh, N.J., Taberlet, P., Widemo, F., P.G.M. Crowsigt, J., 2021. Small shrubs with large importance? Smaller deer may increase the moose-forestry conflict through feeding competition over *Vaccinium* shrubs in the field layer. *For. Ecol. Manage.* 480, 118768. <https://doi.org/10.1016/j.foreco.2020.118768>.
- Spitzer, R., Felton, A., Landman, M., Singh, N.J., Widemo, F., Crowsigt, J.P.G.M., 2020. Fifty years of European ungulate dietary studies: a synthesis. *Oikos* 129 (11), 1668–1680. <https://doi.org/10.1111/oik.07435>.
- Timmons, G.R., Hewitt, D.G., DeYoung, C.A., Fulbright, T.E., Draeger, D.A., 2010. Does supplemental feed increase selective foraging in a browsing ungulate? *J. Wildl. Manage.* 74 (5), 995–1002. <https://doi.org/10.2193/2009-250>.
- van Beest, F.M., Loe, L.E., Mysterud, A., Milner, J.M., 2010. Comparative space use and habitat selection of moose around feeding stations. *J. Wildl. Manage.* 74 (2), 219–227. <https://doi.org/10.2193/2009-109>.
- Wallgren, M., Bergström, R., Bergqvist, G., Olsson, M., 2013. Spatial distribution of browsing and tree damage by moose in young pine forests, with implications for the forest industry. *For. Ecol. Manage.* 305, 229–238. <https://doi.org/10.1016/j.foreco.2013.05.057>.
- Wam, H.K., Hjeljord, O., 2010. Moose summer and winter diets along a large scale gradient of forage availability in southern Norway. *Eur. J. Wildl. Res.* 56 (5), 745–755. <https://doi.org/10.1007/s10344-010-0370-4>.
- Wam, H.K., Hjeljord, O., Solberg, E.J., 2010. Differential forage use makes carrying capacity equivocal on ranges of Scandinavian moose (*Alces alces*). *Can. J. Zool.* 88, 1179–1191. <https://doi.org/10.1139/z10-084>.
- Wam, H.K., Hofstad, O., 2007. Taking timber browsing damage into account: A density dependant matrix model for the optimal harvest of moose in Scandinavia. *Ecol. Econ.* 62 (1), 45–55. <https://doi.org/10.1016/j.ecolecon.2007.01.001>.