

1 Associational relationships at multiple spatial scales
2 affect forest damage by moose

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14

15 **Abstract**

16 Increasing abundance of large herbivores combined with changes in forestry practices has led
17 to increased forest damage in many temperate and boreal forest areas. The role of alternative
18 forage as a driver for browsing pressure on tree species important for forestry has received
19 increased attention. However, actions to reduce damage through altering forage abundance
20 must be carried out at spatial scales that correspond to the behavioral processes that generate
21 the browsing pattern. We used a multi-scaled dataset on browse abundance and utilization in
22 Southern Norway to assess how pine browsing damage was related to abundance and quality
23 of browse measured at different spatial scales. Pine trees had a lower probability to be
24 browsed at high pine abundance at all spatial scales. However, the abundance and quality of
25 alternative browse was negatively related to pine browsing (i.e. associational resistance) at
26 several spatial scales, with the highest explanatory power at the largest spatial scale.
27 Management actions to reduce pine browsing by moose should focus on facilitating high
28 abundance of both pine and alternative high-quality browse, and should be carried out at
29 sufficiently large spatial scales (moose home range scale or larger).

30

31 *Key words: Alces alces; associational relationships; browsing; integrated management;*
32 *moose; pine; Pinus sylvestris; spatial scale*

33 **1. Introduction**

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

46 Perhaps the two most efficient actions to prevent forest damage by browsing herbivores
47 – physical barriers around vulnerable forest stands or trees (e.g. Cutini et al., 2011; Ward et
48 al., 2000) and reducing herbivore abundance by increasing harvesting (e.g. Hothorn and
49 Müller, 2010) – are both costly and may have unwanted ecological and economic side-effects
50 (Kuijper, 2011). Altering the local browsing pressure by changing the amount and/or spatial
51 distribution of forage has therefore received increased interest (Heikkilä and Härkönen, 1996;
52 Mathisen et al., 2014; Putman and Staines, 2004; van Beest et al., 2010). While
53 supplementary feeding can be expensive and logistically challenging, the natural food base
54 can be altered as part of standard silvicultural practices such as pre-commercial cleaning and
55 thinning. Selectively performing these operations can alter both the quantity and quality of
56 alternative browse species with the aim to reduce the browsing pressure on the focal tree
57 species. The association of a browsed species with other preferred or avoided species can

58 either increase (associational susceptibility) or decrease (associational resistance) the
59 detection probability of a focal species (Barbosa et al., 2009). Alternatively, the contrast
60 between a focal species and preferred plants in the surroundings can divert the browsing
61 pressure toward the latter (associational resistance by contrast or attractant-decoy hypothesis;
62 Atsatt and O'Dowd, 1976). Depending on whether the focal species receives associational
63 resistance or susceptibility from abundance of other browse species, increasing quantity
64 and/or quality of alternative forage will reduce or increase forest damage. Accordingly,
65 knowledge about the relationship between forest damage and the food base is needed in order
66 to target actions efficiently.

67 Animals are thought to be distributed in their landscape according to the distribution of
68 resources (e.g. Bjørneraas et al., 2012; Fretwell and Lucas, 1969; Månsson et al., 2012), and
69 one should therefore expect that the browsing pressure per capita food resource should be
70 evenly distributed in space. However, several mechanisms influence animals' behavioural
71 decisions resulting in browsing patterns that do not necessarily reflect the spatial variation in
72 forage abundance. Firstly, the foraging decisions of herbivores are a result of many factors
73 that are not only related to the quality and quantity of forage. Factors such as predation risk
74 and environmental stress can reduce the net gain obtained from a foraging patch (Brown,
75 1999). Such factors may influence the animals at larger spatial scales compared to the local
76 variation in food abundance (Johnson et al., 2001; Rettie and Messier, 2000), and therefore
77 may generate browsing patterns that are disproportionate to the resource distribution (Cassing
78 et al., 2006; Hamilton et al., 1980; Palmer and Truscott, 2003). Secondly, animals forage in
79 landscapes where their resources are unevenly distributed. Optimal foraging theory predicts
80 that the time spent in a foraging patch, and the proportion of resources in the patch that is
81 utilised, depend on the patch quality and costs such as searching time and locomotion costs
82 occurring when moving between patches (Charnov, 1976). Accordingly, in areas with high

83 movement costs the utilisation rate of resources in a foraging patch is expected to be higher
84 (Charnov, 1976).

85 The foraging niche of large herbivores can be separated into three components: quality,
86 quantity and availability of forage (Skogland, 1984; Sæther and Andersen, 1990). The
87 importance of these components for patch utilisation can vary depending on forage
88 characteristics in the surroundings as well as on other environmental conditions in interaction
89 with the decision-making process of the animal (Andersen and Sæther, 1992; Bergman et al.,
90 2005; Sæther and Andersen, 1990). Accordingly, we may expect associational relationships
91 between the surrounding forage and the detection probability and browsing pressure of a
92 focal species (Atsatt and O'Dowd, 1976; Barbosa et al., 2009). A meta-analysis by (Barbosa
93 et al., 2009) suggests that associational resistance is more likely than susceptibility in
94 mammalian herbivores. However, other relationships are also reported, from no significant
95 associational relationships (e.g. Danell et al., 1991a; Edenius, 1991; Jalkanen, 2001), to
96 evidence for associational susceptibility (e.g. Milligan and Koricheva, 2013; Vehvilainen and
97 Koricheva, 2006), indicating that the role of associational relationships is not straightforward
98 for mammalian herbivores. Still, the utilisation of the focal species as food is likely to be
99 affected both by the quantity and quality of alternative forage, but the strength of the
100 association will be shaped by the spatial distribution of the higher and lower quality forage
101 resources (Bergvall et al., 2008).

102 The factors related to management actions and animal foraging decisions described
103 above all require that the characteristics of food sources are interpreted at the appropriate
104 spatial scales. Forestry operations are done at scales dictated by management strategies for
105 forest stands, land properties or other management units. Accordingly, actions should best be
106 done at an appropriate spatial scale that incorporate the ecological mechanisms affecting the
107 distribution of animals and their browsing pressure. However, little is known about the spatial

108 scales of herbivore foraging damages according to ecological mechanisms affecting the
109 distribution of animals and their browsing pressure, and whether or not the forest
110 management scales currently applied are appropriate for addressing these damages. This calls
111 for a multi-scale evaluation of forest herbivore damage in order to target actions to efficiently
112 reduce silviculture-herbivore conflicts (Tanentzap et al., 2011; Weisberg and Bugmann,
113 2003).

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

131 We focused on the following questions: 1) Is the degree of pine browsing affected by
132 quality or quantity of alternative browse in the browsing patch, forest stand, home range or

133 municipality scale? 2) Is the degree of pine browsing in a patch best explained by absolute
134 value of browse (i.e. the abundance of browse of different type), or is it modified by the
135 relative abundance of browse in the surroundings (i.e. the difference in abundance between a
136 browsing patch and the abundance in surrounding areas)? 3) Does the spatial scale of forest
137 management and actions capture the spatial scales at which variation in quality or quantity of
138 alternative browse explains pine browsing frequency?

139

140 **2. Materials and methods**

141 *2.1. Study area*

142 Our study area was made up of 12 sub-areas of approximately 10,000 ha each distributed
143 throughout southern Norway (Fig. 1). With the exception of the two southernmost sub-areas,
144 the sub-areas are situated within the boreal forest zone (Moen, 1999), dominated by Scots
145 pine and Norway spruce (*Picea abies*) mixed with deciduous trees like birches (*Betula* spp.),
146 rowan (*Sorbus aucuparia*), aspen (*Populus tremula*) and goat willow (*Salix caprea*). The two
147 southernmost sub-areas constitute an ecotone between the boreal and temperate forest (i.e.
148 boreo-nemoral zone, Moen, 1999), with oak (*Quercus* spp.) being an additional common tree
149 species. Because of the wide geographical distribution of this study, the areas covered large
150 gradients in plant growth conditions: the start of growing season varied from 20 April to 10
151 May, while the proportion of the range area comprising intermediate to high forest
152 productivity (Site Index \geq G14 on the H40 scale) varied from 27% to 96% (Wam et al.,
153 2010). The H40 Site Index indicates the height of the dominant tree species when the age of
154 the tree (measured at 130 cm height) is 40 years (Tveite, 1977).

155 The timber logging activity was fairly similar between sub-areas: recently cleared forest
156 (stands with dominating tree height $<$ 4 m) covered 5-13% of the range area. The forest had
157 been clear-cut at the commercially mature stage with semi-automated harvesters and

158 forwarders. Tops and branches had been left on ground to decompose around each felled tree.
159 There had been no use of herbicides, artificial fertilizers or mechanical site preparation
160 immediately prior to or at the time of study. Such silvicultural operations are very scarce in
161 the region (Statistics Norway, 2014), and would anyway not co-vary with any of our
162 explanatory variables.

163

164 *2.2. Sampling procedures*

165 We carried out field surveys of moose forage availability and utilization in July-August 2005-
166 2007. Our sampling design was aimed at representing a cross section of the moose range (see
167 Wam and Hjeljord, 2010 for details). Circular plots ($r = 2$ m) were systematically distributed
168 along a-priori determined transects for every 15 metres (paced off by steps) in young forest
169 (class I, II; Table 1) and every 75 metres in older forest, bogs and areas logged within the last
170 year (class 0, III, IV, bog). We had a higher plot frequency in the younger age classes
171 because this is where most of the moose forage occurs (Wam et al., 2010).

172 For each plot we determined forest productivity (FP) and forest height class (Table 1)
173 based on the dominant vegetation on 0.1 ha surrounding the plot. Both indices were
174 determined by visual inspection of vegetation composition, tree volume and height growth.
175 We counted all trees having parts or the whole of their crown within moose browsing height
176 (30-300 cm above ground). Trees branching off < 5 cm above ground were counted as
177 separate trees. We recorded species and whether or not the tree had been browsed by moose.
178 Most browsing was from previous winter (HKW, pers. obs.), but some older browsing was
179 also visible. However, as the abiotic and biotic factors used to explain browsing vary little
180 from year to year, browsing that occurred prior to the previous winter was assumed to have
181 occurred under similar conditions to the previous winter's browsing.

182

183 2.3. Environmental variables and browse abundance

184 Description of variables is provided in Table 1. Snow depth was obtained from the
185 Norwegian Meteorological Institute as gridded (1*1km²) downscaled daily values (Engen-
186 Skaugen et al., 2002). From this dataset, we calculated mean snow depth for all days when
187 snow depth was > 1 cm over the winter for each grid cell. We also calculated number of days
188 during winter with > 50 cm snow. These variables were first calculated annually, and then
189 averaged over the years 2005-2007. Snow condition will have large- and fine-scale spatial
190 variation which can affect browsing pressure differently. We calculated the large-scale
191 (regional) snow conditions by averaging snow depth and length of snow cover at the
192 municipality scale (see below) for each plot (Table 1). The local snow conditions were
193 calculated as the difference between the snow condition at the plot and the regional snow
194 condition. The local snow condition was positive if the plot had higher snow depths or longer
195 period of snow cover than the regional average around the plot, and negative if the snow
196 depth at the plot was lower or the length of snow cover was shorter than the regional average.

197 Topography may affect moose habitat use (e.g. Leblond et al., 2010) and thereby the
198 browsing pressure. We used distance to ridge as a descriptor of topography. Ridges were
199 recognised by applying a terrain algorithm at a raster digital elevation model with resolution
200 25*25 m. The algorithm defined a pixel as a ridge if none or only one of the eight neighbour
201 pixels had higher elevation. We used the minimum Euclidian distance from a plot to a ridge
202 as measure of distance to ridge.

203 We chose four *a priori* set spatial scales, S , to calculate browse abundance: 1)
204 Browsing patch (BP), which is the sampling unit (12.5 m², radius = 2 m), and is the area
205 available for a moose standing in a foraging bout; 2) Forest stand (FS) calculated as the mean
206 size of forest stands in the study area (2 ha, radius = 80 m), which is the basic operational
207 scale of silviculture; 3) Moose home range (HR, 10 km², radius = 1750 m), which represents

208 the average winter home range size of moose in Scandinavia (Cassing et al., 2006; Olsson et
209 al., 2011; Roer and Gangsei, 2008; Rolandsen et al., 2010); and 4) Municipality (MUN),
210 calculated as the mean forested area within a municipality in the study area (415 km², radius
211 = 11.5 km), which represents the spatial scale of moose management and strategic scale for
212 forest management.

213 For each sampling plot we assigned species-specific browse abundance as the species-
214 specific number of browsed and un-browsed trees. The alternative browse (i.e. other browse
215 than pine) was later classified into selected and non-selected browse based on the level of
216 browsing given the abundance (see below). For spatial scales larger than the browsing patch
217 level, we averaged the species-specific number of trees for all plots within a distance that
218 represented a circle with area of the scale of interest. The abundance measures were
219 calculated as number of browsed and un-browsed trees per 12.5 m² (Table 1). The ratio
220 between selected and total browse was used as an index of the quality of the browse within
221 the patch. As measures of differences in browse characteristics between a patch and the
222 surroundings (Δ Pine, Δ Quality, Δ Total), we used the differences between patch-scale browse
223 measures and larger-scale browse measures. High values mean that the patch had more total
224 browse, pine browse, or higher quality than the average plot within the respective scale radius
225 (forest stand, home range, or municipality scale).

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

229

230 *2.4. Statistical analyses*

231 We analysed the probability that a pine tree within a patch was browsed or not (i.e. at least
232 one twig on a tree was removed by moose) by logistic regression with logit link and binomial

233 family. The dependent variable was the number of pine trees with browsing vs the total
234 number of pine trees in the patch. Because pine damage is a problem primarily in young
235 stands, for the response variable we only included sample plots in forest height class II (0.5 –
236 4 m, i.e. trees that were within browsing reach of moose during winter). To account for
237 potential interdependencies between observations (e.g. Bolker et al., 2009), we added sub-
238 area, transect identity and plot identity as random factors in a mixed model setting for all our
239 analyses. Plot identity was added to reduce over-dispersion and to avoid plots with many pine
240 trees being weighted more in the analyses than plots with few pine trees.

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

254 Next we assessed how abiotic factors (local and regional snow condition, forest
255 productivity, distance to ridge) affected pine browsing. See Table 2 for the global model and
256 valid candidate models. The most important variables were used as baseline models that were
257 retained in all further analyses.

258 We then added scale-specific estimates of browse abundance and browse quality to the
259 baseline models, separately for each spatial scale S . To describe the browse characteristics,
260 we used abundance of pine (Pines), total browse abundance (not including pine, Totals), and
261 quality of browse (selected / total browse, Quality_S). The interaction between total abundance
262 and quality is the amount of selected browse, and if this was significant it suggested that it is
263 the preferred browse alone, and not the total browse, that is important for pine browsing. As a
264 final step, we combined the highest ranked scale-specific models into multi-scale models and
265 re-ran AICc-based model selection. We did this to investigate whether significant
266 relationships at one spatial scale were captured by patterns at larger or smaller spatial scales.

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

273 Ranking of candidate models and evaluation of variables importance for explaining
274 pine browsing was done based on AIC, corrected for small sample size (AICc; Burnham and
275 Anderson, 2002). The dependent variable and random structure were similar for all models
276 and AICc-values could therefore be compared directly among models from different spatial
277 scales. Accordingly, we used AICc-values to assess which spatial scale that best predicted
278 pine browsing, and whether the absolute or relative browse characteristics best explained pine
279 browsing. We therefore report both the Δ AICc-value for comparison of models within a
280 spatial scale, and the absolute AICc-value to ease the comparison across spatial scales and
281 between absolute and relative browse measures. The baseline models were retained in all

282 candidate models regarding alternative browse. If an interaction was included in a candidate
283 model, the main effects were also kept in the model.

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

288

289 **3. Results**

290 *3.1. Overall browsing pattern*

291 The probability that a pine tree was browsed ($\beta_{\text{Pine}} = 0.473$, 95% CI: 0.416; 0.526) was not
292 significantly different from the overall browsing probability ($\beta_{\text{All}} = 0.505$, 95% CI: 0.472;
293 0.537, Fig. 2), suggesting that moose utilise pine in a non-selective browsing pattern. Juniper
294 (*Juniperus communis*), oak, rowan-aspen-goat willow (RAG) and other willow species (*Salix*
295 spp.) had a higher probability of being browsed than the overall browsing probability (β_{Juniper}
296 = 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:
297 0.732; 0.813, $\beta_{\text{Willow}} = 0.735$, 95% CI: 0.676; 0.786, Fig. 2), and were considered high quality
298 browse. The browsing probability of birch ($\beta_{\text{Birch}} = 0.494$, 95% CI: 0.440; 0.456) and other
299 deciduous trees ($\beta_{\text{OD}} = 0.486$, 95% CI: 0.423; 0.549) overlapped with the overall browsing
300 probability (Fig. 2). Norway spruce was hardly browsed at all ($\beta_{\text{Spruce}} = 0.014$, 95% CI: 0.005;
301 0.034, Fig. 2). Due to the lack of utilisation of spruce as forage, and that pine and spruce
302 rarely are established in the same forest stand, we omitted Norway spruce from further
303 analyses.

304

305 *3.2. Abiotic factors and pine browsing*

306 The highest ranked model regarding the relationship between pine tree browsing and abiotic
307 variables included local snow depth (SD_{Local}), forest productivity (FP), and their interaction
308 (Table 2). Alternative models with $\Delta AICc < 2$ also included length of snow cover at the
309 regional scale ($SL_{Regional}$), $SD_{Regional}$ or distance to ridge, but SD_{Local} , forest productivity, and
310 their interactions were retained in all high-ranked models so we chose the highest ranked
311 model as the baseline model. According to this model, the browsing probability of pine tree
312 was negatively related to SD_{Local} on patches with high forest productivity (estimate at the
313 logit scale: $\beta = -0.605$, 95% CI: -0.963; -0.248, Fig. 3), whereas in patches with low forest
314 productivity the relationship did not differ from zero (estimate at the logit scale: $\beta = -0.061$,
315 95% CI: -0.390; 0.266, Fig. 3).

316

317 *3.3. Scale-specific browse abundance and pine damage*

318 At the browsing patch scale the highest ranked model included abundance of pine ($Pine_{BP}$),
319 total browse abundance ($Total_{BP}$) and browse quality ($Quality_{BP}$) as well as their two- and
320 three-way interactions (Table 3). No alternative models received considerable support
321 ($\Delta AICc \geq 3.40$). Pine browsing was positively related to $Quality_{BP}$ if $Total_{BP}$ was low and
322 $Pine_{BP}$ was high, and if $Total_{BP}$ was high and $Pine_{BP}$ was low (Fig. 4A). In contrast, if both
323 $Total_{BP}$ and $Pine_{BP}$ was high, there was a negative relationship between $Quality_{BP}$ and pine
324 browsing probability (Fig. 4A), suggesting that a high abundance of high-quality browse
325 decreases the pine browsing only if the abundance of pine is high.

326 The highest ranked model at the forest stand scale included $Pine_{FS}$, $Total_{FS}$ and their
327 interaction, with the second ranked model including only $Pine_{FS}$ and a $\Delta AICc$ of 1.15 (Table
328 3). The highest ranked model suggested that pine browsing was higher if $Pine_{FS}$ was low and
329 $Total_{FS}$ was high, and low if both $Pine_{FS}$ and $Total_{FS}$ were high (Fig. 4B). When pine

330 abundance was high while total browse abundance was low, or if both pine and total browse
331 abundance was low, then pine browsing was intermediate (Fig. 4B).

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

337 The highest ranked model at the municipality scale included Pine_{MUN}, Total_{MUN},
338 Quality_{MUN} and the interaction between Pine_{MUN} and Total_{MUN} (Table 3). These variables and
339 the interaction were included in three of the five highest ranked models, giving support to
340 their importance in explaining the browsing probability of pine trees. According to the
341 highest ranked model, pine browsing was negatively related to the browse quality at the
342 municipality scale (Fig. 4D). In addition, the probability of pine browsing was high if
343 Pine_{MUN} and Total_{MUN} was low, whereas it was lowest when Pine_{MUN} was high and Total_{MUN}
344 was low (Fig. 4D).

345

346 *3.4. Multi-scale and relative browse abundance and pine damage*

347 Across spatial scales, the municipality level model had lowest AICc-value and thus best
348 explained the variation in pine tree browsing among patches. The forest stand model had the
349 highest AICc-value, 11.63 higher than the best model at the municipality level (Table 3).

350 When we combined the highest ranked scale-specific models (Table 3) to a multi-scale model
351 and ran AICc-based model selection on the full model, the highest ranked model did not
352 include any browse measures at the forest stand scale (Table 4). This multi-scale model had a
353 considerably lower AICc-value than any of the single-scale models ($\Delta AICc = -13.09$),
354 suggesting that spatial variation in pine browsing is a result of abundance and quality of

355 browse at multiple spatial scales. Parameter estimates from the highest ranked multi-scale
356 model did not deviate much from corresponding estimates from the single-scale models
357 (Table 5), and therefore the browsing pattern were similar to those shown in Fig. 4A-D.

358 None of the scale-specific models explaining pine browsing with relative browse
359 abundance (Δ Pine, Δ Quality and Δ Total) received support from AICc-values (Table 6).
360 Accordingly, the absolute abundance and quality of browse at multiple spatial scales was
361 better predictor for pine browsing in a patch than the relative differences in these variables
362 between the patch and its surroundings.

363

364 **4. Discussion**

365 Moose browsing on young pine trees have a high impact on the quality and value of the
366 timber (Bergqvist et al., 2013; Edenius et al., 2002). We used an extensive dataset on spatial
367 variation in browse abundance to describe the relationship between level of pine browsing by
368 moose and browse characteristics, as well as environmental characteristics. Our results
369 suggest negative relationships between the level of pine browsing and abundance and/or
370 quality of browse at multiple spatial scales (Fig. 4), supporting that young pine trees receive
371 associational resistance from alternative browse. Moreover, the absolute values of browse
372 characteristics better explained pine browsing level compared to relative differences in
373 browse characteristics between a browsing patch and its surroundings. The results suggest
374 that forest damage from moose browsing is a result of factors operating at multiple spatial
375 scales. However, the large-scale administrative units for moose and forest management
376 (municipality level) best captured the variation in pine damage by moose, suggesting that
377 strategic planning to reduce forest damage by moose requires large-scale collaboration
378 between forest owners.

379 We measured browsing and abundance at the tree level, that is, a tree was browsed or
380 not, and all trees counted equally in the browse abundance estimates, giving clear
381 repeatability and comparability between individual trees. This simplification of the rather
382 complex foraging environment of the moose was done of two main reasons. The first reason
383 is related to how young pine trees are damaged by moose. The most common browsing
384 pattern is removal of the apical leader shoot first (Bergqvist et al., 2001, 2013). Such
385 browsing damages the tree stem and greatly reduces the economic value of the timber.
386 Further browsing intensity will thus not cause major additional damage to timber value, until
387 the browsing intensity reach a level that greatly reduces growth (more than 30% of twigs
388 removed; Danell et al., 1991b; Edenius et al., 1995; Hester et al., 2004; Speed et al., 2013).
389 Accordingly, our decision to simplify recording of browsing into browsed vs un-browsed
390 trees is based on the assumption that this will give a sufficiently robust indication of impacts
391 related to the economic value of the timber. The second reason is related to how silvicultural
392 operations such as pre-commercial thinning and cleaning are done. These operations are
393 performed at the tree level, i.e. the operator chooses to remove a tree of a certain species or
394 not. However, species differ in how much biomass moose forage they provide, both with
395 respect on the biomass of a twig and the number of twigs per tree. Still, for the practical
396 operations the most relevant information is considered to be whether or not the abundance of
397 trees of a specific species affects the likelihood that pine is browsed.

398 Of the abiotic factors, only local snow depth and site productivity influenced the level
399 of pine browsing, with a negative relationship between snow depth and pine browsing at
400 high-productive sites (Fig. 3). Moose movement is likely to be influenced by snow conditions
401 (Leblond et al., 2010). Our result suggests that it is the local snow depth relative to the
402 regional mean that affects pine browsing, and not the absolute depth. This means that a
403 region with low snow depths experienced as much pine browsing as a region with high snow

404 depths, but within a region, local variation in snow depths can have a great impact on the
405 level of pine browsing, particularly on sites of high productivity. The pattern remained even
406 after accounting for abundance and composition of alternative browse, which suggests that
407 the effect of snow condition is not caused by a confounding relationship between snow
408 condition and available browse.

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

423 Our results suggested that pine browsing is related to the characteristics of alternative
424 browse in complex ways that differ among the spatial scales. The species-specific browsing
425 (Fig. 2) confirmed previous findings that oak, rowan, aspen, willow species, and juniper are
426 important parts of moose winter diet and heavily browsed if available (Kullberg and
427 Bergström, 2001; Månsson et al., 2007b; Wam and Hjeljord, 2010). Accordingly, we could
428 expect that these species will have a higher impact on the browsing pressure than species that

429 are less selected (birch and other deciduous species, Fig. 2), either by making areas with high
430 abundance of such species more attractive and increasing the overall browsing pressure
431 (associational susceptibility; Bergman et al., 2005; Milligan and Koricheva, 2013; Wallgren
432 et al., 2013), or by decreasing the browsing pressure on non-attractive species (associational
433 resistance; Atsatt and O'Dowd, 1976; Ward et al., 2008). We found a lower probability of
434 pine browsing at high quality of the alternative browse at both the patch and municipality
435 scale supporting the associational resistance hypothesis (Fig. 4). However, at the browsing
436 patch scale this relationship was only found at high pine abundances in the patch (Fig. 4),
437 which suggests that the spatial resistance from high-quality forage that leads to reduced pine
438 browsing at the municipality scale only operates when pine abundance is high at the browsing
439 patch scale. Similar interactions were also found between pine abundance and total
440 abundance of alternative browse at the browsing patch, forest stand, and municipality scale
441 (Table 3). Although pine was browsed far less than many other species (Fig. 2) and thus is
442 considered less preferred food resource (Kullberg and Bergström, 2001; Månsson et al.,
443 2007b; Wam and Hjeljord, 2010), our results suggest that some pine browsing will always
444 occur even if there is high abundance of alternative browse of high quality (Edenius, 1991).
445 Herbivore foraging patterns represent a complex process involving many physiological and
446 behavioural mechanisms affecting diet composition (DeGabriel et al., 2014). Pine can offer
447 some important compounds that the more selected browse species not contain (Timmons et
448 al., 2010), and diversity in availability of plant species may be an important driver for
449 browsing pressure and diet diversity (Milligan and Koricheva, 2013).

450 The relationship between pine browsing and browse characteristics received support at
451 several spatial scales (Table 3, Fig. 4), but the models at the municipality scale received
452 strongest support (lowest AICc-value, Table 3). This may be because larger spatial scale
453 captures factors such as moose density and landscape characteristics (Cassing et al., 2006;

454 Månsson, 2009). These factors may also influence moose space use (Bjørneraas et al., 2012),
455 and any management actions that seek to incorporate the scale of moose space use should
456 acknowledge the large individual and regional variation that is present in our estimate of
457 average winter home range size of 10 km². Other studies that have assessed moose browsing
458 at the individual moose level suggest that foraging behaviour is mostly related to the tree
459 level characteristics such as species and twig abundance (e.g. Andersen and Sæther, 1992;
460 Danell et al., 1991a). However, for forest management it is the sum of browsing decisions of
461 multiple individuals during the winter that determines the overall level of pine browsing and
462 damage, and this may best be explained by large-scale descriptors of moose forage
463 availability and quality (Cassing et al., 2006). This spatial scale corresponds well with the
464 current spatial scale of moose management, which supports the proposal that moose should
465 be managed at a scale that captures the spatial distribution of a moose population (Nilsen et
466 al., 2009). Reducing forest damage by moose must therefore be solved by adopting
467 management actions at spatial scales larger than common silvicultural management units
468 such as forest stands and most forest estates.

469 The relative differences in browse characteristics between the browsing patch scale and
470 larger spatial scales did not have higher explanatory power than absolute values (Tables 3, 6).
471 Moreover, parameter estimates from the single-scale models did not differ much from
472 corresponding estimates from the multi-scale models, which implies that the observed pattern
473 at a specific scale was not confounded by relationships at larger spatial scales. These findings
474 suggest that browse characteristics at the patch scale and the larger spatial scales operate on
475 pine browsing more or less independent of each other (Cassing et al., 2006; Månsson et al.,
476 2007a). It has been suggested that animal resource utilisation can be considered a hierarchical
477 process, going from large-scale environmental conditions affecting the distribution of the
478 species, to selection of home range, habitat types, and finally resource items (e.g. trees and

479 twigs) at the finest scale (Johnson, 1980), and that mechanisms and factors involved in
480 shaping utilisation patterns at one spatial scale are not necessarily important at a different
481 spatial scale (Herfindal et al., 2009; Johnson et al., 2001, 2002; Nikula et al., 2004). If this
482 also is the case for moose browsing patterns as suggested by our results, mitigation actions
483 should be done hierarchically at multiple spatial scales simultaneously (Gordon et al., 2004;
484 Weisberg and Bugmann, 2003). First, strategic planning of objectives, targets and indicators
485 for forest and moose should be done at the municipality scale. It could be argued that this
486 would be more practical to solve at the forest estate scale. However, the structure of forest
487 estates in Norway is diverse, with a few very large properties and many very small.
488 Accordingly, for most forest owners their forest estate is far too small to capture the spatial
489 scale needed to have any significant impact on the browsing pressure on pine. Moreover,
490 municipalities are highly involved in moose management and integration of wildlife and
491 forest management objectives should be done at this scale. Second, silvicultural operation at
492 the estate and forest stand scales should contribute to these large-scale objectives. As an
493 example, regeneration of pine on clear-cuts should focus on high stocking rate. Yet the
494 optimal stocking that simultaneously minimizes damage by moose and intraspecific
495 competition is unknown. Reduction in growth due to competition could also mean a longer
496 time to escape browsing (Heikkilä and Härkönen, 1996), but this could be balanced by a
497 lower risk of browsing. Similarly, although intensive and early pre-commercial thinning has
498 been reported to provide the greatest diameter growth (Huuskonen and Hynynen, 2006), this
499 advantage can be reduced by a higher browsing risk for residuals trees.. Third, at the scale
500 of forest workers having to make decisions on which competing stems to clear or leave, pre-
501 commercial thinning rules should be done with caution, favouring keeping preferred
502 deciduous stems if pine density is high, as these will provide associational resistance. At low
503 pine densities, however, cleaning of deciduous browse may reduce pine browsing.

504

505 **Acknowledgements**

506 We thank Olav Hjeljord for assistance with the field survey design. The project was
507 supported by the Research Council of Norway (RCN project #215647/E40; Intensified
508 harvesting of forests – implications for enterprises related to wild and domestic ungulates).
509 We thank two anonymous referees for helpful comments on the manuscript.

510

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714

715

716 Tables

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

Name (Abbreviation)	Description
Forest height class	0: cleared the previous year, I: height of focal tree species < 50 cm, II: height between 50 and 400 cm, III: height between 4 and 10 m, IV: height > 10 m.
Forest productivity (FP)	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 ($HSI > F11$).
Regional snow depth (SD_{Regional})	Mean snow depth during period with snow cover, averaged over the municipality scale of for each sample plot.
Local snow depth (SD_{Local})	The difference between the mean snow depth during days with snow cover at the browsing patch (BP) and its regional snow depth ($SD_{\text{BP}} - SD_{\text{Regional}}$). SD_{Local} indicates whether snow depth at the browsing patch is higher or lower than the regional mean.
Regional length of snow cover (SL_{Regional})	The number of days with > 50 cm of snow, averaged over the municipality scale of each sample plot.
Local length of snow cover (SL_{Local})	The difference between the number of days with snow cover > 50 cm at the browsing patch and the regional length of snow cover ($SL_{\text{BP}} - SL_{\text{Regional}}$). SL_{Local} indicates whether the length of the period with snow cover at the location is longer or shorter than the regional mean.
Distance to ridge (DR)	Distance from a sample plot to the closest pixel ($25 \times 25 \text{ m}^2$) 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).
Total browse abundance	The abundance of all browse species, except pine. $Total_{\text{BP}}$ is number of

(Total _{BP} , Total _{FS} , Total _{HR} , Total _{MUN})	trees in the browsing patch (12.5 m ²). 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 km ²), MUN = municipality (415 km ²).
Pine abundance (Pine _{Scale})	The abundance of pine trees at a given spatial scale, where "Scale" is BP, FS, HR, or MUN (see above).
Browse quality (Quality _{Scale})	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).
Browse difference (Δ Pine _{Scale} , Δ Quality _{Scale} , Δ Total _{Scale})	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.

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720

721 Table 2. AICc-based ranking of candidate models with abiotic factors explaining the
 722 probability that a pine tree was browsed by moose. For variables abbreviation, see Table 1.

Dependent	FP	SD _{Regional}	SL _{Regional}	SD _{Local}	SL _{Local}	DR	DR ²	SF*SD _{Local}	SF*SL _{Local}	SF*DR	SF*DR ²	ΔAICc	AICc-w
Tree level	X			X				X				0.00	0.087
browsing	X		X	X				X				1.08	0.051
	X	X		X				X				1.27	0.046
	X			X		X		X				1.37	0.044
	X			X	X			X				2.06	0.031

723

724 Table 3. AICc-based ranking of models of pine browsing by moose in relation to abundance
 725 of pine and abundance and quality of alternative browse at four spatial scales. The baseline
 726 model (see Table 2) was included in all candidate models. The highlighted model is the best,
 727 according to AICc, among all four spatial scales.

Scale	Pine	Quality	Total	Pine*Quality	Pine*Total	Quality*Total	Pine*Quality*Total	AICc	Δ AICc	AICc-w
Browsing patch	X	X	X	X	X	X	X	1132.54	0.00	0.564
	X	X		X				1135.94	3.40	0.103
	X	X	X	X	X			1137.23	4.91	0.054
								1137.82	5.91	0.040
	X		X	X				1138.03	5.81	0.036
Forest stand	X		X		X			1136.13	0.00	0.194
	X							1137.28	1.15	0.109
								1137.82	1.69	0.083
	X	X	X		X			1137.91	1.78	0.080
	X	X	X	X	X			1138.09	1.96	0.073
Home range	X							1126.76	0.00	0.208
	X	X						1127.14	0.37	0.173
	X		X					1127.56	0.79	0.140
	X		X		X			1128.18	1.42	0.103
	X	X	X					1128.49	1.72	0.088
Municipality	X	X	X		X			1124.50	0.00	0.221
	X	X	X	X				1124.87	0.37	0.184
	X	X	X	X	X			1125.60	1.10	0.128
	X	X		X				1125.90	1.40	0.110
	X	X	X		X	X		1126.58	2.07	0.078

728

729

730 Table 4 AICc-based ranking of multi-scale models explaining the probability that a pine tree
 731 in a browse patch was browsed by moose. The baseline model (see Table 2) was included in
 732 all candidate models. Explanatory variables and interactions were chosen from the highest
 733 ranked single-scale models (Table 3).

PineBP	QualityBP	TotalBP	PineBP*QualityBP	PineBP*TotalBP	QualityBP*TotalBP	PineBP*QualityBP*TotalBP	PineFS	TotalFS	PineFS*TotalFS	PineHR	PineMUN	QualityMUN	TotalMUN	PineMUN*TotalMUN	AICc	ΔAICc	AICc-w
X	X	X	X	X	X	X				X	X	X	X	X	1111.41	0.00	0.158
X	X	X	X	X	X	X	X	X		X	X	X	X	X	1113.04	1.63	0.069
X	X	X	X	X	X	X	X			X	X	X	X	X	1113.51	2.09	0.055
X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	1114.035	2.62	0.042
										X	X	X	X	X	1114.54	3.12	0.033

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735

736

737 Table 5. Parameter estimates (SE) for the highest ranked single-scale models (Table 3) and
 738 the multi-scale model (Table 4). All estimates are at the logit scale. See also Fig. 4.

739

Variable	Single-scale estimates	Multi-scale estimates
Pine _{BP}	0.011 (0.045)	0.033 (0.044)
Quality _{BP}	-0.461 (0.960)	-0.128 (0.940)
Total _{BP}	0.008 (0.022)	0.012 (0.022)
Pine _{BP} *Quality _{BP}	0.260 (0.218)	0.240 (0.212)
Pine _{BP} *Total _{BP}	-0.001 (0.004)	-0.001 (0.003)
Quality _{BP} *Total _{BP}	0.165 (0.071)	0.148 (0.069)
Pine _{BP} *Quality _{BP} *Total _{BP}	-0.053 (0.019)	-0.049 (0.018)
Pine _{FS}	0.059 (0.123)	
Total _{FS}	0.056 (0.046)	
Pine _{FS} *Total _{FS}	-0.025 (0.012)	
Pine _{HR}	-2.065 (0.591)	-1.670 (0.596)
Pine _{MUN}	-11.906 (3.512)	-9.544 (3.380)
Quality _{MUN}	-6.569 (1.813)	-5.066 (1.762)
Total _{MUN}	-1.064 (0.406)	-1.102 (0.396)
Pine _{MUN} *Total _{MUN}	1.395 (0.653)	1.381 (0.639)

740

741

742 Table 6. AICc-based ranking of models regarding pine browsing by moose in relation to the
 743 abundance of pine and alternative browse in the browsing patch relative to that found at three
 744 larger spatial scales. See Table 1 for details regarding the explanatory variables. The baseline
 745 model (see Table 2) was included in all candidate models. The highlighted models are the
 746 best, according to AICc, across all spatial scales.

Scale	Δ Pine	Δ Quality	Δ Total	Δ Pine* Δ Quality	Δ Pine* Δ Total	Δ Quality* Δ Total	Δ Pine* Δ Quality* Δ Total	AICc	Δ AICc	AICc-w
Forest stand								1137.82	0.00	0.282
	X							1139.17	1.35	0.144
			X					1139.48	1.66	0.123
		X						1139.88	2.06	0.100
	X	X	X	X				1140.76	2.94	0.065
Home range								1137.82	0.00	0.182
	X		X	X				1138.54	0.72	0.128
	X							1138.57	0.74	0.126
		X						1139.23	1.41	0.090
			X					1139.88	2.06	0.065
Municipality								1137.82	0.00	0.144
	X							1138.15	0.33	0.122
	X		X	X				1138.47	0.65	0.104
		X						1138.66	0.84	0.095
	X	X		X				1138.75	0.93	0.091

747

748

749 Figure legends

750 Fig. 1. Location of the study areas in Norway.

751

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

756

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

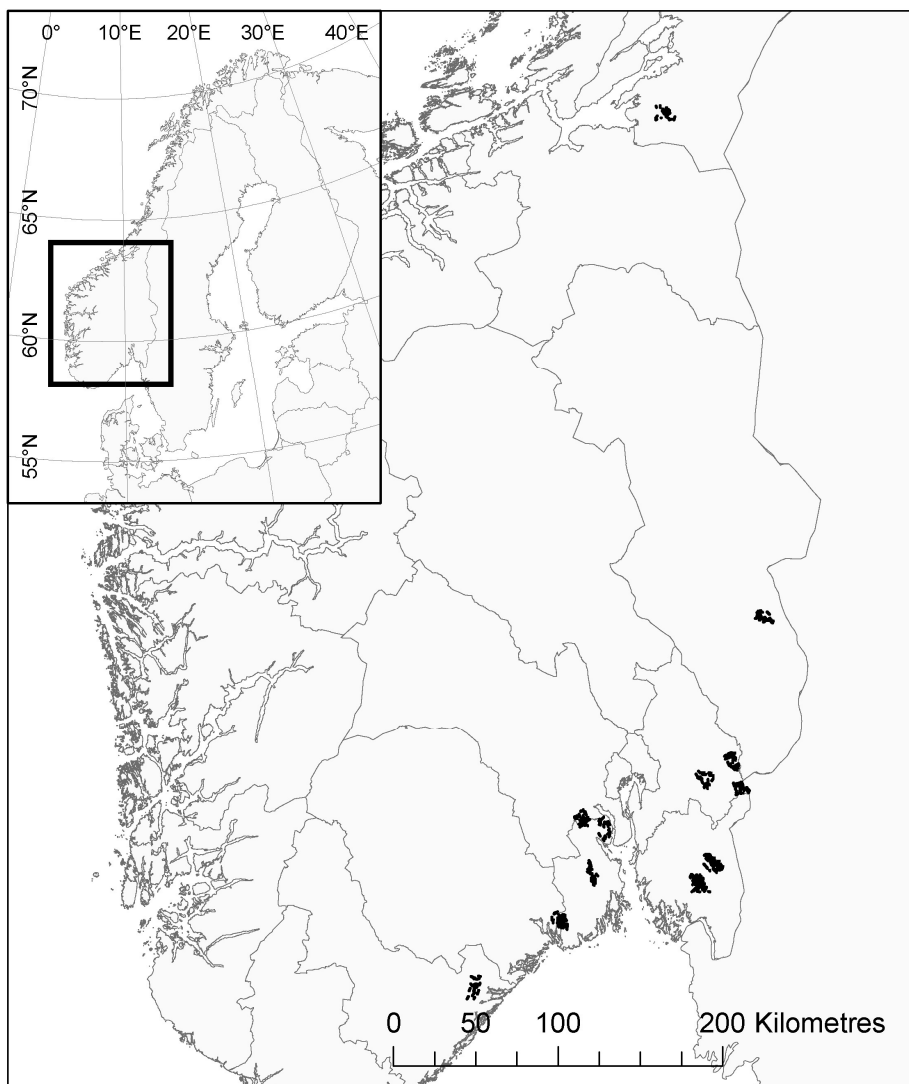
762

763 Fig. 4. The relationship between pine tree browsing probability, and quality of alternative
764 forage measured at four spatial scales; browsing plot (BP, 12.5 m²), forest stand (FS, 10 ha),
765 moose winter home range (HR, 10 km²), and municipality (MUN, 415 km²). The relationship
766 is shown for high and low levels of abundance of pine and total alternative browse at the
767 spatial scales. Relationships are based on the highest ranked models in Table 3 (see Table 5
768 for parameter estimates). If the lines are horizontal the highest ranked model did not include
769 browse quality as explanatory variable.

770

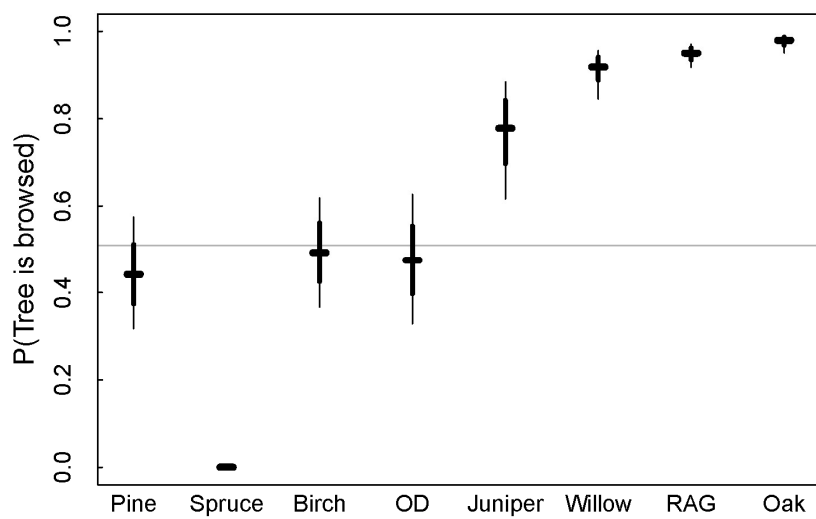
771 Figures

772 Fig. 1



773

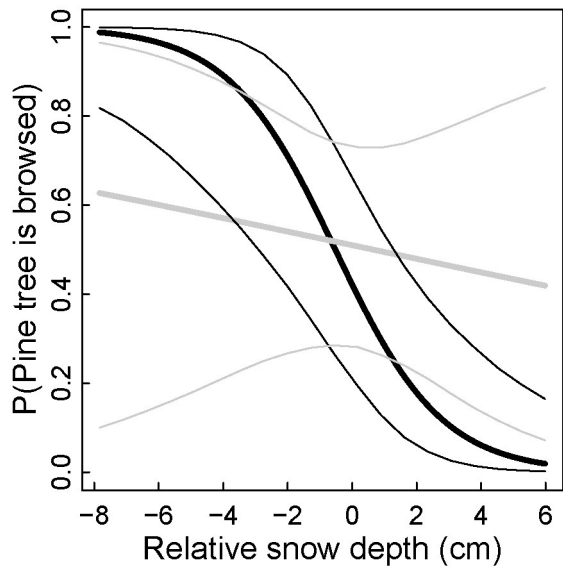
774 Fig. 2



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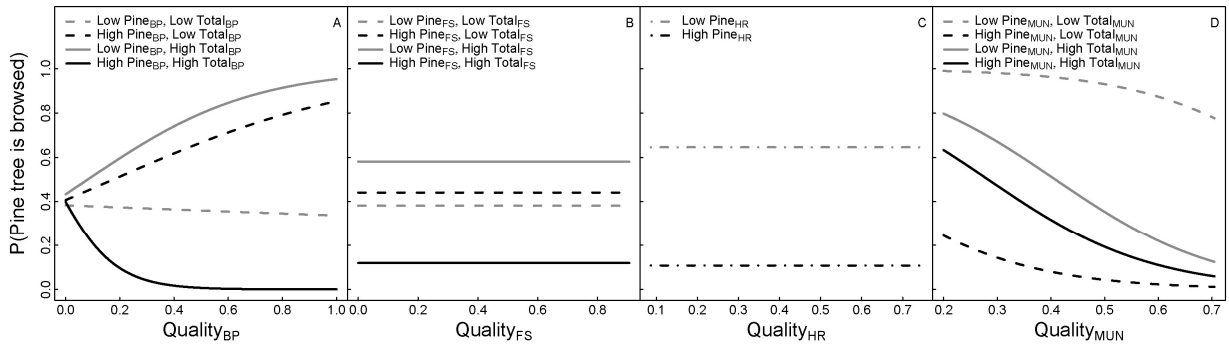
777 Fig. 3



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780 Fig. 4



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