Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Predictors of browsing damage on commercial forests – A study linking nationwide management data

Sabine E. Pfeffer[a,*], Navinder J. Singh[a], Joris P.G.M. Cromsigt[a], Christer Kalén[b], Fredrik Widemo[a]

[a] Department of Wildlife, Fish and Environmental Studies, Swedish University of Agricultural Sciences, 901 83 Umeå, Sweden
[b] Swedish Forest Agency, P.O. Box 343, 501 13 Borås, Sweden

ABSTRACT

Population sizes and species distributions of wild ungulates in Europe have increased during the past decades, and continue to do so. As a result, browsing pressure in forests is increasing and concerns about the effects of increasingly common multi-species deer communities on forestry are rising. However, we currently lack an understanding of how the composition of deer communities affects browsing damage, particularly with respect to the role of species with different dietary requirements. Further, the relative importance of predictors of browsing damage in systems with multiple browsers remains elusive. Here, we used data from Swedish management, which is monitoring ungulates and their damage to forests, to test how deer densities, forage availability, and winter severity predict browsing damage on commercially important Scots pine (*Pinus sylvestris*) at national and regional scales. Moose (*Alces alces*) is the main browser of Scots pine, but competes with other deer over more preferred forage. During winter, a higher index of moose density was associated with higher browsing damage in northern Sweden, where there is low competition from other deer. In southern Sweden, competition from other deer is higher and a higher density index of roe deer (*Capreolus capreolus*) was associated with higher winter damage. However, there was no relationship between moose density and damage. We suggest that moose are forced to browse more pine due to interspecific competition over alternative forage resources in the south, yielding stronger relationships between densities of competing deer species and damage than between moose density and damage. Pine density, a proxy for forage availability, was an equally or more important determinant for browsing damage as deer density indices in most regions. Increasing pine density was associated with reduced browsing damage caused in winter in all regions and reduced damage caused in summer in central Sweden. Increased winter severity, as an index of snow depth, predicted increased winter damage in the northern region only. To reduce winter damage, our results suggest that management should consider deer densities and forage availability simultaneously, while adopting a multi-species approach. Results varied among regions, with densities of other deer being more relevant in the south and winter severity more relevant in the north. Management data did not predict summer damage well. Since national models did not capture regional variations, we conclude that management decisions and actions need to be tailored to the regional or local scale.

1. Introduction

Across Europe, deer numbers and species distributions have increased partly as a result of wildlife management actions, including adapted harvesting strategies, species (re)introductions, and translocations (Apollonio et al., 2010; Ferretti and Lovari, 2014). In parallel, human land-use has been intensified (Iacolina et al., 2019) and contributed to increasing deer numbers through improving forage availability and habitat suitability (Presley et al., 2019). While increasing deer populations may provide ecosystem services, e.g. through hunting or wildlife watching, at the same time population increases may lead to strong browsing and grazing pressures, limiting production in forestry and agriculture. As a result, human-wildlife conflicts have become increasingly evident (Reimoser and Putman, 2011).

In the boreal zone, even-aged forest management of conifers is the most profitable and commonly used forestry practice (Kuuluvainen et al., 2012; Chen et al., 2017). For deer, young forest stands resulting from regenerated clear-cut areas are a major source of forage. Due to high forage quantity, deer commonly concentrate their foraging to such stands (Kuijper et al., 2009; Bergqvist et al., 2018), where future

* Corresponding author.
  E-mail addresses: sabine.pfeffer@slu.se (S.E. Pfeffer), navinder.singh@slu.se (N.J. Singh), joris.cromsigt@slu.se (J.P.G.M. Cromsigt), christer.kalen@skogsstyrelsen.se (C. Kalén), fredrik.widemo@slu.se (F. Widemo).

production stems are especially susceptible to browsing damage from deer (Reimoser, 2003; Gerhardt et al., 2013).

Hofmann (1989) classified the main European deer species, including the species occurring in the boreal zone, into different feeding types. *Sensu* Hofmann (1989), moose (*Alces alces*) and roe deer (*Capreolus capreolus*) are concentrate selectors, foraging on trees, shrubs, and forbs, whereas red deer (*Cervus elaphus*) and fallow deer (*Dama dama*) are intermediate feeders, having a significant proportion of grass in their diet. However, all four species may shift their diets seasonally and generally increase the amount of woody plants in their winter diet (Mysterud, 2000; Spitzer et al., 2020). Based on this, one would expect moose and roe deer to affect forestry through summer and winter browsing, whereas the impact of intermediate feeders should be more severe during winter. Competition among these species may further affect their browsing patterns and thus levels of browsing damage (Spitzer, 2019). The relative importance of deer species and determinants of browsing damage may change depending on the composition of the deer community (Ferretti et al., 2011; Richard et al., 2010). Typically, studies on browsing damage have focused on the effect of one or two deer species in winter only (e.g. Ward et al., 2008; Bergqvist et al., 2014). A better understanding of damage patterns in multi-species deer communities is beneficial for wildlife management, as multi-species deer communities are becoming more complex and common.

In this study, we investigated the predictors of browsing damage in young forest stands across Sweden in a multi-species deer setting. We focused on damage to Scots pine (*Pinus sylvestris*, hereafter referred to as pine), which is an important production tree in the boreal zone. While not being the most preferred forage, pine is an important forage source especially for moose during winter (Cederlund et al., 1980; Shipley et al., 1998; Månsson et al., 2007b). Further, moose is the largest, most widely distributed, and after roe deer the second most common deer species in Sweden (Liberg et al., 2010). Therefore, conflicts between forestry and deer management have been centered on moose and pine in Scandinavia and the extensive scientific literature has mainly focused on the effects of moose during winter so far (e.g. Andrén and Angelstam, 1993; Danell et al., 2003; Månsson et al., 2007a). However, as elsewhere in Europe, the Swedish ungulate community has changed and multi-species communities are now more and more common, possibly increasing interspecific competition over forage (Spitzer, 2019). Results from some studies suggest that this may force moose to increase their use of pine in areas with high densities of competing smaller deer (Nichols and Spong, 2014; Spitzer, 2019). Further, browsing on pine has become more common during the vegetation period (Bergqvist et al., 2013) and moose has been shown to be the main browser of pine also in summer (Nichols and Spong, 2014; Spitzer, 2019). However, the importance of interspecific competition for determining levels of summer damage has not been investigated yet.

We combined data mainly collected for formulating plans in local moose management to investigate patterns and determinants of browsing damage caused during winter and summer. We did this both at the national and at the regional scale in Sweden in order to capture the strong latitudinal gradient in deer communities, land-use, and winter severity. We investigated the importance of the composition of the deer community for browsing damage on pine. We predicted a weaker relationship between moose density and browsing damage in areas where competing ungulate species are abundant. Two different, but not necessarily exclusive, mechanisms could explain this weaker relation. First, the relation would become weaker if the smaller deer species would be responsible for a larger share of browsing damage. Second, moose may increase their use of pine due to interspecific competition from smaller deer regardless of moose density (Spitzer, 2019). Furthermore, we determined the relative importance of deer densities, forage availability, and winter severity on browsing damage on pine in a multi-species setting. We predicted a stronger effect of winter severity in northern Sweden, where winters are coldest and longest. In southern Sweden, where densities of the smaller deer species

are highest, we predicted that the combined effect of all smaller deer would be larger than the effect of moose alone. Finally, we compared the predictors of browsing damage on pine caused during winter and summer. In general, we predicted the levels of summer damage to be lower than levels of winter damage. We also predicted that our deer density and forage availability indices would explain less variation in summer than in winter damage due to higher availability of alternative forage during summer.

Our approach exploits an opportunity to use management data for elucidating ecological relationships, whilst evaluating the potential for predicting the outcome of actions in local management using existing management data. We discuss the implications of our results for ungulate management in Sweden, which currently has a strong single- rather than multi-species focus.

2. Material and methods

2.1. Study system

In Sweden, the forestry sector is of high national importance due to the large exports of pulp, paper, and timber throughout the world (Swedish Forest Industries Federation, 2019). Simultaneously, Sweden holds one of the densest moose populations in the world (Jensen et al., 2020) and populations of other, smaller deer species are increasing (Danell and Bergström, 2010; Viltövervakningen, 2018). Multi-species ungulate communities exist in Sweden due to the natural distribution of native species (e.g. moose and roe deer), but also due to the introductions of non-native species (e.g. fallow deer) and translocations of native species (e.g. red deer) towards the north (Liberg et al., 2010).

In 2012, an adaptive co-management system was introduced for moose in Sweden with moose management areas (MMAs, in Swedish *Älgförvaltningsområde*) being the focal unit. The system's guidelines state that a MMA should cover an area equivalent to the distribution of at least one migratory moose population (Naturvårdsverket, 2011). Thus, the annual range use of local moose populations determines the size and boundaries of MMAs, in addition to geographical barriers and administrative borders (Naturvårdsverket, 2011). Reflecting differences in migration patterns, MMA sizes increase from the south towards the north (see Fig. 1). During the years of this study (2015 and 2016), Sweden was divided into 148 MMAs (Fig. 1).

First, we performed analyses at the national scale (all moose management areas; *n* = 148). However, due to Sweden's strong latitudinal and, thus, environmental and climatic gradient, we expected different ecological processes and drivers to play a role in different regions along this north–south gradient. To explore patterns at this regional scale and compare them to the national scale, we performed, in a second step, separate analyses for the three Swedish regions where *Norrland* (33 MMAs) represents northern Sweden, *Svealand* (61 MMAs) central-Sweden, and *Götaland* (54 MMAs) southern Sweden (Fig. 1). These three regions map geographical groupings often used by management institutions and forestry and follow the broad climatic and land-use gradient across the country.

2.2. Databases

We compiled information on browsing damage in young forest stands, deer density indices, forage availability across the landscape, and winter severity (see Table 1 for variables per category). Data used in this study was collected by several national institutions that are responsible for providing publicly available monitoring data on an annual basis (see Appendix, Table A.1). Where necessary, we aggregated data to the common scale of MMAs (see Sections 2.2.2 and 2.2.4 for further description). We present a national overview of the raw data per MMA for each variable used in Appendix, Fig. A.1-4 and list mean values at the national and regional scale in Table 1.
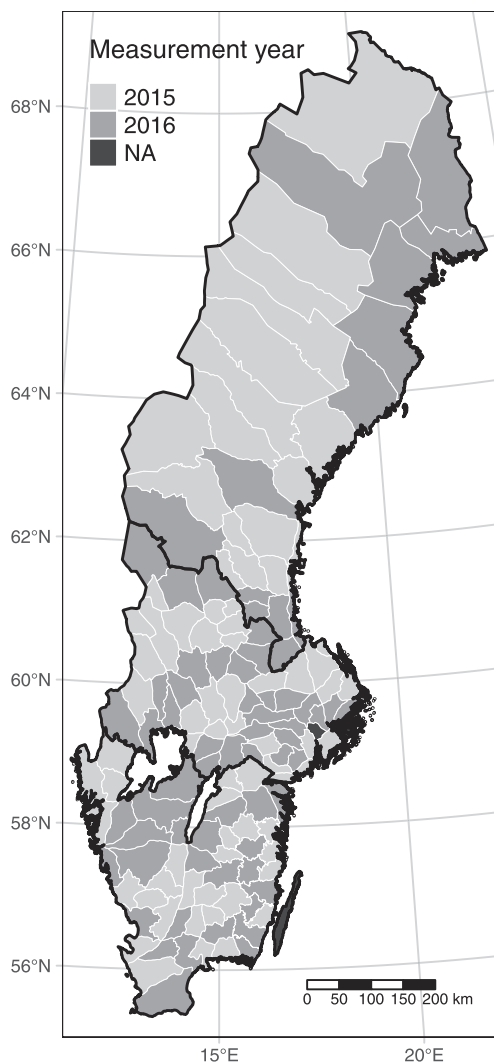
Fig. 1. Sweden and its moose management areas (MMA, *n* = 148; white outlines) during the hunting season of 2015/16. MMA sizes vary considerably from ~22,500 ha to ~3,000,000 ha. Black outlines divide the country into its regions *Norrland* (northern region; *n* = 33), *Svealand* (center region; *n* = 61), and *Götaland* (southern region; *n* = 54). Different grey scales highlight the measurement year of the browsing damage inventory per MMA.

2.2.1. Browsing damage inventory

Since the year 2000, the Swedish Forest Agency (SFA, *Skogsstyrelsen*) carries out a 'moose browsing inventory' (*Älgbetesinventering*). The inventory assesses browsing on trees in young forest stands. However, browsing on lateral shoots is not recorded, as the main target of the inventory originally was to monitor browsing that affects wood quality negatively. Thus, three types of damage are recorded for the central stem of the tree; browsed apical leader (top shoot), stripped bark, and broken stem. These three types of damage affect the quality of the butt log and thus reduce wood quality (Liberg et al., 2010). In this study, we refer to 'browsing' damage if stems showed at least one of the three types of damage since top shoot browsing is most common (Roberge et al., 2012). Although the inventory was designed to capture mainly moose damage, browsing by other species, such as red deer, cannot be excluded based on the visual assessment (Nichols et al., 2012). Thus, the main objective of the inventory is to record the amount of damaged stems by deer in young forest stands (Skogsstyrelsen, 2016). Here, we refer to the scheme as a 'browsing damage inventory' rather than a 'moose browsing inventory'.

Table 1

Detailed information on response variables of the category 'browsing damage' and explanatory variables of the categories 'deer density indices', 'forage availability', and 'winter severity' based on the measurement years of the browsing damage inventory. Original resolution, sample size (*n*) representing the number of moose management areas (MMAs) with available data, measurement unit, transformed unit for analyses, and mean (± SD) values at the national and regional scale according to the transformed units are listed per variable. Values presented for all explanatory variables are set in relation to the analyses of winter damage (2014/15–2015/16). Values for analyzing summer damage (2013/14–2014/15) were quantitatively similar.

Category	Variable	n	Measurement unit	Original resolution	Unit for analyses	Sweden	Norrland	Svealand	Götaland
Browsing damage	Winter damage	145	Prop. damaged stems	MMA	Prop. damaged stems	0.118 (± 0.078)	0.084 (± 0.043)	0.105 (± 0.061)	0.154 (± 0.097)
	Summer damage	143	Prop. damaged stems	MMA	Prop. damaged stems	0.051 (± 0.061)	0.034 (± 0.050)	0.052 (± 0.063)	0.061 (± 0.063)
Deer density indices	Moose observations	135	Seen animals h^{-1}	MMA	Seen animals h^{-1}	0.066 (± 0.020)	0.055 (± 0.014)	0.067 (± 0.014)	0.072 (± 0.025)
	Moose harvest	148	Shot animals	MMA	Shot animals 1000 ha^{-1}	2.30 (± 0.87)	2.44 (± 1.00)	2.14 (± 0.70)	2.40 (± 0.99)
	Roe deer harvest	148	Shot animals	Hunting district	Shot animals 1000 ha^{-1}	4.80 (± 3.58)	0.99 (± 1.12)	3.68 (± 2.39)	8.38 (± 2.16)
	Red deer harvest	148	Shot animals	Hunting district	Shot animals 1000 ha^{-1}	0.48 (± 1.28)	0.01 (± 0.03)	0.69 (± 1.53)	0.53 (± 1.25)
	Fallow deer harvest	148	Shot animals	Hunting district	Shot animals 1000 ha^{-1}	1.86 (± 5.01)	0.00 (± 0.00)	2.33 (± 6.47)	2.46 (± 4.41)
Forage availability	Pine density	145	Stems ha^{-1}	MMA	Stems ha^{-1}	738.4 (± 521.3)	1156.3 (± 448.7)	848.0 (± 496.0)	356.2 (± 284.6)
	Birch density	145	Stems ha^{-1}	MMA	Stems ha^{-1}	2973.0 (± 1557.6)	1844.8 (± 841.8)	2920.0 (± 1445.9)	3734.5 (± 1596.4)
	Young forest area	148	ha	MMA	Proportion	0.077 (± 0.037)	0.089 (± 0.036)	0.075 (± 0.027)	0.072 (± 0.045)
Winter severity	Temperature < 0 °C	148	Daily values	Weather station	Proportion	0.175 (± 0.124)	0.328 (± 0.126)	0.169 (± 0.089)	0.090 (± 0.043)
	≥10 cm snow	148	Daily values	Weather station	Proportion	0.241 (± 0.240)	0.513 (± 0.242)	0.223 (± 0.159)	0.096 (± 0.170)
	≥20 cm snow	148	Daily values	Weather station	Proportion	0.143 (± 0.203)	0.397 (± 0.261)	0.117 (± 0.114)	0.017 (± 0.037)
	≥30 cm snow	148	Daily values	Weather station	Proportion	0.091 (± 0.177)	0.305 (± 0.258)	0.053 (± 0.086)	0.003 (± 0.013)

Since 2015, young forest stands are monitored annually in roughly half of the MMAs per county after snowmelt and before bud burst of deciduous trees (approx. April in southern Sweden and June in northern Sweden). However, in the two northern-most counties, all MMAs are monitored each year. Combining the years 2015 and 2016 gave us the first available complete dataset for all but three MMAs (see Appendix, Table A.2) using a new standardized methodology. In previous years, different regions used different methods. When MMAs were measured in both years ($n = 13$), we randomly selected data from one of the two years (see Appendix, Table A.2). This resulted in a dataset of 75 MMAs measured in 2015 and 70 MMAs in 2016 covering 145 out of 148 MMAs (Fig. 1). There were no significant differences between the two years in winter damage across (Beta regression, $z = 0.98$, $p = 0.33$) or within regions (Beta regressions, $z \leq 1.32$, $p \geq 0.19$). Summer damage between the two years differed across regions (Beta regression, $z = 2.15$, $p = 0.03$), however only within *Norrland* (Beta regression, $z = 2.38$, $p = 0.02$), but not within *Svealand* or *Götaland* (Beta regression, $z \leq 1.82$, $p \geq 0.07$).

The SFA monitors browsing damage in young forest stands that have a mean height between 1 and 4 m and a size of at least 0.5 ha (see Appendix B.1 for detailed description of stand selection). Selected young forest stands contain up to 15 sampling plots, with a sampling area of 38.5 m^2 (radius = 3.5 m) each. In each sampling plot, browsing damage is recorded as either 'winter damage' (from last winter; considered as fresh damage), 'summer damage' (from the vegetation period preceding last winter; summer top shoot browsing is visible as damage on not yet lignified top shoot), or old damage (from earlier years). Browsing damage above the height of 0.3 m is recorded on all coniferous stems, which are taller than half of the average height of the two tallest coniferous trees per sampling location. Thus, browsing damage is not recorded on short stems that potentially are outcompeted and unlikely to contribute to future wood biomass. In 2015 and 2016, stems were also sub-evaluated as future production stems (i.e. estimated as retained after future pre-commercial thinning). Winter damage on pine production stems correlated positively to winter damage on all pine stems (Pearson's $r > 0.9$). We focused our analysis on damaged production stems only, since production stems are economically most important to forest owners. Summer damage was only recorded for production stems. We used the proportion of damaged production stems as response variable for winter and summer damage since the proportion of damaged stems is the main damage variable presented by the SFA and is the indicator of acceptable browsing damage used in Swedish management, including setting moose harvest quotas. The forestry sector and the SFA have stated an official target of maximum 5% annual browsing damage (winter + summer) on pine trees in young forests. For comparisons, we present the mean absolute numbers of all and damaged pine production stems in Appendix, Table A.3. We analyzed the effects on winter and summer damage separately.

2.2.2. Deer density indices

We used harvest data reported by hunters as an index of population density per deer species. As moose harvest goals are influenced by the results of the browsing damage inventory, there might be a causal link between browsing damage and moose harvest. Thus, moose harvest might not be an ideal proxy for estimating moose density when the aim is to predict browsing damage as in this study. However, moose harvest has been suggested to be a good predictor of moose density (Ueno et al., 2014). The issue of causality is less obvious for the other deer species since hunters do not use damage data for setting harvest quotas of these smaller deer species. To be able to compare results among species, we ran analyses with harvest data for all species including moose. In addition, we included moose observations (*Älgobs*) as an independent index of moose density. Moose observations are based on the records of moose seen during the start of the hunting season by Swedish hunters (for details see Ericsson and Kindberg, 2011; Singh et al., 2014) and are used within management to track changes in moose populations inside

management areas and units (Ericsson and Kindberg, 2011). Spatial variation in detectability due to differences in visibility caused by varying topography and forest cover may result in biases when using moose observations to predict moose densities across monitoring units, even though the relation between moose observations and actual density is generally positive (Ericsson and Wallin, 1999). Thus, neither of the two indices of moose density may be ideal for predicting actual moose density or the relationship between density and damage. However, these are the only two measures widely available to us and constitute what is being used in management for setting harvest goals in an attempt to reduce damage. Therefore, we included both moose observations and moose harvest as indices of moose density in our models.

We extracted absolute moose harvest numbers and moose observations per observational hour for each MMA for the hunting seasons of 2014/15 and 2015/16 to link them to winter damage measured in 2015 and 2016, respectively. Additionally, we extracted absolute moose harvest numbers and moose observations per observational hour for each MMA for the hunting season of 2013/14. We linked data from the hunting seasons of 2013/14 and 2014/15 to summer damage caused in 2014 and 2015, respectively. We had to exclude 11 of the 148 MMAs (see Appendix, Table A.2) from models predicting winter and summer damage using moose observations as explanatory variable due to insufficient numbers of observational hours (< 5000 h, see Ericsson and Kindberg, 2011).

For roe deer, red deer, and fallow deer, we extracted absolute harvest numbers from hunting reports for the hunting seasons of 2014/15 and 2015/16 per hunting district (*Jaktvårdskrets*; $n = 322$) to link them to winter damage measured in 2015 and 2016, respectively. Additionally, we extracted absolute harvest numbers for each hunting district for the hunting season of 2013/14. We linked data from the hunting seasons of 2013/14 and 2014/15 to summer damage caused in 2014 and 2015, respectively. Since hunting district borders do not always overlap directly with MMA borders, we assumed an equal hunting pressure within each hunting district and used the proportion of terrestrial overlap between hunting districts and MMAs to assign harvest numbers per MMA (see Appendix B.2 and B.3 for detailed method descriptions). We transformed absolute harvest numbers of roe deer, red deer, fallow deer, and moose to harvest 1000 ha^{-1} per terrestrial land per MMA.

2.2.3. Forage availability

For each MMA, we used three proxies for forage availability; stem densities of pine and birch (*Betula* sp.) in young forest stands and the proportion of young forest area. Stem densities were monitored as part of the SFA's browsing damage inventory per young forest stand. Data on young forest area per MMA were available in 2016 from the SFA's forage prediction analyses (*Foderprognos*). The SFA uses satellite imagery to estimate the area of young forest stands per MMA, defined as stands with an average height between 1 and 6 m. We calculated the proportion of young forest area based on the terrestrial area per MMA (see Appendix B.2 for detailed method description).

2.2.4. Winter severity

We used snow depth and temperature during winter (Oct–April) as proxies for winter severity. We extracted daily values of snow depth and maximum temperature from the nearest weather station of the Swedish Meteorological and Hydrological Institute (*SMHI*) to the centroid of each MMA. Since most weather stations had winter days where data on snow depth was missing, we calculated a winter severity index as the number of days with snow in relation to the total number of days with snow data available for each weather station during the winters of 2014/15 and 2015/16. We did this for three different snow depths; days with ≥10 cm, ≥20 cm, and ≥30 cm of snow. For temperature, we calculated a winter severity index as the number of days with a maximum temperature below 0 °C in relation to the total number of days during winter. We did not test for winter severity when predicting

summer damage. Thus, we matched winter severity from 2014/15 to damage data measured in 2015 and winter severity from 2015/16 to damage data measured in 2016.

2.3. Statistical analyses

For all statistical analyses, we used the software R 3.6.2 (The R Foundation, 2019) and a significance level of alpha = 0.05.

2.3.1. Winter damage

'Winter damage' captured the proportion of pine production stems that were damaged by deer during the winter preceding the measurement. We applied beta regression models using the *betareg* function of the same-named package (Cribari-Neto and Zeileis, 2010), which is appropriate for analyzing response variables within the standard unit interval (0, 1). To be able to compare the relative influence of each explanatory variable, we standardized explanatory variables according to the z-score transformation in all statistical models (Abdi, 2007). To identify patterns at the national scale, the initial model comprised all explanatory variables representing deer density indices and forage availability. Additionally, the initial model contained either temperature or one of the three categories for snow depth as index for winter severity; meaning that the effects of temperature and different snow depths on winter damage were tested separately due to strong correlations between variables of winter severity (see Appendix, Table C.1). Further, we tested strongly correlated explanatory variables (Pearson's r ≥ +0.7 or ≤–0.7; see Appendix, Table C.1) in separate models including all other variables. For all modelling scenarios, we adopted a stepwise deletion approach and verified the removal of variables with likelihood ratio tests. If ΔAIC was < 2, we selected the more parsimonious model. To identify if patterns at the regional scale differed from the national scale, we repeated the same stepwise deletion procedure as described above for each of the three regions.

The proportion of winter days with ≥10 cm and ≥20 cm did not significantly explain winter damage independent of spatial context. Thus, we present only the results including the proportion of winter days with ≥30 cm of snow (in the remainder of the paper referred to as 'snow depth'). Independent of scale, modelling scenarios with temperature as index for winter severity revealed similar results as models with snow depth. Thus, we presented only the effects of snow depth as index for winter severity on winter damage. Model selection tables for winter damage are presented in Appendix, Table D.1.

2.3.2. Summer damage

'Summer damage' captured the proportion of pine production stems that were damaged by deer during the growing season preceding last winter. For summer damage, we used the same analysis approach as described for winter damage. However, since data on summer damage contained several 0-values, we transformed data according to [y · (n - 1) + 0.5] / n, where *n* is sample size, when applying a beta regression (Smithson and Verkuilen, 2006). Winter severity was not included in analyses on summer damage. Correlation coefficients and model selection tables for summer damage are presented in Appendix, Table C.2 and D.2, respectively.

3. Results

3.1. General patterns in deer density indices

There was a general decreasing pattern of deer density indices from south to north (Appendix, Fig. A.2). Moose observations differed regionally (Kruskal-Wallis, $\chi^2 \geq 13.50$, $p \leq 0.001$), with lower observations in *Norrland* compared to *Svealand* (Mann-Whitney *U* test, $p \leq 0.001$) and *Götaland* (Mann-Whitney *U* test, $p \leq 0.0014$), respectively. Moose observations and moose harvest were weakly correlated at the national scale (n = 137, Pearson's r > 0.28, $p \leq 0.001$). Roe deer harvest varied across all regions (Kruskal-Wallis, $\chi^2 \geq 97.59$, $p < 0.0001$), with lower harvest in *Norrland* than in *Svealand* (Mann-Whitney *U* test, $p < 0.0001$) and higher harvest in *Götaland* than in *Svealand* (Mann-Whitney *U* test, $p < 0.0001$). Red deer harvest varied in a similar manner across Sweden (Kruskal-Wallis, $\chi^2 \geq 28.77$, $p < 0.0001$), with lower harvest in *Norrland* as compared to *Svealand* (Mann-Whitney *U* test, $p < 0.0001$) and *Götaland* (Mann-Whitney *U* test, $p < 0.0001$), respectively. Similarly, fallow deer harvest varied across all three regions (Kruskal-Wallis, $\chi^2 \geq 58.06$, $p < 0.0001$), with the lowest harvest in *Norrland*, higher in *Svealand* than in *Norrland* (Mann-Whitney *U* test, $p < 0.0001$) and higher in *Götaland* than in *Svealand* (Mann-Whitney *U* test, $p \leq 0.01$). No other pairwise comparisons of density indices between regions were significant.

3.2. Drivers of winter damage

Winter damage differed across the three Swedish regions (Appendix, Fig. A.1), with higher winter damage in *Götaland* as compared to *Svealand* (Beta regression, z = 3.05, p = 0.003) and *Norrland* (Beta regression, z = 3.80, p = 0.0001), respectively. There was a tendency

Table 2
Estimates including standard errors (SE), z- and p-values for explanatory variables after model selection of a beta regression with winter damage on Scots pine (*Pinus sylvestris*) as response variable. *Sweden* represents the final model on the national scale (all MMAs), whereas *Norrland*, *Svealand*, and *Götaland* represent the final model per Swedish region from north to south. p-values ≤0.05 are marked in bold.

Explanatory Variables	Sweden n = 145			Norrland n = 31			Svealand n = 59			Götaland n = 53		
	Estimate (SE)	z-value	*p*	Estimate (SE)	z-value	*p*	Estimate (SE)	z-value	*p*	Estimate (SE)	z-value	*p*
Moose observations [h^{-1}]	·	·	·	0.25 (0.11)	2.32	**0.020**	·	·	·	·	·	·
Moose harvest [1000 ha^{-1}]	·	·	·	·	·	·	·	·	·	·	·	·
Roe deer harvest [1000 ha^{-1}]	0.25 (0.07)	3.63	**< 0.001**	·	·	·	·	·	·	0.35 (0.09)	4.02	**< 0.001**
Red deer harvest [1000 ha^{-1}]	·	·	·	·	·	·	·	·	·	0.17 (0.09)	1.85	0.064
Fallow deer harvest [1000 ha^{-1}]	·	·	·	–	–	–	·	·	·	·	·	·
Pine density [ha^{-1}]	-0.23 (0.07)	-3.25	**0.001**	-0.26 (0.10)	-2.51	**0.012**	-0.18 (0.08)	-2.49	**0.013**	-0.26 (0.09)	-2.86	**0.004**
Birch density [ha^{-1}]	·	·	·	·	·	·	·	·	·	·	·	·
Prop. young forest area	0.09 (0.04)	1.99	**0.047**	·	·	·	·	·	·	·	·	·
Prop. days with ≥30 cm snow	0.14 (0.06)	2.28	**0.022**	0.27 (0.11)	2.48	**0.013**	·	·	·	·	·	·
r^2		0.271			0.211			0.086			0.420	

'·' for explanatory variables that were included in the starting model but were removed during model selection. '–' for explanatory variables that were not included into the starting model: fallow deer harvest was excluded in the modelling for 'Norrland' due to the absence of the species in most MMAs and no expected ecological effect. Red deer and fallow deer harvest were tested independent of each other in the modelling for 'Svealand' due to Pearson's r > 0.7. Both did not influence the final model. For details on Pearson correlation coefficients, see Appendix, Table C.1. Model selection tables are presented in Appendix, Table D.1.

for a higher level of winter damage in *Svealand* as compared to *Norrland* (Beta regression, $z = 1.71$, $p = 0.09$).

Independent of spatial context, winter damage in 2015 and 2016 decreased with increasing pine density (Table 2). Additionally, winter damage increased with increasing roe deer harvest, the proportion of young forest area, and snow depth at the national scale (Table 2). Pine density and roe deer harvest predicted winter damage to a similar degree (Table 2). However, the proportion of young forest area and snow depth only predicted winter damage about half as much as pine density and roe deer harvest (Table 2). Together, the four variables explained 27.1 % variation in the observed winter damage to pine. In *Norrland*, winter damage increased with increasing moose observations and snow depth (Table 2). Both variables predicted winter damage to a similar degree as pine density (Table 2). The three explanatory variables explained 21.1 % variation in winter damage in *Norrland*. In *Svealand*, pine density was the only significant predictor on winter damage (Table 2). Pine density explained 8.6 % variation in winter damage in *Svealand*. In *Götaland*, winter damage increased with increasing roe deer harvest, which predicted winter damage about ⅓ more than pine density (Table 2). Together with the non-significant effect of red deer harvest, these variables explained 42.0 % variation in winter damage in *Götaland*.

3.3. Drivers of summer damage

Levels of summer damage were lower than levels of winter damage across regions (Beta regression, $z = 2.42$, $p = 0.015$), especially within *Götaland* (Beta regression, $z = 2.18$, $p = 0.03$). There was a tendency for a lower level of summer damage compared to winter damage in *Norrland* (Beta regression, $z = 1.86$, $p = 0.06$). Winter and summer damage were weakly correlated (n = 143, Pearson's r = 0.23, $p = 0.006$). Levels of summer damage did not differ across regions (Appendix, Fig. A.1), but showed a tendency for a higher level of summer damage in *Götaland* as compared to *Norrland* (Beta regression, $z = 1.82$, $p = 0.07$).

For summer damage, pine density was the only significant predictor. Summer damage in 2014 and 2015 decreased with increasing pine density but only at the national scale and in *Svealand* explaining 6.3% and 18.6% of the variation, respectively. In *Norrland* and *Götaland*, none of the tested variables showed a significant effect on summer damage (Table 3).

4. Discussion

Our analyses on the determinants of browsing damage showed that pine density is one of the most important predictors of browsing damage at the national scale, as well as across regions for winter damage and partly for summer damage. However, other variables that are important at the national scale did not affect browsing damage consistently across regions. Instead, our analyses yielded different results per region and no regional result matched the results from the analyses at the national scale. For each region, management decisions based solely on national analyses would either incorporate non-significant regional effects or omit significant regional effects. This was true both for winter and for summer damage. Given the pronounced latitudinal gradient in the composition and density of deer communities, land-use, forest composition, and climate, these differences are not surprising. For these reasons, we focus the discussion on the results of our regional analyses and patterns.

4.1. Deer communities and density indices

The deer community was dominated by moose in *Norrland*, whereas deer communities in *Svealand* and *Götaland* were dominated by the smaller deer species. In *Norrland*, winter damage increased with increasing moose observations. We did not find a relationship between moose harvest and browsing damage regardless of spatial scale. In *Svealand*, deer density indices and damage levels were intermediate. However, our deer density indices did not explain browsing damage in *Svealand*. In *Götaland*, where overall deer densities and damage levels were highest, winter damage increased with increasing roe deer harvest. Further, we found a trend between winter damage and red deer harvest, both increasing in relation to each other, while there was no relationship with the indices of moose density. Thus, our results support our prediction of a weaker effect of moose density on browsing damage in the presence of other deer species partly competing over the same food resources (Spitzer et al., 2020). The effect of the smaller deer species, in particular roe deer, was larger than the effect of moose alone. We did not find any effects of fallow deer, even though fallow deer densities can be high at some locations. This might be an effect of aggregated distributions of fallow deer, with few moose management areas containing high densities during this study.

From our results, we cannot say whether roe deer and potentially red deer indirectly forced moose to browse more pine *per capita* due to competition over alternative food resources or whether these species

Table 3

Estimates including standard errors (SE), z- and p-values for explanatory variables after model selection of a beta regression with summer damage on Scots pine (*Pinus sylvestris*) as response variable. *Sweden* represents the final model on the national scale (all MMAs), whereas *Norrland*, *Svealand*, and *Götaland* represent the final model per Swedish region from north to south. Deer density indices were extracted one year prior to the browsing damage inventory and thus marked with 'S' indicating 'summer'. p-values ≤ 0.05 are marked in bold.

Explanatory Variables	Sweden n = 143			Norrland n = 31			Svealand n = 59			Götaland n = 52		
	Estimate (SE)	z-value	*p*	Estimate (SE)	z-value	*p*	Estimate (SE)	z-value	*p*	Estimate (SE)	z-value	*p*
Moose observations^S [h^{-1}]	·	·	·	·	·	·	·	·	·	-0.22 (0.13)	-1.69	0.092
Moose harvest^S [1000 ha^{-1}]	·	·	·	·	·	·	·	·	·	0.23 (0.14)	1.66	0.098
Roe deer harvest^S [1000 ha^{-1}]	·	·	·	·	·	·	·	·	·	·	·	·
Red deer harvest^S [1000 ha^{-1}]	·	·	·	·	·	·	·	·	·	·	·	·
Fallow deer harvest^S [1000 ha^{-1}]	·	·	·	–	–	–	·	·	·	·	·	·
Pine density [ha^{-1}]	-0.18 (0.07)	-2.48	**0.013**	·	·	·	-0.29 (0.11)	-2.57	**0.010**	·	·	·
Birch density [ha^{-1}]	·	·	·	·	·	·	·	·	·	·	·	·
Prop. of young forest area	·	·	·	0.18 (0.17)	1.06	0.29	·	·	·	·	·	·
r^2		0.063			0.029			0.186			0.069	

'·' for explanatory variables that were included in the starting model but were removed during model selection. '–' for explanatory variables that were not included into the starting model: fallow deer harvest was excluded in 'Norrland' due to the absence of the species in most MMAs and no expected ecological effect. Red deer and fallow deer harvest were tested independent of each other in the modelling for 'Svealand' due to Pearson's r > 0.7. Both did not influence the final model. For details on Pearson correlation coefficients, see Appendix, Table C.2. Model selection tables are presented in Appendix, Table D.2.

increased damage directly by browsing on pine in *Götaland*. Data on the diet of the different deer species from Sweden shows that moose is the deer species whose diet contains most pine (Cederlund et al., 1980; Spitzer, 2019). Even though pine is also observed in roe deer diets (Spitzer, 2019), roe deer are smaller in size and damage caused by roe deer is unlikely to be detected in the investigated browsing damage inventory, which focuses on monitoring damage from the larger moose in taller stands. Studies of browsing on deciduous trees show that red deer may browse at heights covered by the browsing damage inventory (Nichols et al., 2015), but DNA analyses of browsed pine in an area with increasing red deer densities in *Götaland* showed that moose caused most of the damage on pine (Nichols and Spong, 2014). Thus, we suggest that the increased browsing damage in southern Sweden observed in this study probably mainly is a direct effect of moose browsing, but may result from interspecific competition over shared forage resources from roe deer and red deer. Moose is the deer species most restricted in diet diversity, which may make moose populations sensitive to the influx of large numbers of deer with different foraging preferences (Spitzer et al., 2020). With increasing densities of the smaller deer species, moose diets have been shown to contain more pine and less *Vaccinium spp.* potentially due to interspecific competition (Spitzer, 2019). To disentangle the direct and indirect effects of the different deer species, further research is needed. However, regardless of whether the increased damage is a result of direct or indirect mechanisms, or both, our results suggest that management of damage levels on pine at the tested scale requires more focus and potential direct actions in terms of regulations of populations of sympatric deer species, rather than of moose alone.

4.2. The relative importance of deer density, forage availability, and winter severity

Some studies suggested negative impacts of deer densities on tree regeneration and wood quality (Månsson, 2009; Hothorn and Müller, 2010; Chevrier et al., 2011; Rao, 2017). Other studies suggested that forage availability may play a crucial role in determining levels of browsing damage (Nevalainen et al., 2016; Bergqvist et al., 2018). In accordance with previous studies from Sweden (Andrén and Angelstam, 1993; Månsson et al., 2007a; Wallgren et al., 2013), Norway (Herfindal et al., 2015), and Finland (Nevalainen et al., 2016), our results support that winter browsing on pine decreases with increasing pine density, as an index of forage availability in young forest stands. In contrast to Bergqvist et al. (2013), we also found that an increasing pine density is associated with decreasing summer damage in *Svealand*. With increasing tree densities, the effect of browsing is diluted by a higher forage availability (Bergqvist et al., 2014; Díaz-Yáñez et al., 2017). In our analyses, pine density was one of the most important predictors being an equally or more important determinant for winter and summer damage on pine as compared to deer density indices in all regions, except for winter damage in *Götaland* where the effect of roe deer harvest was larger than the effect of pine density. Our results support previous findings from southern and central Sweden, showing that pine availability is a more important predictor of pine damage than moose densities (Månsson, 2009; Bergqvist et al., 2014). However, taking the complete deer community into account, deer densities and pine availability appear to have comparable effects on winter damage in most regions.

Pine is not the most preferred forage by moose (Månsson et al., 2007b). Thus, adapting forest management to increase alternative forage in the landscape can also reduce damage and thus wildlife-forestry conflicts (Kuijper, 2011). However, within the Swedish management system, measures of alternative forage are limited in detail. Forage availability is assessed mainly by measuring the area of young forest stands inside moose management areas. We did not find any relationships between this measure and levels of damage in our regional analyses. We suggest that monitoring forage availability in greater

detail might provide a better understanding and predictive power. In particular, the shrub layer appears to be a very important source of food for all deer (Spitzer, 2019). Monitoring the shrub layer would be a valuable addition.

In *Norrland*, snow depth explained as much variation in damage as pine density as well as moose observations, respectively. This was expected as snow cover is most frequent in this region in comparison to southern regions. We found no consistent effect of 'days with snow depth above 10 cm or 20 cm'. However, we found corresponding patterns for the highly correlated variables 'days with snow depth above 30 cm' (i.e. snow depth) and 'days with temperature below zero'. We suggest that the detected effects come mainly from the snow accumulation, which impedes animal movements and the accessibility to forage within the field layer (e.g. dwarf shrubs) for large herbivores (Visscher et al., 2006; Allen et al., 2016). Thus, available tree species such as pine are browsed even if they are not the most preferred food resource (Månsson et al., 2007b), but simply because they are among the few resources available with increasing snow depth. Forage limitation due to snow might be comparable with a limited amount of forage due to resource competition among co-existing deer species, which leads to increased winter damage to pine. Also, energy expenditure of deer is higher when snow depth increases (Gerhardt et al., 2013), making it more efficient for moose to spend more time in young pine stands with more available forage per hectare to reduce movement.

4.3. Comparing winter and summer damage

As predicted, levels of summer damage on pine were lower than levels of winter damage. This is likely due to the increased availability of alternative and more preferred forage during the vegetation period (Herfindal et al., 2015) and species diversifying their space use and diets, especially with the availability of agricultural crops (Allen et al., 2016; Spitzer, 2019). A more diverse number of environmental as well as land-use factors may therefore influence browsing patterns in summer as opposed to winter. As expected, our results support this with summer damage models having a lower explanatory power than winter damage models. Further, this may partly be a result due to a more difficult determination of the damage agent (e.g. deer, insect, etc.) almost one year after the damage occurred. Our models explained similar levels of variation in winter damage as compared to previous studies (Månsson et al., 2007a; Bergqvist et al., 2014) at most scales.

There was only a weak correlation between winter and summer damage, suggesting that different factors influence summer and winter damage, respectively. Monitoring winter and summer damage separately may thus be of importance while considering a multi-species approach in order to understand determinants of damage on pine.

4.4. Combining data from different sources across spatial and temporal scales

Using management data allowed us to analyze the predictors of browsing damage on pine across all of Sweden and our results highlight the importance of adapting management to local and regional conditions. The conventional approach of collecting scientific data in limited study areas and trying to extrapolate the results to fit management needs would not have given us such a comprehensive understanding. Even though all variables were collected for management rather than research purposes, we believe that the quality of the data is high and relevant for the research questions we outline in this study. All datasets we used were collected according to clear protocols, in a highly repeatable manner gathering amounts of data deemed sufficient for making management decisions in validations of the methods. Further, the monitoring methods have been scientifically evaluated and data on deer density indices are validated by the responsible institutions (Rolander et al., 2011; SLU, 2020).

4.5. Management implications

Overall, 60–80% of the variation in damage often remained un-explained, indicating that there may be other important predictors that determine browsing damage or that random variation is high. Our results were arrived at using the same data used in management. Thus, the explanatory power of our models, and the relative importance of the different factors, may give an idea of the effect of management actions based on the same data.

Nevertheless, our results emphasize the importance of simulta-neously managing forage availability and deer densities for managing browsing damage on pine. Regulating moose numbers alone may not cause a corresponding decrease in relative damage. Successful man-agement of browsing damage may require the regulation of deer den-sities using a multi-species approach at the local and regional scale besides managing forage availability. Roe deer densities appear to have the strongest effects on damage levels in our study. Developing methods for monitoring the different deer species with higher precision and at the same scale might be an advantage to understand and regulate da-mage levels. Currently, a national management plan for moose and red deer in Sweden is being formulated at the national scale by the Swedish Environmental Protection Agency (*Naturvårdsverket*) and the SFA (Naturvårdsverket, 2018). This is good insofar as it is a step towards multi-species management, where moose and red deer are managed and potentially regulated in relation to one another. However, making re-gional management decisions based on national analyses across a large latitudinal gradient runs a considerable risk of targeting unimportant factors, while omitting factors that are important. Thus, management actions and plans need to be adapted to regional and local conditions in order to increase the likelihood of reducing damage.

Our results show the importance of pine density to regulate winter damage at the scale of the MMAs. However, in order to reduce browsing on pine, many individual forest owners are currently regenerating forests using less palatable spruce on sites more suitable for pine (Felton et al., 2019). We suggest that a joint effort collectively regenerating with pine on land suitable for pine regeneration would increase pine availability at the landscape level and, thus, might be beneficial for forest owners collectively. Such projects already exist (e.g. SFA's project 'Mera tall/More pine') and should be given a high priority by the re-sponsible institutions.

CRediT authorship contribution statement

Sabine E. Pfeffer: Conceptualization, Data curation, Formal ana-lysis, Writing - original draft, Visualization. **Navinder J. Singh:** Conceptualization, Writing - original draft, Funding acquisition. **Joris P.G.M. Cromsigt:** Conceptualization, Writing - review & editing, Funding acquisition. **Christer Kalén:** Provision of data, Writing - re-view & editing. **Fredrik Widemo:** Conceptualization, Formal analysis, Writing - original draft, Funding acquisition.

Declaration of Competing Interest

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

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2020.118597.

References

Abdi, H., 2007. Z-scores. In: Salkind, N. (Ed.), Encyclopedia of Measurement and Statistics. Sage, Thousand Oaks, California, pp. 1055–1058.

Allen, A.M., Månsson, J., Sand, H., Malmsten, J., Ericsson, G., Singh, N.J., 2016. Scaling up movements: from individual space use to population patterns. Ecosphere 7 (10), e01524. https://doi.org/10.1002/ecs2.1524.

Andrén, H., Angelstam, P., 1993. Moose browsing on Scots pine in relation to stand size and distance to forest edge. J. Appl. Ecol. 30 (1), 133–142. https://doi.org/10.2307/2404277.

Apollonio, M., Andersen, R., Putman, R., 2010. European Ungulates and their Management in the 21st Century. Cambridge University Press, Cambridge, UK.

Bergqvist, G., Bergström, R., Wallgren, M., 2013. Summer browsing by moose on Scots pine. Scand. J. For. Res. 28 (2), 110–116. https://doi.org/10.1080/02827581.2012.725767.

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 avail-ability, moose population density and site productivity. Silva Fennica 48 (1). 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. 419–420, 170–178. https://doi.org/10.1016/j.foreco.2018.03.049.

Cederlund, G., Ljungqvist, H., Markgren, G., Stålfelt, F., 1980. Foods of moose and roe deer at Grimsö in Central Sweden – Results of rumen content analyses. Grimsö Research Station, Swedish Wildlife Research 11, 169–247.

Chen, S., Shahi, C., Chen, H.Y.H., McLaren, B., 2017. Economic analysis of forest man-agement alternatives: Compositional objectives, rotation ages, and harvest methods in boreal forests. For. Policy Econ. 85, 124–134. https://doi.org/10.1016/j.forpol.2017.09.006.

Chevrier, T., Saïd, S., Widmer, O., Hamard, J.-P., Saint-Andrieux, C., Gaillard, J.-M., 2011. The oak browsing index correlates linearly with roe deer density: a new in-dicator for deer management? Eur. J. Wildl. Res. 58 (1), 17–22. https://doi.org/10.1007/s10344-011-0535-9.

Cribari-Neto, F., Zeileis, A., 2010. Beta Regression in R. J. Stat. Softw. 34 (2), 1–24. https://doi.org/10.18637/jss.v034.i02.

Danell, K., Bergström, R., 2010. Vilt, människa, samhälle. Liber AB, Stockholm.

Danell, K., Bergström, R., Edenius, L., Ericsson, G., 2003. Ungulates as drivers of tree population dynamics at module and genet levels. For. Ecol. Manage. 181, 67–76. https://doi.org/10.1016/s0378-1127(03)00116-6.

Díaz-Yáñez, O., Mola-Yudego, B., González-Olabarria, J.R., 2017. What variables make a forest stand vulnerable to browsing damage occurrence? Silva Fennica 51 (2). https://doi.org/10.14214/sf.1693.

Ericsson, G., Kindberg, J., 2011. Inventering för adaptiv älgförvaltning i älgförvaltningsområden (ÄFO) – Älgobservationer (Älgobs). Manual nr 2 · Version 1.0. Institutionen för vilt, fisk och miljö Sveriges lantbruksuniveristet, Umeå.

Ericsson, G., Wallin, K., 1999. Hunter observations as an index of moose Alces alces population parameters. Wildl. Biol. 5 (1), 177–185. https://doi.org/10.2981/wlb.1999.022.

Felton, A., Petersson, L., Nilsson, O., Witzell, J., Cleary, M., Felton, A.M., Björkman, C., Sang, Å.O., Jonsell, M., Holmström, E., 2019. The tree species matters: Biodiversity and ecosystem service implications of replacing Scots pine production stands with Norway spruce. Ambio 1–15. https://doi.org/10.1007/s13280-019-01259-x.

Ferretti, F., Lovari, S., 2014. Introducing aliens: problems associated with invasive exo-tics. In: Putman, R.J., Apollonio, M. (Eds.), Behaviour and Management of European Ungulates. Whittles Publishing, Dunbeath, UK, pp. 78–109.

Ferretti, F., Sforzi, A., Lovari, S., 2011. Behavioural interference between ungulate spe-cies: roe are not on velvet with fallow deer. Behav. Ecol. Sociobiol. 65 (5), 875–887. https://doi.org/10.1007/s00265-010-1088-8.

Gerhardt, P., Arnold, J.M., Hackländer, K., Hochbichler, E., 2013. Determinants of deer impact in European forests – A systematic literature analysis. For. Ecol. Manage. 310, 173–186. https://doi.org/10.1016/j.foreco.2013.08.030.

Herfindal, 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.

Hofmann, R.R., 1989. Evolutionary steps of ecophysiological adaptation and diversification of ruminants: a comparative view of their digestive system. Oecologia 78 (4), 443–457. https://doi.org/10.1007/bf00378733.

Hothorn, T., Müller, J., 2010. Large-scale reduction of ungulate browsing by managed sport hunting. For. Ecol. Manage. 260 (9), 1416–1423. https://doi.org/10.1016/j.foreco.2010.07.019.

Iacolina, L., Corlatti, L., Buzan, E., Safner, T., Šprem, N., 2019. Hybridisation in European ungulates: an overview of the current status, causes, and consequences. Mammal Rev. 49 (1), 45–59. https://doi.org/10.1111/mam.12140.

Jensen, W.F., Rea, R.V., Penner, C.E., Smith, J.R., Bragina, E.V., Razenkova, E., Balciauskas, L., Bao, H., Bystiansky, S., Csányi, S., Chovanova, Z., Done, G., Hackländer, K., Heurich, M., Jiang, G., Kazarez, A., Pusenius, J., Solberg, E.J., Veeroja, R., Widemo, F., 2020. A review of circumpolar moose populations with emphasis on Eurasian moose distributions and densities. Alces 56.

Kuijper, D.P.J., 2011. Lack of natural control mechanisms increases wildlife-forestry conflict in managed temperate European forest systems. Eur. J. Forest Res. 130 (6), 895–909. https://doi.org/10.1007/s10342-011-0523-3.

Kuijper, D.P.J., Cromsigt, J.P.G.M., Churski, M., Adam, B., Jędrzejewska, B., Jędrzejewski, W., 2009. Do ungulates preferentially feed in forest gaps in European temperate forest? For. Ecol. Manage. 258 (7), 1528–1535. https://doi.org/10.1016/j.foreco.2009.07.010.

Kuuluvainen, T., Tahvonen, O., Aakala, T., 2012. Even-aged and uneven-aged forest management in boreal Fennoscandia: a review. Ambio 41 (7), 720–737. https://doi.org/10.1007/s13280-012-0289-y.

Liberg, O., Bergström, R., Kindberg, J., Von Essen, H., 2010. Ungulates and their management in Sweden. In: Apollonio, M., Andersen, R., Putman, R. (Eds.), European Ungulates and their Management in the 21st Century. Cambridge University Press, Cambridge, UK, pp. 37–70.

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., Andrén, H., Pehrson, Å., Bergström, R., 2007a. Moose browsing and forage availability: a scale-dependent relationship? Can. J. Zool. 85 (3), 372–380. https://doi.org/10.1139/Z07-015.

Månsson, J., Kalén, C., Kjellander, P., Andrén, H., Smith, H., 2007b. 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.

Mysterud, A., 2000. Diet overlap among ruminants in Fennoscandia. Oecologia 124 (1), 130–137. https://doi.org/10.1007/s004420050032.

Naturvårdsverket, 2011. Naturvårdsverkets författningssamling 2011:7 - Naturvårdsverkets föreskrifter och allmänna råd om jakt efter älg och kronhjort. Swedish Environmental Protection Agency ISSN 1403-8234.

Naturvårdsverket, 2018. Uppföljning av mål inom älgförvaltningen - Redovisning av regeringsuppdrag. NV-08872-17. Swedish Environmental Protection Agency, Stockholm, Sweden.

Nevalainen, S., Matala, J., Korhonen, K., Ihalainen, A., 2016. Moose damage in National Forest Inventories (1986–2008) in Finland. Silva Fennica 50 (2). https://doi.org/10.14214/sf.1410.

Nichols, R.V., Cromsigt, 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.

Nichols, R.V., Konigsson, H., Danell, K., Spong, G., 2012. Browsed twig environmental DNA: diagnostic PCR to identify ungulate species. Mol. Ecol. Resour. 12 (6), 983–989. https://doi.org/10.1111/j.1755-0998.2012.03172.x.

Nichols, R.V., Spong, G., 2014. Ungulate browsing on conifers during summer as revealed by DNA. Scand. J. For. Res. 29 (7), 650–652. https://doi.org/10.1080/02827581.2014.960895.

Presley, S.J., Cisneros, L.M., Klingbeil, B.T., Willig, M.R., 2019. Landscape ecology of mammals. J. Mammal. 100 (3), 1044–1068. https://doi.org/10.1093/jmammal/gyy169.

Rao, S.J., 2017. Effect of reducing red deer *Cervus elaphus* density on browsing impact and growth of Scots pine *Pinus sylvestris* seedlings in semi-natural woodland in the Cairngorms, UK. Conserv. Evid. 14, 22–26.

Reimoser, F., 2003. Steering the impacts of ungulates on temperate forests. J. Nature Conserv. 10 (4), 243–252. https://doi.org/10.1078/1617-1381-00024.

Reimoser, F., Putman, 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.

Richard, E., Gaillard, J.-M., Saïd, S., Hamann, J.-L., Klein, F., 2010. High red deer density depresses body mass of roe deer fawns. Oecologia 163 (1), 91–97. https://doi.org/10.1007/s00442-009-1538-z.

Roberge, J.-M., Månsson, J., Edenius, L., Lindqvist, S., Ericsson, G., 2012. Vad visar inventeringar av älgskador och betestryck i skog? Nr 12 Sveriges lantbruksuniversitet.

Rolander, M., Kalén, C., Bergquist, J., 2011. Älgbetesinventering - Skogliga inventeringsmetoder i en kunskapsbaserad älgförvaltning 1 Swedish Forest Agency.

Shipley, L.A., Blomquist, S., Danell, K., 1998. Diet choices made by free-ranging moose in northern Sweden in relation to plant distribution, chemistry, and morphology. Can. J. Zool. 76 (9), 1722–1733. https://doi.org/10.1139/z98-110.

Singh, N.J., Danell, K., Edenius, L., Ericsson, G., 2014. Tackling the motivation to monitor: success and sustainability of a participatory monitoring program. Ecol. Soc. 19 (4). https://doi.org/10.5751/ES-06665-190407.

Skogsstyrelsen, 2016. Skogsstyrelsens Information om älgbetesinventeringen 2016. Swedish Forest Agency.

SLU, 2020. Manualer och rapporter [Online]. Swedish University of Agricultural Sciences. Available: https://www.slu.se/centrumbildningar-och-projekt/algforvaltning/manualer/ [accessed 2020-03-23].

Smithson, M., Verkuilen, J., 2006. A better lemon squeezer? Maximum-likelihood regression with beta-distributed dependent variables. Psychol. Methods 11 (1), 54. https://doi.org/10.1037/1082-989X.11.1.54.

Spitzer, R., 2019. Trophic resource use and partitioning in multispecies ungulate communities. Doctoral Thesis. Department of Wildlife, Fish and Environmental Studies, Swedish University of Agricultural Sciences, Umeå, Sweden, ISBN 978-91-7760-465-5.

Spitzer, R., Felton, A., Landman, M., Singh, N.J., Widemo, F., Cromsigt, J.P.G.M., 2020. Fifty years of European ungulate dietary studies: a synthesis. Oikos. https://doi.org/10.1111/oik.07435.

Swedish Forest Industries Federation, 2019. Facts and figures [Online]. Stockholm, Sweden. Available: https://www.forestindustries.se/forest-industry/facts-and-figures [accessed 2019-08-23].

The R Foundation, 2019. The R Project for Statistical Computing [Online]. The R Foundation. Available: https://www.R-project.org/ [accessed 2020-01-30].

Ueno, M., Solberg, E.J., Iijima, H., Rolandsen, C.M., Gangsei, L.E., 2014. Performance of hunting statistics as spatiotemporal density indices of moose (Alces alces) in Norway. Ecosphere 5 (2). https://doi.org/10.1890/es13-00083.1.

Viltövervakningen, 2018. Om Viltövervakning [Online]. Available: https://jagareforbundet.se/vilt/viltovervakning/om-viltovervakning/ [accessed 2020-02-03].

Visscher, D.R., Merrill, E.H., Fortin, D., Frair, J.L., 2006. Estimating woody browse availability for ungulates at increasing snow depths. For. Ecol. Manage. 222 (1–3), 348–354. https://doi.org/10.1016/j.foreco.2005.10.035.

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.

Ward, A.I., White, P.C.L., Walker, N.J., Critchley, C.H., 2008. Conifer leader browsing by roe deer in English upland forests: Effects of deer density and understorey vegetation. For. Ecol. Manage. 256 (6), 1333–1338. https://doi.org/10.1016/j.foreco.2008.06.034.