Associational relationships at multiple spatial scales affect forest damage by moose

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Abstract

Increasing abundance of large herbivores combined with changes in forestry practices has led to increased forest damage in many temperate and boreal forest areas. The role of alternative forage as a driver for browsing pressure on tree species important for forestry has received increased attention. However, actions to reduce damage through altering forage abundance must be carried out at spatial scales that correspond to the behavioral processes that generate the browsing pattern. We used a multi-scaled dataset on browse abundance and utilization in Southern Norway to assess how pine browsing damage was related to abundance and quality of browse measured at different spatial scales. Pine trees had a lower probability to be browsed at high pine abundance at all spatial scales. However, the abundance and quality of alternative browse was negatively related to pine browsing (i.e. associational resistance) at several spatial scales, with the highest explanatory power at the largest spatial scale.

Management actions to reduce pine browsing by moose should focus on facilitating high abundance of both pine and alternative high-quality browse, and should be carried out at sufficiently large spatial scales (moose home range scale or larger).

Key words: Alces alces; associational relationships; browsing; integrated management; moose; pine; Pinus sylvestris; spatial scale
Many populations of large herbivores have experienced large increase in abundance during recent decades following reduced abundance of natural predators, changes in harvesting strategies, and increased availability of food due to changes in human land use practices (Apollonio et al., 2010). In many areas this increase represents a re-establishment of previous densities of herbivores after decades of decline, and is in some cases considered positive for biodiversity conservation reasons or for the recreational or economic value associated with the herbivore species (Putman et al., 2011a). High abundances of large herbivores do, however, also come with costs, both from an ecological (Côté et al., 2004) and human perspective (Putman et al., 2011a, 2011b). For instance, some of the most valuable tree species for forest economy are also important forage for herbivores (e.g. Edenius et al., 2002; Milner et al., 2013; Tremblay et al., 2007), giving rise to increased human-wildlife conflicts (Putman et al., 2011a; Weisberg and Bugmann, 2003).

Perhaps the two most efficient actions to prevent forest damage by browsing herbivores – physical barriers around vulnerable forest stands or trees (e.g. Cutini et al., 2011; Ward et al., 2000) and reducing herbivore abundance by increasing harvesting (e.g. Hothorn and Müller, 2010) – are both costly and may have unwanted ecological and economic side-effects (Kuijper, 2011). Altering the local browsing pressure by changing the amount and/or spatial distribution of forage has therefore received increased interest (Heikkilä and Härkönen, 1996; Mathisen et al., 2014; Putman and Staines, 2004; van Beest et al., 2010). While supplementary feeding can be expensive and logistically challenging, the natural food base can be altered as part of standard silvicultural practices such as pre-commercial cleaning and thinning. Selectively performing these operations can alter both the quantity and quality of alternative browse species with the aim to reduce the browsing pressure on the focal tree species. The association of a browsed species with other preferred or avoided species can
either increase (associational susceptibility) or decrease (associational resistance) the
detection probability of a focal species (Barbosa et al., 2009). Alternatively, the contrast
between a focal species and preferred plants in the surroundings can divert the browsing
pressure toward the latter (associational resistance by contrast or attractant-decoy hypothesis;
Atsatt and O'Dowd, 1976). Depending on whether the focal species receives associational
resistance or susceptibility from abundance of other browse species, increasing quantity
and/or quality of alternative forage will reduce or increase forest damage. Accordingly,
knowledge about the relationship between forest damage and the food base is needed in order
to target actions efficiently.

Animals are thought to be distributed in their landscape according to the distribution of
resources (e.g. Bjørneraas et al., 2012; Fretwell and Lucas, 1969; Månsson et al., 2012), and
one should therefore expect that the browsing pressure per capita food resource should be
evenly distributed in space. However, several mechanisms influence animals' behavioural
decisions resulting in browsing patterns that do not necessarily reflect the spatial variation in
forage abundance. Firstly, the foraging decisions of herbivores are a result of many factors
that are not only related to the quality and quantity of forage. Factors such as predation risk
and environmental stress can reduce the net gain obtained from a foraging patch (Brown,
1999). Such factors may influence the animals at larger spatial scales compared to the local
variation in food abundance (Johnson et al., 2001; Rettie and Messier, 2000), and therefore
may generate browsing patterns that are disproportionate to the resource distribution (Cassing
et al., 2006; Hamilton et al., 1980; Palmer and Truscott, 2003). Secondly, animals forage in
landscapes where their resources are unevenly distributed. Optimal foraging theory predicts
that the time spent in a foraging patch, and the proportion of resources in the patch that is
utilised, depend on the patch quality and costs such as searching time and locomotion costs
occurring when moving between patches (Charnov, 1976). Accordingly, in areas with high
movement costs the utilisation rate of resources in a foraging patch is expected to be higher (Charnov, 1976).

The foraging niche of large herbivores can be separated into three components: quality, quantity and availability of forage (Skogland, 1984; Sæther and Andersen, 1990). The importance of these components for patch utilisation can vary depending on forage characteristics in the surroundings as well as on other environmental conditions in interaction with the decision-making process of the animal (Andersen and Sæther, 1992; Bergman et al., 2005; Sæther and Andersen, 1990). Accordingly, we may expect associational relationships between the surrounding forage and the detection probability and browsing pressure of a focal species (Atsatt and O'Dowd, 1976; Barbosa et al., 2009). A meta-analysis by (Barbosa et al., 2009) suggests that associational resistance is more likely than susceptibility in mammalian herbivores. However, other relationships are also reported, from no significant associational relationships (e.g. Danell et al., 1991a; Edenius, 1991; Jalkanen, 2001), to evidence for associational susceptibility (e.g. Milligan and Koricheva, 2013; Vehvilainen and Koricheva, 2006), indicating that the role of associational relationships is not straightforward for mammalian herbivores. Still, the utilisation of the focal species as food is likely to be affected both by the quantity and quality of alternative forage, but the strength of the association will be shaped by the spatial distribution of the higher and lower quality forage resources (Bergvall et al., 2008).

The factors related to management actions and animal foraging decisions described above all require that the characteristics of food sources are interpreted at the appropriate spatial scales. Forestry operations are done at scales dictated by management strategies for forest stands, land properties or other management units. Accordingly, actions should best be done at an appropriate spatial scale that incorporate the ecological mechanisms affecting the distribution of animals and their browsing pressure. However, little is known about the spatial
scales of herbivore foraging damages according to ecological mechanisms affecting the
distribution of animals and their browsing pressure, and whether or not the forest
management scales currently applied are appropriate for addressing these damages. This calls
for a multi-scale evaluation of forest herbivore damage in order to target actions to efficiently
reduce silviculture-herbivore conflicts (Tanentzap et al., 2011; Weisberg and Bugmann,
2003).

We used a large dataset on winter browse availability and utilisation by moose (*Alces
alces*) in Southern Norway to assess how browse abundance and composition at several
spatial scales affected browsing damage on Scots pine (*Pinus sylvestris*). The Norwegian
moose population has increased considerably since the 1960's (Lavsund et al., 2003; Solberg
et al., 2006), and in many areas current moose densities are probably higher than ever before
(Rosvold et al., 2012). The high moose abundance represents a considerable income for land-
owners through hunting permits and hunting-related services (Storaas et al., 2001, but see
also Wam and Hofstad, 2007). During the same period forestry practice changed from
selective felling of trees to clear cutting (Lavsund et al., 2003). This opened large areas which
provided concentrated abundances of high-quality forage for moose, and this has been
proposed as an important reason for the increase in moose density (Lavsund et al., 2003;
Milner et al., 2013). However, regeneration of pine-dominated forest stands is compromised
in many areas due to intense browsing by moose during winter (Edenius et al., 2002). Pine is
an important part of moose winter diet if the availability of alternative browse is scarce
(Hörnberg, 2001; Wam and Hjeljord, 2010), but its quality as moose forage is considered to
be of moderate value compared to several deciduous species (Histøl and Hjeljord, 1993;
Hjeljord et al., 1982, 1994).

We focused on the following questions: 1) Is the degree of pine browsing affected by
quality or quantity of alternative browse in the browsing patch, forest stand, home range or
municipality scale? 2) Is the degree of pine browsing in a patch best explained by absolute value of browse (i.e. the abundance of browse of different type), or is it modified by the relative abundance of browse in the surroundings (i.e. the difference in abundance between a browsing patch and the abundance in surrounding areas)? 3) Does the spatial scale of forest management and actions capture the spatial scales at which variation in quality or quantity of alternative browse explains pine browsing frequency?

2. Materials and methods

2.1. Study area

Our study area was made up of 12 sub-areas of approximately 10,000 ha each distributed throughout southern Norway (Fig. 1). With the exception of the two southernmost sub-areas, the sub-areas are situated within the boreal forest zone (Moen, 1999), dominated by Scots pine and Norway spruce (*Picea abies*) mixed with deciduous trees like birches (*Betula* spp.), rowan (*Sorbus aucuparia*), aspen (*Populus tremula*) and goat willow (*Salix caprea*). The two southernmost sub-areas constitute an ecotone between the boreal and temperate forest (i.e. boreo-nemoral zone, Moen, 1999), with oak (*Quercus* spp.) being an additional common tree species. Because of the wide geographical distribution of this study, the areas covered large gradients in plant growth conditions: the start of growing season varied from 20 April to 10 May, while the proportion of the range area comprising intermediate to high forest productivity (Site Index ≥ G14 on the H40 scale) varied from 27% to 96% (Wam et al., 2010). The H40 Site Index indicates the height of the dominant tree species when the age of the tree (measured at 130 cm height) is 40 years (Tveite, 1977).

The timber logging activity was fairly similar between sub-areas: recently cleared forest (stands with dominating tree height < 4 m) covered 5-13% of the range area. The forest had been clear-cut at the commercially mature stage with semi-automated harvesters and
forwarders. Tops and branches had been left on ground to decompose around each felled tree.

There had been no use of herbicides, artificial fertilizers or mechanical site preparation immediately prior to or at the time of study. Such silvicultural operations are very scarce in the region (Statistics Norway, 2014), and would anyway not co-vary with any of our explanatory variables.

2.2. Sampling procedures

We carried out field surveys of moose forage availability and utilization in July-August 2005-2007. Our sampling design was aimed at representing a cross section of the moose range (see Wam and Hjeljord, 2010 for details). Circular plots (r = 2 m) were systematically distributed along a-priori determined transects for every 15 metres (paced off by steps) in young forest (class I, II; Table 1) and every 75 metres in older forest, bogs and areas logged within the last year (class 0, III, IV, bog). We had a higher plot frequency in the younger age classes because this is where most of the moose forage occurs (Wam et al., 2010).

For each plot we determined forest productivity (FP) and forest height class (Table 1) based on the dominant vegetation on 0.1 ha surrounding the plot. Both indices were determined by visual inspection of vegetation composition, tree volume and height growth.

We counted all trees having parts or the whole of their crown within moose browsing height (30-300 cm above ground). Trees branching off < 5 cm above ground were counted as separate trees. We recorded species and whether or not the tree had been browsed by moose.

Most browsing was from previous winter (HKW, pers. obs.), but some older browsing was also visible. However, as the abiotic and biotic factors used to explain browsing vary little from year to year, browsing that occurred prior to the previous winter was assumed to have occurred under similar conditions to the previous winter's browsing.
2.3. Environmental variables and browse abundance

Description of variables is provided in Table 1. Snow depth was obtained from the Norwegian Meteorological Institute as gridded (1*1km$^2$) downscaled daily values (Engen-Skaugen et al., 2002). From this dataset, we calculated mean snow depth for all days when snow depth was > 1 cm over the winter for each grid cell. We also calculated number of days during winter with > 50 cm snow. These variables were first calculated annually, and then averaged over the years 2005-2007. Snow condition will have large- and fine-scale spatial variation which can affect browsing pressure differently. We calculated the large-scale (regional) snow conditions by averaging snow depth and length of snow cover at the municipality scale (see below) for each plot (Table 1). The local snow conditions were calculated as the difference between the snow condition at the plot and the regional snow condition. The local snow condition was positive if the plot had higher snow depths or longer period of snow cover than the regional average around the plot, and negative if the snow depth at the plot was lower or the length of snow cover was shorter than the regional average.

Topography may affect moose habitat use (e.g. Leblond et al., 2010) and thereby the browsing pressure. We used distance to ridge as a descriptor of topography. Ridges were recognised by applying a terrain algorithm at a raster digital elevation model with resolution 25*25 m. The algorithm defined a pixel as a ridge if none or only one of the eight neighbour pixels had higher elevation. We used the minimum Euclidian distance from a plot to a ridge as measure of distance to ridge.

We chose four a priori set spatial scales, S, to calculate browse abundance: 1) Browsing patch (BP), which is the sampling unit (12.5 m$^2$, radius = 2 m), and is the area available for a moose standing in a foraging bout; 2) Forest stand (FS) calculated as the mean size of forest stands in the study area (2 ha, radius = 80 m), which is the basic operational scale of silviculture; 3) Moose home range (HR, 10 km$^2$, radius = 1750 m), which represents...
the average winter home range size of moose in Scandinavia (Cassing et al., 2006; Olsson et al., 2011; Roer and Gangsei, 2008; Rolandsen et al., 2010); and 4) Municipality (MUN), calculated as the mean forested area within a municipality in the study area (415 km$^2$, radius $= 11.5$ km), which represents the spatial scale of moose management and strategic scale for forest management.

For each sampling plot we assigned species-specific browse abundance as the species-specific number of browsed and un-browsed trees. The alternative browse (i.e. other browse than pine) was later classified into selected and non-selected browse based on the level of browsing given the abundance (see below). For spatial scales larger than the browsing patch level, we averaged the species-specific number of trees for all plots within a distance that represented a circle with area of the scale of interest. The abundance measures were calculated as number of browsed and un-browsed trees per 12.5 m$^2$ (Table 1). The ratio between selected and total browse was used as an index of the quality of the browse within the patch. As measures of differences in browse characteristics between a patch and the surroundings ($\Delta$Pine, $\Delta$Quality, $\Delta$Total), we used the differences between patch-scale browse measures and larger-scale browse measures. High values mean that the patch had more total browse, pine browse, or higher quality than the average plot within the respective scale radius (forest stand, home range, or municipality scale).

A total of 8221 sample plots were used to describe different spatial scales of browse abundance for the 497 plots that were located in young stands of pine forest (i.e. where pine were within moose browsing height and vulnerable to browsing damage).

2.4. Statistical analyses

We analysed the probability that a pine tree within a patch was browsed or not (i.e. at least one twig on a tree was removed by moose) by logistic regression with logit link and binomial
family. The dependent variable was the number of pine trees with browsing vs the total number of pine trees in the patch. Because pine damage is a problem primarily in young stands, for the response variable we only included sample plots in forest height class II (0.5 – 4 m, i.e. trees that were within browsing reach of moose during winter). To account for potential interdependencies between observations (e.g. Bolker et al., 2009), we added sub-area, transect identity and plot identity as random factors in a mixed model setting for all our analyses. Plot identity was added to reduce over-dispersion and to avoid plots with many pine trees being weighted more in the analyses than plots with few pine trees.

We first investigated the overall species-specific browsing pattern to assess species-specific estimates of browsing pressure. We used a resource selection probability function (i.e. sampling design I according to Manly et al., 2002), with number of browsed and total number of trees in a patch as dependent variable and tree species as the explanatory variable in a mixed logistic regression. The model provided species-specific estimates of proportion of trees that were browsed by moose, and these estimates were compared against a null-model which represents the overall browsing pressure. Species that were browsed more than the overall browsing pressure (95% credible interval did not overlap with the estimate for the overall browsing pressure) were considered to be selected by moose and thus of high quality (referred to as "high quality browse"). Species with browsing pressure not significantly different from the overall browsing pressure were termed "other browse". Only one species (Norway spruce) was browsed significantly less than the overall browsing, and was excluded from further analyses (see 3.1. Overall browsing pattern). Pine was kept in a separate class.

Next we assessed how abiotic factors (local and regional snow condition, forest productivity, distance to ridge) affected pine browsing. See Table 2 for the global model and valid candidate models. The most important variables were used as baseline models that were retained in all further analyses.
We then added scale-specific estimates of browse abundance and browse quality to the baseline models, separately for each spatial scale $S$. To describe the browse characteristics, we used abundance of pine ($\text{Pine}_S$), total browse abundance (not including pine, $\text{Total}_S$), and quality of browse (selected / total browse, $\text{Quality}_S$). The interaction between total abundance and quality is the amount of selected browse, and if this was significant it suggested that it is the preferred browse alone, and not the total browse, that is important for pine browsing. As a final step, we combined the highest ranked scale-specific models into multi-scale models and re-ran AICc-based model selection. We did this to investigate whether significant relationships at one spatial scale were captured by patterns at larger or smaller spatial scales.

We were particularly interested in whether pine browsing was best predicted by the absolute abundance and quality of available browse at the patch or at larger spatial scales, or by the relative difference in abundance and quality of browse between the browsing patch and its surrounding. As a final step we therefore ran models with $\Delta\text{Pine}$, $\Delta\text{Total}$, and $\Delta\text{Quality}$ at the forest stand, home range, and municipality scale as explanatory variables. The full models included all two- and three-way interactions (see Table 6).

Ranking of candidate models and evaluation of variables importance for explaining pine browsing was done based on AIC, corrected for small sample size (AICc; Burnham and Anderson, 2002). The dependent variable and random structure were similar for all models and AICc-values could therefore be compared directly among models from different spatial scales. Accordingly, we used AICc-values to assess which spatial scale that best predicted pine browsing, and whether the absolute or relative browse characteristics best explained pine browsing. We therefore report both the $\Delta\text{AICc}$-value for comparison of models within a spatial scale, and the absolute AICc-value to ease the comparison across spatial scales and between absolute and relative browse measures. The baseline models were retained in all
candidate models regarding alternative browse. If an interaction was included in a candidate model, the main effects were also kept in the model.

All analyses were run in R version 3.1.0 (R Core Team, 2014), where the mixed models were run within the lme4 package (Bates et al., 2014). Uncertainty of parameter estimates was assessed based on 10,000 resampling of the posterior distribution of the parameter estimates using the function sim from the R-package arm (Gelman and Su, 2014).

3. Results

3.1. Overall browsing pattern

The probability that a pine tree was browsed ($\beta_{\text{Pine}} = 0.473$, 95% CI: 0.416; 0.526) was not significantly different from the overall browsing probability ($\beta_{\text{All}} = 0.505$, 95% CI: 0.472; 0.537, Fig. 2), suggesting that moose utilise pine in a non-selective browsing pattern. Juniper (Juniperus communis), oak, rowan-aspen-goat willow (RAG) and other willow species ($\beta_{\text{Juniper}} = 0.626$, 95% CI: 0.543; 0.704, $\beta_{\text{Oak}} = 0.841$, 95% CI: 0.783; 0.890, $\beta_{\text{RAG}} = 0.777$, 95% CI: 0.732; 0.813, $\beta_{\text{Willow}} = 0.735$, 95% CI: 0.676; 0.786, Fig. 2), and were considered high quality browse. The browsing probability of birch ($\beta_{\text{Birch}} = 0.494$, 95% CI: 0.440; 0.456) and other deciduous trees ($\beta_{\text{OD}} = 0.486$, 95% CI: 0.423; 0.549) overlapped with the overall browsing probability (Fig. 2). Norway spruce was hardly browsed at all ($\beta_{\text{Spruce}} = 0.014$, 95% CI: 0.005; 0.034, Fig. 2). Due to the lack of utilisation of spruce as forage, and that pine and spruce rarely are established in the same forest stand, we omitted Norway spruce from further analyses.

3.2. Abiotic factors and pine browsing
The highest ranked model regarding the relationship between pine tree browsing and abiotic variables included local snow depth (SD_{Local}), forest productivity (FP), and their interaction (Table 2). Alternative models with ΔAICc < 2 also included length of snow cover at the regional scale (SL_{Regional}), SD_{Regional} or distance to ridge, but SD_{Local}, forest productivity, and their interactions were retained in all high-ranked models so we chose the highest ranked model as the baseline model. According to this model, the browsing probability of pine tree was negatively related to SD_{Local} on patches with high forest productivity (estimate at the logit scale: $\beta = -0.605$, 95% CI: -0.963; -0.248, Fig. 3), whereas in patches with low forest productivity the relationship did not differ from zero (estimate at the logit scale: $\beta = -0.061$, 95% CI: -0.390; 0.266, Fig. 3).

3.3. Scale-specific browse abundance and pine damage

At the browsing patch scale the highest ranked model included abundance of pine (Pine_{BP}), total browse abundance (Total_{BP}) and browse quality (Quality_{BP}) as well as their two- and three-way interactions (Table 3). No alternative models received considerable support (ΔAICc ≥ 3.40). Pine browsing was positively related to Quality_{BP} if Total_{BP} was low and Pine_{BP} was high, and if Total_{BP} was high and Pine_{BP} was low (Fig. 4A). In contrast, if both Total_{BP} and Pine_{BP} was high, there was a negative relationship between Quality_{BP} and pine browsing probability (Fig. 4A), suggesting that a high abundance of high-quality browse decreases the pine browsing only if the abundance of pine is high.

The highest ranked model at the forest stand scale included Pine_{FS}, Total_{FS} and their interaction, with the second ranked model including only Pine_{FS} and a ΔAICc of 1.15 (Table 3). The highest ranked model suggested that pine browsing was higher if Pine_{FS} was low and Total_{FS} was high, and low if both Pine_{FS} and Total_{FS} were high (Fig. 4B). When pine
abundance was high while total browse abundance was low, or if both pine and total browse abundance was low, then pine browsing was intermediate (Fig. 4B).

At the moose home range scale, the highest ranked model included only Pine$_{HR}$, with an alternative model also including Quality$_{HR}$ ($\Delta$AICc = 0.37, Table 3). As Quality$_{HR}$ was not included in the third and fourth ranked model, we did not consider it as important for explaining pine tree browsing. Accordingly, pine tree browsing was negatively related to the abundance of pine at the moose home range scale (Fig. 4C).

The highest ranked model at the municipality scale included Pine$_{MUN}$, Total$_{MUN}$, Quality$_{MUN}$ and the interaction between Pine$_{MUN}$ and Total$_{MUN}$ (Table 3). These variables and the interaction were included in three of the five highest ranked models, giving support to their importance in explaining the browsing probability of pine trees. According to the highest ranked model, pine browsing was negatively related to the browse quality at the municipality scale (Fig. 4D). In addition, the probability of pine browsing was high if Pine$_{MUN}$ and Total$_{MUN}$ was low, whereas it was lowest when Pine$_{MUN}$ was high and Total$_{MUN}$ was low (Fig. 4D).

### 3.4. Multi-scale and relative browse abundance and pine damage

Across spatial scales, the municipality level model had lowest AICc-value and thus best explained the variation in pine tree browsing among patches. The forest stand model had the highest AICc-value, 11.63 higher than the best model at the municipality level (Table 3). When we combined the highest ranked scale-specific models (Table 3) to a multi-scale model and ran AICc-based model selection on the full model, the highest ranked model did not include any browse measures at the forest stand scale (Table 4). This multi-scale model had a considerably lower AICc-value than any of the single-scale models ($\Delta$AICc = -13.09), suggesting that spatial variation in pine browsing is a result of abundance and quality of

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Parameter estimates from the highest ranked multi-scale model did not deviate much from corresponding estimates from the single-scale models (Table 5), and therefore the browsing pattern were similar to those shown in Fig. 4A-D. None of the scale-specific models explaining pine browsing with relative browse abundance (ΔPine, ΔQuality and ΔTotal) received support from AICc-values (Table 6). Accordingly, the absolute abundance and quality of browse at multiple spatial scales was better predictor for pine browsing in a patch than the relative differences in these variables between the patch and its surroundings.

4. Discussion

Moose browsing on young pine trees have a high impact on the quality and value of the timber (Bergqvist et al., 2013; Edenius et al., 2002). We used an extensive dataset on spatial variation in browse abundance to describe the relationship between level of pine browsing by moose and browse characteristics, as well as environmental characteristics. Our results suggest negative relationships between the level of pine browsing and abundance and/or quality of browse at multiple spatial scales (Fig. 4), supporting that young pine trees receive associational resistance from alternative browse. Moreover, the absolute values of browse characteristics better explained pine browsing level compared to relative differences in browse characteristics between a browsing patch and its surroundings. The results suggest that forest damage from moose browsing is a result of factors operating at multiple spatial scales. However, the large-scale administrative units for moose and forest management (municipality level) best captured the variation in pine damage by moose, suggesting that strategic planning to reduce forest damage by moose requires large-scale collaboration between forest owners.
We measured browsing and abundance at the tree level, that is, a tree was browsed or not, and all trees counted equally in the browse abundance estimates, giving clear repeatability and comparability between individual trees. This simplification of the rather complex foraging environment of the moose was done of two main reasons. The first reason is related to how young pine trees are damaged by moose. The most common browsing pattern is removal of the apical leader shoot first (Bergqvist et al., 2001, 2013). Such browsing damages the tree stem and greatly reduces the economic value of the timber. Further browsing intensity will thus not cause major additional damage to timber value, until the browsing intensity reach a level that greatly reduces growth (more than 30% of twigs removed; Danell et al., 1991b; Edenius et al., 1995; Hester et al., 2004; Speed et al., 2013). Accordingly, our decision to simplify recording of browsing into browsed vs un-browsed trees is based on the assumption that this will give a sufficiently robust indication of impacts related to the economic value of the timber. The second reason is related to how silvicultural operations such as pre-commercial thinning and cleaning are done. These operations are performed at the tree level, i.e. the operator chooses to remove a tree of a certain species or not. However, species differ in how much biomass moose forage they provide, both with respect on the biomass of a twig and the number of twigs per tree. Still, for the practical operations the most relevant information is considered to be whether or not the abundance of trees of a specific species affects the likelihood that pine is browsed.

Of the abiotic factors, only local snow depth and site productivity influenced the level of pine browsing, with a negative relationship between snow depth and pine browsing at high-productive sites (Fig. 3). Moose movement is likely to be influenced by snow conditions (Leblond et al., 2010). Our result suggests that it is the local snow depth relative to the regional mean that affects pine browsing, and not the absolute depth. This means that a region with low snow depths experienced as much pine browsing as a region with high snow
depths, but within a region, local variation in snow depths can have a great impact on the level of pine browsing, particularly on sites of high productivity. The pattern remained even after accounting for abundance and composition of alternative browse, which suggests that the effect of snow condition is not caused by a confounding relationship between snow condition and available browse.

Pine is generally considered to be of intermediate quality as forage for moose, and the utilisation rate by moose during winter is often lower than many deciduous tree species (Månsson et al., 2007b; Wam and Hjeljord, 2010). Still, a high proportion of pine trees were browsed, suggesting that it is an important food source for moose during winter (Wam and Hjeljord, 2010). The abundance of pine itself could thus be expected to influence to what extent it is utilised by moose (Bergqvist et al., 2014). Indeed, we found a negative relationship between the abundance of pine and pine browsing at several spatial scales after accounting for alternative browse (Fig. 4). For instance, at the browsing patch level and at intermediate quantity and quality of alternative browse at a pine abundance of two trees per patch, the estimated average number of damaged and undamaged trees in the patch is 0.86 and 1.14, respectively (75 % damaged trees). Increasing the pine abundance to 6 trees per patch, the corresponding numbers are 2.30 damaged and 3.70 undamaged pine trees (62 % damaged trees). Accordingly, when pine abundance is high the utilisation rate decreases (Bergqvist et al., 2013, 2014).

Our results suggested that pine browsing is related to the characteristics of alternative browse in complex ways that differ among the spatial scales. The species-specific browsing (Fig. 2) confirmed previous findings that oak, rowan, aspen, willow species, and juniper are important parts of moose winter diet and heavily browsed if available (Kullberg and Bergström, 2001; Månsson et al., 2007b; Wam and Hjeljord, 2010). Accordingly, we could expect that these species will have a higher impact on the browsing pressure than species that
are less selected (birch and other deciduous species, Fig. 2), either by making areas with high 
abundance of such species more attractive and increasing the overall browsing pressure 
(associational susceptibility; Bergman et al., 2005; Milligan and Koricheva, 2013; Wallgren 
et al., 2013), or by decreasing the browsing pressure on non-attractive species (associational 
resistance; Atsatt and O'Dowd, 1976; Ward et al., 2008). We found a lower probability of 
pine browsing at high quality of the alternative browse at both the patch and municipality 
scale supporting the associational resistance hypothesis (Fig. 4). However, at the browsing 
patch scale this relationship was only found at high pine abundances in the patch (Fig. 4), 
which suggests that the spatial resistance from high-quality forage that leads to reduced pine 
browsing at the municipality scale only operates when pine abundance is high at the browsing 
patch scale. Similar interactions were also found between pine abundance and total 
abundance of alternative browse at the browsing patch, forest stand, and municipality scale 
(Table 3). Although pine was browsed far less than many other species (Fig. 2) and thus is 
considered less preferred food resource (Kullberg and Bergström, 2001; Månsson et al., 
2007b; Wam and Hjeljord, 2010), our results suggest that some pine browsing will always 
occur even if there is high abundance of alternative browse of high quality (Edenius, 1991). 
Herbivore foraging patterns represent a complex process involving many physiological and 
behavioural mechanisms affecting diet composition (DeGabriel et al., 2014). Pine can offer 
some important compounds that the more selected browse species not contain (Timmons et 
al., 2010), and diversity in availability of plant species may be an important driver for 
browsing pressure and diet diversity (Milligan and Koricheva, 2013).

The relationship between pine browsing and browse characteristics received support at 
several spatial scales (Table 3, Fig. 4), but the models at the municipality scale received 
strongest support (lowest AICc-value, Table 3). This may be because larger spatial scale 
captures factors such as moose density and landscape characteristics (Cassing et al., 2006;
Månsson, 2009). These factors may also influence moose space use (Bjørneraas et al., 2012), and any management actions that seek to incorporate the scale of moose space use should acknowledge the large individual and regional variation that is present in our estimate of average winter home range size of 10 km². Other studies that have assessed moose browsing at the individual moose level suggest that foraging behaviour is mostly related to the tree level characteristics such as species and twig abundance (e.g. Andersen and Sæther, 1992; Danell et al., 1991a). However, for forest management it is the sum of browsing decisions of multiple individuals during the winter that determines the overall level of pine browsing and damage, and this may best be explained by large-scale descriptors of moose forage availability and quality (Cassing et al., 2006). This spatial scale corresponds well with the current spatial scale of moose management, which supports the proposal that moose should be managed at a scale that captures the spatial distribution of a moose population (Nilsen et al., 2009). Reducing forest damage by moose must therefore be solved by adopting management actions at spatial scales larger than common silvicultural management units such as forest stands and most forest estates.

The relative differences in browse characteristics between the browsing patch scale and larger spatial scales did not have higher explanatory power than absolute values (Tables 3, 6). Moreover, parameter estimates from the single-scale models did not differ much from corresponding estimates from the multi-scale models, which implies that the observed pattern at a specific scale was not confounded by relationships at larger spatial scales. These findings suggest that browse characteristics at the patch scale and the larger spatial scales operate on pine browsing more or less independent of each other (Cassing et al., 2006; Månsson et al., 2007a). It has been suggested that animal resource utilisation can be considered a hierarchical process, going from large-scale environmental conditions affecting the distribution of the species, to selection of home range, habitat types, and finally resource items (e.g. trees and
twigs) at the finest scale (Johnson, 1980), and that mechanisms and factors involved in shaping utilisation patterns at one spatial scale are not necessarily important at a different spatial scale (Herfindal et al., 2009; Johnson et al., 2001, 2002; Nikula et al., 2004). If this also is the case for moose browsing patterns as suggested by our results, mitigation actions should be done hierarchically at multiple spatial scales simultaneously (Gordon et al., 2004; Weisberg and Bugmann, 2003). First, strategic planning of objectives, targets and indicators for forest and moose should be done at the municipality scale. It could be argued that this would be more practical to solve at the forest estate scale. However, the structure of forest estates in Norway is diverse, with a few very large properties and many very small. Accordingly, for most forest owners their forest estate is far too small to capture the spatial scale needed to have any significant impact on the browsing pressure on pine. Moreover, municipalities are highly involved in moose management and integration of wildlife and forest management objectives should be done at this scale. Second, silvicultural operation at the estate and forest stand scales should contribute to these large-scale objectives. As an example, regeneration of pine on clear-cuts should focus on high stocking rate. Yet the optimal stocking that simultaneously minimizes damage by moose and intraspecific competition is unknown. Reduction in growth due to competition could also mean a longer time to escape browsing (Heikkilä and Härkönen, 1996), but this could be balanced by a lower risk of browsing. Similarly, although intensive and early pre-commercial thinning has been reported to provide the greatest diameter growth (Huuskonen and Hynynen, 2006), this advantage can be reduced by a higher browsing risk for residuals threes. Third, at the scale of forest workers having to make decisions on which competing stems to clear or leave, pre-commercial thinning rules should be done with caution, favouring keeping preferred deciduous stems if pine density is high, as these will provide associational resistance. At low pine densities, however, cleaning of deciduous browse may reduce pine browsing.
Acknowledgements

We thank Olav Hjeljord for assistance with the field survey design. The project was supported by the Research Council of Norway (RCN project #215647/E40; Intensified harvesting of forests – implications for enterprises related to wild and domestic ungulates).

We thank two anonymous referees for helpful comments on the manuscript.

References


Table 1. Variables used in the analyses of moose browsing of pine. Variable abbreviation is given in parentheses.

<table>
<thead>
<tr>
<th>Name (Abbreviation)</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Forest height class</td>
<td>0: cleared the previous year, I: height of focal tree species &lt; 50 cm, II: height between 50 and 400 cm, III: height between 4 and 10 m, IV: height &gt; 10 m.</td>
</tr>
<tr>
<td>Forest productivity (FP)</td>
<td>The forest productivity was classified into five classes based on the H40 Site Index (HSI) during field work, and reclassified into two for analysis: low (bogs, unproductive, and HSI ( \leq ) F11) and high (HSI &gt; F11).</td>
</tr>
<tr>
<td>Regional snow depth (SD_{Regional})</td>
<td>Mean snow depth during period with snow cover, averaged over the municipality scale of each sample plot.</td>
</tr>
<tr>
<td>Local snow depth (SD_{Local})</td>
<td>The difference between the mean snow depth during days with snow cover at the browsing patch (BP) and its regional snow depth (SD_{BP} - SD_{Regional}). SD_{Local} indicates whether snow depth at the browsing patch is higher or lower than the regional mean.</td>
</tr>
<tr>
<td>Regional length of snow cover (SL_{Regional})</td>
<td>The number of days with &gt; 50 cm of snow, averaged over the municipality scale of each sample plot.</td>
</tr>
<tr>
<td>Local length of snow cover (SL_{Local})</td>
<td>The difference between the number of days with snow cover &gt; 50 cm at the browsing patch and the regional length of snow cover (SL_{BP} - SD_{Regional}). SL_{Local} indicates whether the length of the period with snow cover at the location is longer or shorter than the regional mean.</td>
</tr>
<tr>
<td>Distance to ridge (DR)</td>
<td>Distance from a sample plot to the closest pixel (25x25 m²) that had one or zero of the neighbouring eight pixels with altitude equal to or higher than the focal pixel (i.e. the pixel was at a ridge).</td>
</tr>
<tr>
<td>Total browse abundance</td>
<td>The abundance of all browse species, except pine. Total_{BP} is number of</td>
</tr>
</tbody>
</table>
(Total_{BP}, Total_{FS}, Total_{HR}, Total_{MUN}) trees in the browsing patch (12.5 m²). At larger scales: the average number of trees from all patches within a circle corresponding to the spatial scale.

FS = Forest stand (10 ha), HR = moose winter home range (10 km²), MUN = municipality (415 km²).

Pine abundance The abundance of pine trees at a given spatial scale, where "Scale" is BP, FS, HR, or MUN (see above).

(Pine_{Scale}) Browse quality The ratio between the abundance of browse that was selected by moose (see Fig. 2) and the total browse at a given spatial scale (see above).

(Quality_{Scale}) Browse difference The difference in pine abundance, browse quality, and total browse abundance, between the browsing patch and measures at the larger spatial scales (FS, HR, or MUN, see above). High values mean that the browsing patch had higher abundance or higher quality than the average surrounding area.

(ΔPine_{Scale}, ΔQuality_{Scale}, ΔTotal_{Scale})
Table 2. AICc-based ranking of candidate models with abiotic factors explaining the probability that a pine tree was browsed by moose. For variables abbreviation, see Table 1.

<table>
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<tr>
<th>Dependent</th>
<th>FP</th>
<th>SD&lt;sub&gt;Regional&lt;/sub&gt;</th>
<th>SL&lt;sub&gt;Regional&lt;/sub&gt;</th>
<th>SD&lt;sub&gt;Local&lt;/sub&gt;</th>
<th>SL&lt;sub&gt;Local&lt;/sub&gt;</th>
<th>DR</th>
<th>DR&lt;sup&gt;2&lt;/sup&gt;</th>
<th>SF*SD&lt;sub&gt;Local&lt;/sub&gt;</th>
<th>SF*SL&lt;sub&gt;Local&lt;/sub&gt;</th>
<th>SF*DR</th>
<th>ΔAICc</th>
<th>AICc&lt;sub&gt;W&lt;/sub&gt;</th>
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<td>X</td>
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Table 3. AICc-based ranking of models of pine browsing by moose in relation to abundance of pine and abundance and quality of alternative browse at four spatial scales. The baseline model (see Table 2) was included in all candidate models. The highlighted model is the best, according to AICc, among all four spatial scales.

<table>
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<tr>
<th>Scale</th>
<th>Pine</th>
<th>Quality</th>
<th>Total</th>
<th>Pine*Quality</th>
<th>Pine<em>Quality</em>Total</th>
<th>AICc</th>
<th>ΔAICc</th>
<th>AICc-w</th>
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</table>
Table 4 AICc-based ranking of multi-scale models explaining the probability that a pine tree in a browse patch was browsed by moose. The baseline model (see Table 2) was included in all candidate models. Explanatory variables and interactions were chosen from the highest ranked single-scale models (Table 3).
Table 5. Parameter estimates (SE) for the highest ranked single-scale models (Table 3) and the multi-scale model (Table 4). All estimates are at the logit scale. See also Fig. 4.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Single-scale estimates</th>
<th>Multi-scale estimates</th>
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</thead>
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<tr>
<td>PineBP</td>
<td>0.011 (0.045)</td>
<td>0.033 (0.044)</td>
</tr>
<tr>
<td>QualityBP</td>
<td>-0.461 (0.960)</td>
<td>-0.128 (0.940)</td>
</tr>
<tr>
<td>TotalBP</td>
<td>0.008 (0.022)</td>
<td>0.012 (0.022)</td>
</tr>
<tr>
<td>PineBP*QualityBP</td>
<td>0.260 (0.218)</td>
<td>0.240 (0.212)</td>
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<tr>
<td>PineBP*TotalBP</td>
<td>-0.001 (0.004)</td>
<td>-0.001 (0.003)</td>
</tr>
<tr>
<td>QualityBP*TotalBP</td>
<td>0.165 (0.071)</td>
<td>0.148 (0.069)</td>
</tr>
<tr>
<td>PineBP<em>QualityBP</em>TotalBP</td>
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<td>-0.049 (0.018)</td>
</tr>
<tr>
<td>PineFS</td>
<td>0.059 (0.123)</td>
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</tr>
<tr>
<td>TotalFS</td>
<td>0.056 (0.046)</td>
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<td>PineFS*TotalFS</td>
<td>-0.025 (0.012)</td>
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</tr>
<tr>
<td>PineHR</td>
<td>-2.065 (0.591)</td>
<td>-1.670 (0.596)</td>
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<td>PineMUN</td>
<td>-11.906 (3.512)</td>
<td>-9.544 (3.380)</td>
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<td>QualityMUN</td>
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<td>TotalMUN</td>
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<td>PineMUN*TotalMUN</td>
<td>1.395 (0.653)</td>
<td>1.381 (0.639)</td>
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Table 6. AICc-based ranking of models regarding pine browsing by moose in relation to the abundance of pine and alternative browse in the browsing patch relative to that found at three larger spatial scales. See Table 1 for details regarding the explanatory variables. The baseline model (see Table 2) was included in all candidate models. The highlighted models are the best, according to AICc, across all spatial scales.

<table>
<thead>
<tr>
<th>Scale</th>
<th>ΔPine</th>
<th>ΔQuality</th>
<th>ΔTotal</th>
<th>ΔPine*ΔQuality</th>
<th>ΔPine*ΔTotal</th>
<th>ΔQuality*ΔTotal</th>
<th>ΔPine<em>ΔQuality</em>ΔTotal</th>
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<th>ΔAIC</th>
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Fig. 1. Location of the study areas in Norway.

Fig. 2. The species-specific probabilities that a tree was browsed by moose. Thick and thin bars represent standard errors and 95% credibility intervals, respectively. The grey line shows the overall probability that a tree was browsed by moose. OD and RAG is Other deciduous trees and Rowan, Aspen, Goat willow, respectively.

Fig. 3. The relationship between the probability that a pine tree is browsed and local snow depth in the browsing patch. Black lines represent high forest productivity in the browsing patch, whereas dashed lines represent low forest productivity. Thin lines show 95% credible interval based on 10000 MCMC resampling of the posterior distribution of the parameter estimates.

Fig. 4. The relationship between pine tree browsing probability, and quality of alternative forage measured at four spatial scales; browsing plot (BP, 12.5 m$^2$), forest stand (FS, 10 ha), moose winter home range (HR, 10 km$^2$), and municipality (MUN, 415 km$^2$). The relationship is shown for high and low levels of abundance of pine and total alternative browse at the spatial scales. Relationships are based on the highest ranked models in Table 3 (see Table 5 for parameter estimates). If the lines are horizontal the highest ranked model did not include browse quality as explanatory variable.
Figures

Fig. 1
Fig. 3

P(Plant tree is browsed) vs. Relative snow depth (cm)