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Title: Landscape structure influences browsing on a keystone tree species in conservation areas

Year: 2020

Version: Accepted version (Final draft)

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Please cite the original version:

Komonen, A., Tuominen, L., Purhonen, J., & Halme, P. (2020). Landscape structure influences browsing on a keystone tree species in conservation areas. *Forest Ecology and Management*, 457, Article 117724. <https://doi.org/10.1016/j.foreco.2019.117724>

1 **Landscape structure influences browsing on a keystone tree species in conservation areas**

2

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8

9 **Abstract**

10 Aspen is a keystone species in boreal forests. The future of aspen in many conservation areas is
11 threatened by ungulate browsing. Our aim was to study the effect of browsing on aspen
12 regeneration and population structure in conservation areas in Central Finland, and the effect of
13 surrounding landscape structure on browsing. Aspen density varied greatly among and within
14 conservation areas. In about half of the conservation areas, middle-sized aspens were scarce or
15 missing, which indicates heavy browsing in the recent past. In addition, the number of dead, large
16 aspens in advanced decay stages were rare. Browsing pressure varied greatly among the areas, but
17 on average, a bit more than half of the living aspens had been browsed. Landscape structure
18 influenced browsing so that increasing proportion of farmland within 1 km and 3 km of the
19 conservation areas decreased browsing pressure. The poor recruitment of aspen in many
20 conservation areas jeopardizes the accumulation of large living and dead aspens. This means that
21 many aspen-associated threatened species are in the risk of local extinction, unless aspen
22 recruitment is enhanced by management.

23

24 Keywords: *Alces alces*, biodiversity, boreal forest, disturbance, landscape, *Populus tremula*

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29 Introduction

30 Keystone species are species, which have – considering their abundance – disproportionate positive
31 effect on biodiversity (Paine 1969, Mills et al. 1993). In boreal forests, aspen (*Populus* spp.) is a
32 keystone species, as it hosts many generalist and specialist species, many of which are red-listed
33 (Worrell 1995, Crites & Dale 1998, Tikkanen et al. 2006). Especially large living and dead aspens
34 provide resources for herbivorous and saproxylic invertebrates, saproxylic fungi, epiphytic lichens
35 and bryophytes, as well as nest sites for birds and mammals. Alkaline aspen litter neutralizes the
36 acidic boreal forest soil, and thus enhances conditions for several ground-living organisms (Koivula et
37 al. 1999, Suominen et al. 2003). The lack of stand-replacing natural disturbances and the high
38 ungulate browsing pressure threaten aspen regeneration in many regions (Romme et al. 1995,
39 Latva-Karjanmaa et al. 2007, Myking et al. 2011, Beschta et al. 2018), which may cause deterministic
40 local extinctions of threatened aspen-associated species (Kouki et al. 2004).

41 Eurasian aspen (*Populus tremula* L.) is a fast-growing pioneer tree that is not commercially valuable
42 in Fennoscandia. It competes with trees that are more valuable and is the host for pine twisting rust
43 (*Melampsora pinitorqua*). Thus, aspens have been extensive removed from managed forests and,
44 consequently, large living and dead aspens have become scarce (Latva-Karjanmaa et al. 2007,
45 Myking et al. 2011). Although modern forest management acknowledges the importance of aspen
46 for biodiversity and aims to retain aspen trees in forestry operations, conservation areas are crucial
47 in maintaining natural aspen population structures in the long-term. Aspen reproduces both sexually
48 by seeds and asexually by root suckers; sexual regeneration occurs mainly after forest fires and
49 other stand-replacing disturbances (Bärring 1988, Worrell 1995, Turner et al. 2003). In the absence
50 of such disturbances, aspens persist as individual canopy trees, and recruitment occurs only after
51 occasional gap disturbances from root suckers (Cumming et al. 2000). However, this recruitment is
52 not sufficient to replace the dying canopy trees (Latva-Karjanmaa et al. 2007), especially due to high
53 browsing pressure on young age cohorts in many conservation areas (Kouki et al. 2004, Myking et al.
54 2011). In Finland, only about 10% of the present aspen volume in old-growth forests has been
55 estimated to remain over the next 100 years (Latva-Karjanmaa et al. 2007).

56 Browsing has diverse effects on tree individuals and populations. It affects vegetative and seedling
57 recruitment, growth rate, morphology, size, seed production, chemical defense and longevity
58 (reviewed in Myking et al. 2011). The legacy of past browsing is revealed in the size-structure of
59 aspen populations in that missing or scarce age cohorts indicate past browsing pressure (Kouki et al.
60 2004, Edenius & Ericsson 2007). Many mammals, such as moose (*Alces alces*), roe deer (*Capreolus*

61 *capreolus*) and mountain hare (*Lepus timidus*) browse aspen (Helle 1980, Hjältén et al. 2004, de
62 Chantal & Granström 2007), but browsing by large ungulates is often the most important source of
63 growth loss or mortality (Edenius et al. 2002a, Härkönen et al. 2008, Beschta et al. 2018). In
64 Fennoscandian and Central Finnish boreal forests, moose is by far the most abundant large ungulate.
65 Clear-cut forestry provides saplings as abundant food for moose, and thus sustains large population
66 size (Edenius et al. 2011, Myking et al. 2011). Moose prefers aspen in its diet (Månsson et al. 2007),
67 and in some conservation areas moose can browse nearly 100% of small aspens (Härkönen et al.
68 2008). In recent decades, also roe deer has become more abundant in Central Finland (Burbaite &
69 Csányi 2009; Natural Resources Institute Finland 2019b).

70 Habitat selection of ungulates is a hierarchical process guided by local and landscape factors.
71 Landscape structure and land use affect the habitat selection of ungulates directly and indirectly
72 (Cederlund 1983, Ericsson et al. 2001, Edenius et al. 2002b, Kjellander et al. 2004, Nikula et al. 2004,
73 Dussault et al. 2005). For example, aspen stands near young pine forests may attract moose
74 (Ericsson et al. 2001), whereas roe deer avoids wetlands and clear cuts (Cederlund 1983). Due to
75 variation in habitat selection, ungulate densities and hence browsing pressure vary spatially
76 (Cederlund 1983, Ericsson et al. 2001, Edenius et al. 2002a, Kjellander et al. 2004). At the stand scale,
77 aspen density may or may not influence foraging behavior and browsing pressure (Ericsson et al.
78 2001, Edenius et al. 2002b). Older forests (e.g. conservation areas) may function as refuges for aspen
79 regeneration if browsers avoid them or there are large sapling stands available nearby (Ericsson et
80 al. 2001). Habitat selection differs also between seasons; for example, in winter open areas with
81 deep snow are avoided (Cederlund 1983, Nikula et al. 2004, Dussault et al. 2005). Although the
82 effect of ungulate browsing on aspen regeneration and population structure have been studied
83 earlier, there are few explicit analyses at the landscape scale.

84 Our overall aim was to investigate the effect of browsing on aspen regeneration in conservation
85 areas. More specifically, our aim was to investigate the relationship between landscape structure,
86 aspen population structure and browsing. Our study questions and hypotheses were: 1) What is the
87 size distribution of aspen in conservation areas? We predict that aspens with diameter at breast
88 height (dbh) 5 cm - 15 cm are underrepresented, due to a high browsing pressure. 2) How does the
89 landscape structure influence browsing pressure in conservation areas? We predict the larger the
90 area of agricultural land and young forest, the higher the probability of browsing.

91 2 MATERIALS AND METHODS

92 2.1 Study areas

93 This study was conducted in the year 2017 in Central Finland, belonging to the boreal vegetation
94 zone (Ahti et al. 1968). After excluding three National parks as too large in comparison with the
95 other conservation areas, as well as lake, island and peatland sites, the study sites ($n = 23$) were
96 randomly selected from the total of 131 suitable sites (Appendix 1). The size of the conservation
97 areas varied from 1 to 206 hectares. The maximum tree age ranged from 83 to 174 years (mean =
98 126) (Appendix 2). Total tree volumes ranged from 93 to 289 m^3ha^{-1} (mean = 190). Based on tree
99 volumes, almost all sites were dominated by conifers. About half of the sites were dominated by
100 spruce and another half by pine; a few sites had rather equal share of spruce, pine and broadleaved
101 trees. Mesic heath forest covered the largest area in most conservation areas.

102 In 2016, the year prior to our fieldwork, moose density in the study region was 4.0-4.5 animals per
103 1000 ha, and in 2015 it was 3.5-4.0, respectively (Natural Resources Institute Finland 2019a). In
104 general, the moose density is rather uniform across Central Finland at the 5 km x 5 km resolution.
105 There are no density estimates for roe deer and hare, but the annual harvest of roe deer in Central
106 Finland was 81 in the year 2015 and 210 in 2016; these statistics are based on hunters' voluntary
107 reports.

108 2.2 Field methods

109 Aspen and browsing data were collected from eight randomly placed plots (20 m x 20 m) in each
110 conservation area, which equals 0.32 hectares per area. Within the plots, all living and dead aspens
111 were counted. The height was measured for all saplings ≤ 130 cm and the diameter at breast height
112 (dbh) for all trees > 130 cm. All individual stems were treated as separate individuals and divided in
113 six size classes: 1) height ≤ 130 cm, 2) height > 130 cm and dbh < 5 cm, 3) dbh 5–14.9 cm, 4) dbh 15–
114 24.9 cm, 5) dbh 25–34.9 cm, and 6) dbh ≥ 35 cm. Dead trees were recorded separately. The decay
115 stage of dead trees was evaluated using a knife method: 1) a knife hardly penetrates the wood, 2) 1–
116 2 cm penetration, 3) 3–5 cm penetration, 4) knife goes in completely, and 5) the wood falling into
117 pieces (only for lying trees) (Siitonen et al. 2000). The browsing damage (yes or no) was recorded for
118 each stem. The mean browsing pressure was calculated as the proportion of aspens with feeding
119 marks in a given size class.

120 Due to constant sampling effort across conservation areas (study plots covered 0.16–32% of the
121 area), smaller areas faced proportionally higher sampling effort than larger; thus, it is possible that
122 the aspen density estimates in the larger areas are less accurate. To test for this, we used the
123 Pearson correlation between the area of the conservation areas and the coefficient of variation
124 among study plots in each site for living aspens. There was no correlation between the area of the
125 conservation areas and the coefficient of variation ($r_p = 0.14$, $n = 21$, $p = 0.53$), suggesting no
126 substantial bias.

127 **2.3 GIS analyses**

128 The landscape structure, more specifically the land use and forest characteristics within and around
129 the conservation areas were estimated to model its relationship with browsing. Land use types were
130 obtained from the CORINE Land Cover data from year 2012 with pixel size 20 m x 20 m (CORINE land
131 cover, 2012, Shape, 2016-10-04, Finnish Environment Institute, CSC). Similar land use types were
132 merged to reduce the number of variables in the statistical model (Appendix 3); for example, urban
133 areas, roads and mining sites were grouped together as browsers likely avoid these areas. Tree age,
134 forest type and tree volume data are based on the National Forest Inventory (Natural Resources
135 Institute Finland 2015). Mature forests were separated from young forests (< 20 years old). Mature
136 mixed forests and coniferous forests were merged. Young forests, sapling forests and transitional
137 forests (including clear-cuts) were merged. Water bodies and wetlands were merged.

138 In the GIS analysis, we calculated the proportion of each land use class within 1 and 3 km radii from
139 the center point of each conservation area, using the coordinate center point of each conservation
140 area as the center point for the buffers; the conservation areas were included within the buffers.
141 These radii were chosen because they reflect both the size of roe deer (0.5-1 km²; Kjellander et al.
142 2004) and moose territories (10-20 km²; Cederlund & Sand 1994), respectively. The home range size
143 of mountain hare is similar to roe deer (Dahl & Willebrand 2005, Kauhala et al. 2005). All pixels that
144 had their center point inside the buffers were included. With a 1000 m radius, the circles of
145 Palosenranta and Vuorilammi were overlapping 9%, and with a 3000 m radius 50%. Because the
146 overlap was minor, the overlapping areas were included in the analyses. The estimations were
147 conducted with ArcGIS program.

148 2.4 Statistical analysis

149 To study the relationship between landscape structure and aspen browsing, we used mixed effects
150 logistic regression (McCullagh & Nelder 1989). The response variable was the presence or absence of
151 browsing damage on each living aspen (≤ 130 cm). Because the proportion of living aspens (≤ 130
152 cm) browsed, correlated strongly with the proportion of living aspens (dbh < 5 cm) browsed ($r_p =$
153 0.941, $n = 21$, $p < 0.01$; these categories were not mutually exclusive), our analysis was robust to the
154 chosen size classification. Two conservation areas did not have living aspens in this size category, so
155 these were excluded from the analyses. Explanatory variables were: 1) the size of the conservation
156 area, because it indicates the area of seminatural forest surrounding the study plots and can serve as
157 shelters for moose; 2) the density of aspens (dbh < 5 cm), because aspen thickets could attract
158 moose; and 3) the landscape variables within the 1 km or 3 km radii (Appendix 4). Although our
159 study focused on the landscape characteristics, we also did an additional analysis on the relationship
160 between the local characteristics (maximum tree age, tree-species specific volumes and forest types)
161 of the conservation areas and browsing damage.

162 We standardized the explanatory variables by subtracting their mean and dividing then with their
163 standard deviation. We used logit link function and binomial error distribution, and the site identity
164 was included as random effect affecting the intercept. The analysis was executed with the function
165 “glmer” from the package “lme4” (Bates et al. 2015). A list of models with all possible explanatory
166 variable combinations (only individual effects were included) was constructed by using function
167 “dredge” from the package “MuMIn” (Barton 2019). We performed model selection based on the
168 corrected Akaike information criterion (AICc) (Burnham & Anderson 2002). The model performance
169 was estimated with function “r.squaredGLMM” in the package “MuMIn” (Barton 2019), which
170 calculates the marginal R^2 value for the fixed effects, and the conditional R^2 value for fixed and
171 random effects.

172 Spatial autocorrelation in the proportion of browsed aspens between the study sites (for all aspens,
173 as well as < 130 cm and > 130 cm aspens separately) was analysed using Moran’s I statistic standard
174 deviate with one, two and four nearest neighbours. Because there was no indication of
175 autocorrelation (Moran’s I = -0.77-0.86, $p > 0.24$), final statistical analyses were done without
176 autocorrelation. The statistical analyses were done with R software version 3.5.1 (R core team 2018).
177 The relationship between the size of the conservation area and the density of living aspens was
178 analysed with linear regression, and the relationship between the density of middle-sized aspens

179 and the proportion of browsed aspens with Pearson correlation. These analyses were conducted
180 with SPSS Statistics 24.0

181 **3 RESULTS**

182 **3.1 Aspen population structure**

183 In total, 2313 aspens were recorded in the 184 study plots covering 7.36 hectares. The mean \pm SE
184 density of living and dead aspens was 239 ± 36 and $75 \pm 24 \text{ ha}^{-1}$, respectively (Table 1). The number
185 of living aspens in different size classes varied among conservation areas, but generally the smallest
186 size class was numerically dominant (Figure 1; Appendix 5). In only five areas, there were living
187 aspens in all the size classes. In six areas, large trees ($\text{dbh} \geq 15 \text{ cm}$) were absent, and in seven areas
188 middle-sized aspens ($\text{dbh} = 5 \text{ to } 24.9 \text{ cm}$) were missing. There was a positive relationship between
189 the size of the conservation area and the density of living aspens $\text{dbh} < 5 \text{ cm}$ ($F_{1,21} = 6.2$, $p = 0.02$, R^2
190 $= 0.23$), but not between the area and other size classes. Most dead aspens were small ($\text{dbh} < 5 \text{ cm}$;
191 only 11 dead aspens had $\text{dbh} > 20 \text{ cm}$) and recently died (89% belonged to decay stage 1 or 2)
192 (Figure 2).

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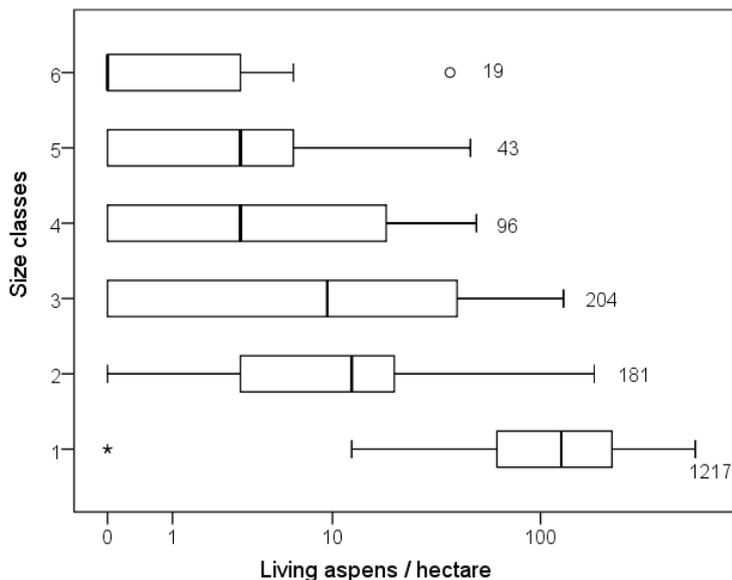
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199

200 **Table 1.** Summary of the aspen population structure in the conservation areas.

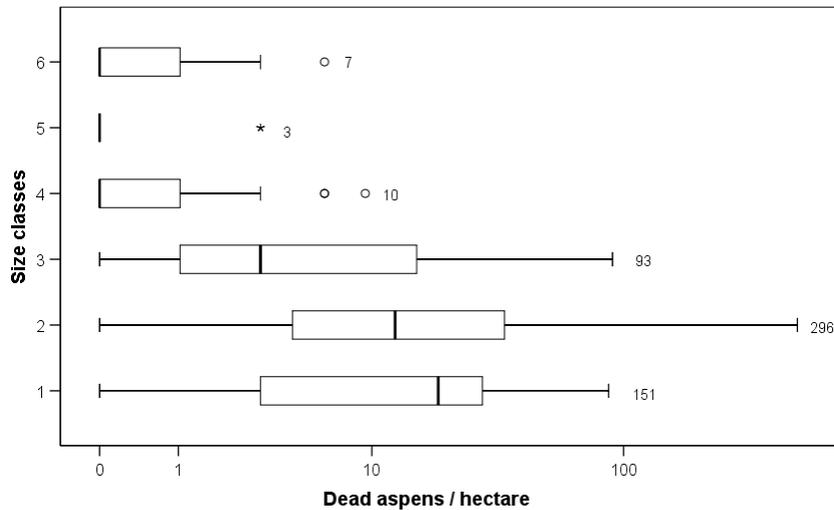
Site	# of small trees ¹	# of large trees ²	# of large trees	Density ³ of trees	Density of small trees ¹	Density of large trees ²	Density of dead trees	Average browsed per plot (SD)	Plots browsed/ not browsed
Hallalähde	25	32	15	178	78	100	47	1.1 (1.8)	3/5
Hintonniemi	42	59	27	316	131	184	84	4.0 (4.3)	5/3
Hirvijärvi	91	8	12	309	284	25	38	7.9 (13.9)	3/5
Hitonhaudanvuori	70	12	20	256	219	38	63	5.5 (7.1)	4/4
Hopeaharju	0	1	1	3	0	3	3	0.0 (0.0)	0/8
Ilvesjoen lehto	53	57	45	344	166	178	141	2.5 (4.6)	4/4
Isolähteenpuro	19	4	4	72	59	13	13	1.5 (2.3)	4/4
Kaitajärvi	115	9	2	388	359	28	6	10.9 (29.2)	4/4
Kanavuori	102	8	17	344	319	25	53	7.9 (10.3)	5/3
Limpsinginrotko	9	0	6	28	28	0	19	1.0 (1.8)	3/5
Listonniemi	138	27	18	516	431	84	56	13.0 (15.8)	6/2
Louhuvuori	42	35	24	241	131	109	75	4.9 (11.1)	4/4
Matolammi	41	2	14	134	128	6	44	4.0 (8.1)	3/5
Metsokangas	168	4	17	538	525	13	53	14.0 (34.0)	4/4
Myllykolun lehto	65	51	176	363	203	159	550	3.5 (5.9)	4/4
Palosenranta	33	0	6	103	103	0	19	2.8 (5.1)	2/6
Rajala	35	2	6	116	109	6	19	3.0 (7.7)	2/6
Ristiniemen lähteikkö	5	3	5	25	16	9	16	0.4 (0.7)	2/6
Ruokomäki	59	3	14	194	184	9	44	6.8 (7.6)	7/1
Ryönien lehto	123	31	62	481	384	97	194	11.0 (10.8)	6/2
Teerikangas	20	0	33	63	63	0	103	0.9 (1.5)	3/5
Tervajärvi	0	0	1	0	0	0	3	0.0 (0.0)	0/8
Vuorilammin alue	143	13	29	488	447	41	91	9.6 (18.45)	5/3
Total	1398	361	554						83/101
Average	61	16	24	239	190	49	75	5.0	3.6

201 1) diameter at breast height < 5 cm; 2) diameter at breast height ≥ 5 cm; 3) all densities are per ha.



202 **Figure 1.** Median density of living aspens in different size classes in the studied conservation areas.
 203 The boxes indicate 25% to 75% percentiles. Whiskers extend to 1.5 times the interquartile range or
 204 to the minimum or maximum values, if there were no outliers. The numbers in the panel indicate the
 205

206 total numbers of trees in different size classes. Size classes: 1) height \leq 130 cm, 2) height $>$ 130 cm
 207 and dbh $<$ 5 cm, 3) dbh 5–14.9 cm, 4) dbh 15–24.9 cm, 5) dbh 25–34.9 cm, and 6) dbh \geq 35 cm.



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209

210 **Figure 2.** Median density of dead aspens in different size classes in the studied conservation areas.
 211 The boxes indicate 25% to 75% percentiles. Whiskers extend to 1.5 times the interquartile range or
 212 to the minimum or maximum values, if there were no outliers. The numbers in the panel indicate the
 213 total numbers of trees in different size classes. Size classes: 1) height \leq 130 cm, 2) height $>$ 130 cm
 214 and dbh $<$ 5 cm, 3) dbh 5–14.9 cm, 4) dbh 15–24.9 cm, 5) dbh 25–34.9 cm, and 6) dbh \geq 35 cm.

215 3.2 Browsing and landscape structure

216 On average, 51% (16–89% per site) of living aspens had been browsed. On average 58% (20–80%) of
 217 small aspens (height \leq 130 cm) and 29% (0–100%) of tall aspens had been browsed. Moreover, on
 218 average 66% (0–100%) of dead aspens had been browsed. The density of middle-sized (dbh 5–15
 219 cm) aspens correlated negatively with the proportion of browsed aspens ($r_p = -0.50$, $n = 21$, $p = 0.02$).

220 Within a 1 km and 3 km buffer from the conservation area, the proportion of small (\leq 130 cm)
 221 aspens browsed declined with increasing proportion of farmland (Table 2 & 3). The results (not
 222 shown) were qualitatively similar if the response variable was browsed aspens dbh $<$ 5 cm, rather
 223 than browsed aspens height \leq 130 cm. Considering only the local characteristics (maximum tree age,
 224 tree-species specific volumes and forest types) of the conservation areas, pine volume had a positive
 225 relationship with browsing damage ($z = 3.2$, $p = 0.001$). When pine volume was included in the
 226 landscape models (not shown), it increased the proportion of explained variance about 0.5%, i.e.

227 11% increase in model performance. Nevertheless, farmland area remained the most significant
 228 factor in the models.

229

230 **Table 2.** The relationship between browsing (≤ 130 cm aspens browsed) and landscape variables
 231 within a 1 km buffer. Young forests were not included, because their area correlated strongly
 232 negatively with the area of mature forests (see Appendix 6 for an analysis with young forests). R^2m is
 233 the explained variation without random variables, R^2c without random variables. Only models with
 234 delta value < 3 are shown.

Model	Incpt	Area	Density	Farmland	Human impact	Mature forest	Waters	df	logLik	AICc	delta	weight	R^2m	R^2c
21	0.52			-0.46		-0.16		4	-802.0	1612.0	0.00	0.11	0.06	0.07
5	0.53			-0.42				3	-803.1	1612.3	0.30	0.10	0.05	0.07
22	0.52	0.11		-0.44		-0.21		5	-801.5	1613.1	1.11	0.07	0.06	0.07
13	0.53			-0.42	0.11			4	-802.6	1613.3	1.32	0.06	0.05	0.07
23	0.50		-0.07	-0.49		-0.15		5	-801.7	1613.4	1.46	0.06	0.06	0.07
7	0.50		-0.09	-0.45				4	-802.8	1613.6	1.63	0.05	0.05	0.07
29	0.51			-0.49	-0.1	-0.24		5	-801.8	1613.7	1.73	0.05	0.06	0.07
53	0.52			-0.46		-0.16	0	5	-802.0	1614.0	2.01	0.04	0.06	0.07
15	0.50		-0.11	-0.46	0.13			5	-802.1	1614.2	2.20	0.04	0.05	0.07
24	0.50	0.13	-0.09	-0.47		-0.21		6	-801.1	1614.2	2.25	0.04	0.06	0.08
37	0.53			-0.42			0.02	4	-803.1	1614.2	2.26	0.04	0.05	0.07
6	0.53	0.01		-0.41				4	-803.1	1614.3	2.30	0.04	0.05	0.07
30	0.51	0.11		-0.46	-0.11	-0.3		6	-801.4	1614.8	2.78	0.03	0.06	0.07

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242 **Table 3.** The relationship between browsing (≤ 130 cm aspens browsed) and landscape variables
 243 within a 3 km buffer. R^2m is the explained variation without random variables, R^2c without random
 244 variables. Only models with delta value < 3 are shown.

Model	Incpt	Area	Density	Farmland	Human impact	Mature forest	Young forest	Waters	df	logLik	AICc	delta	weight	R^2m	R^2c
13	0.52			-0.36	0.22				4	-806.9	1621.9	0.00	0.08	0.03	0.08
5	0.50			-0.32					3	-808.2	1622.4	0.57	0.06	0.03	0.07
14	0.53	0.12		-0.32	0.24				5	-806.5	1623.0	1.17	0.04	0.04	0.08
29	0.52			-0.33	0.27	0.10			5	-806.7	1623.4	1.53	0.04	0.03	0.08
77	0.52			-0.37	0.23			-0.08	5	-806.7	1623.4	1.57	0.04	0.03	0.08
15	0.50		-0.05	-0.38	0.24				5	-806.8	1623.7	1.86	0.03	0.03	0.08
45	0.52			-0.37	0.23		0.03		5	-806.9	1623.8	1.97	0.03	0.03	0.08
6	0.51	0.10		-0.29					4	-807.9	1623.9	2.08	0.03	0.03	0.09
78	0.53	0.16		-0.33	0.25			-0.12	6	-806.0	1624.1	2.24	0.03	0.04	0.08
30	0.53	0.15		-0.27	0.31	0.13			6	-806.0	1624.1	2.29	0.02	0.04	0.08
69	0.50			-0.34				-0.07	4	-808.1	1624.2	2.33	0.02	0.03	0.08
21	0.50			-0.33		-0.02			4	-808.2	1624.4	2.57	0.02	0.03	0.08
7	0.51		0.01	-0.32					4	-808.2	1624.4	2.57	0.02	0.03	0.08
37	0.50			-0.32			-0.01		4	-808.2	1624.4	2.58	0.02	0.03	0.08
16	0.50	0.16	-0.10	-0.34	0.28				6	-806.2	1624.5	2.61	0.02	0.04	0.08
85	0.51			-0.52		-0.36		-0.39	5	-807.2	1624.5	2.68	0.02	0.03	0.08
46	0.53	0.14		-0.34	0.25		0.06		6	-806.4	1624.8	2.99	0.02	0.04	0.08

245

246

247 **4 DISCUSSION**

248 Our study revealed that the aspen size structure and browsing vary widely among and within the
 249 studied conservation areas. In many areas, certain size classes were scarce or missing, indicating that
 250 aspen has not been regenerating well in the recent past. There were also very few large, dead aspen
 251 trunks in advanced decay stages. Landscape structure (proportion of farmland) influenced browsing
 252 negatively.

253 **4.1 Aspen population structure**

254 The overall size structure of aspen, combining all studied conservation areas, resembled a reverse J-
 255 curve. This is typical for trees, which face high mortality in youngest cohorts and increasing survival
 256 in older cohorts (Hett & Loucks 1976). In old-growth forests, however, the size structure of aspen
 257 often resembles Gaussian curve (Latva-Karjanmaa et al. 2007), but this depends greatly on the

258 disturbance regime. Indeed, the size distribution was very variable among the studied conservation
259 areas (see also Kouki et al. 2004).

260 Overall, the density of living aspens was larger than in other conservation areas in Finland: the mean
261 density of saplings (dbh < 5 cm) and that of larger trees (dbh ≥ 5 cm) were 17 and 10 times larger,
262 respectively, than in eastern Finland (cf. Kouki et al. 2004). The difference is even greater compared
263 to another eastern Finnish study (cf. Latva-Karjanmaa et al. 2007). In about half of the study areas,
264 middle-sized (dbh 5–24.9 cm) aspens were missing or there were only very few individuals. Since
265 middle-sized aspens are about 15-80 years old (Latva-Karjanmaa et al. 2007), this supports our
266 hypothesis that aspen has not regenerated well in the past few decades. Similar results have been
267 documented for other conservation areas in Finland (Kouki et al. 2004, Latva-Karjanmaa et al. 2007).
268 In addition to browsing, there are naturally other factors (e.g. disturbances or land use), which have
269 shaped the current aspen population structure in conservation areas. These factors could explain the
270 structure of the older age cohorts, but it is unlikely that they would explain visible browsing damage.

271 In some conservation areas, the number of aspen saplings was rather large, which indicates that
272 some areas have disproportionate effect on aspen recruitment (Edenius & Ericsson 2007). However,
273 most aspens do not survive beyond the sapling phase due to browsing, self-thinning and other
274 environmental factors (Edenius et al. 2011). Therefore, a radical abundance decline after the
275 youngest age cohorts is not alarming as such, but beyond that the age classes should remain more
276 stable. Despite poor recruitment in many conservation areas, aspen population is likely to persist at
277 a landscape scale. Most dead aspens were recently died saplings, and only a few large trunks were
278 observed. Dead aspens in advanced decay stages were also very rare. Because a large proportion of
279 the aspen-dependent species is saproxylic and requires coarse dead wood, the studied conservation
280 areas are unlikely to maintain viable populations, unless the amount of aspen dead wood increases.
281 Also many epiphytes require living or dead large trunks, so their persistence may be jeopardized as
282 well. For the aspen-dependent species, it is crucial to ensure the aspen density is locally and
283 regionally large enough to support viable populations, and that the species can colonize suitable
284 sites.

285 The positive relationship between the size of the conservation area and the density of living aspens
286 (dbh < 5 cm) suggests that browsing pressure is smaller and, consequently, aspen regeneration
287 better in larger conservation areas. In extreme cases, habitat management, such as enhancing aspen
288 regeneration by gap felling to create a continuum, may be necessary (see also Latva-Karjanmaa et
289 al. 2007). However, the effect of such measures is likely to be transient, unless ungulate populations

290 are regulated simultaneously. Fencing may provide best protection against browsing but is probably
291 too expensive.

292 **4.2 Browsing damage**

293 Browsing was one major factor affecting aspen regeneration and size structure in conservation
294 areas. The mean percentage of browsing of living and dead aspens was 50% and 66%, respectively.
295 Many living aspens had been browsed continuously and excessive branching was common. Because
296 most dead aspens had browsing damage, it is likely that browsing was at least the partial cause for
297 mortality (see also Kay & Bartos 2000). Even if browsing does not kill trees, it can still affect the size
298 structure by slowing down aspen regeneration and growth. Browsing pressure varied greatly among
299 and within the conservation areas, which could influence the future distribution of aspen in the
300 landscape (see also Ericsson et al. 2001).

301 The density of middle-sized (dbh 5–14.9 cm) aspens correlated negatively with the browsing
302 pressure. This provides some indication that the past intense browsing hindered regeneration (see
303 also Kouki et al. 2004, Latva-Karjanmaa et al. 2007, Myking et al. 2011) and caused the current gap in
304 the middle-sized aspens. Indeed, moose population size in Central Finland in the year 2000 was
305 double the current size (Natural Resources Institute Finland 2019a). Due to the effective clonal
306 regeneration, aspen can recover heavy browsing, unless browsing is continuous. The mean browsing
307 pressure on aspens <130 cm and >130 cm in height was about 50% and 30%, respectively. Higher
308 browsing pressure on smaller trees could indicate that moose feeds preferably on such trees, or
309 smaller trees face additional browsing from hares and roe deer (Hjältén et al. 2004; but see de
310 Chantal & Granström 2007). Both species can be very abundant locally in Central Finland (Natural
311 Resources Institute Finland 2019b). Although it was impossible to distinguish damages by different
312 herbivores with certainty, this does not change the observation of poor aspen regeneration in
313 conservation areas in Central Finland.

314 **4.3. Influence of landscape structure**

315 Landscape structure influenced browsing probability. At both 1 km and 3 km scales, the proportion
316 of the farmland had a negative relationship with the browsing of living aspen saplings (height \leq 130
317 cm or dbh < 5 cm). At 1 km scale also the proportion of mature forest (negative effect), and at the 3
318 km scale, the proportion of human impacted area (positive effect), were included in the best models.
319 In summer, moose prefers mature forests and avoids human settlements, and in winter, it avoids

320 agricultural areas and human settlements (Nikula et al. 2004). This may well explain the observed
321 negative relationship between farmland area and browsing. In Central Finland, agricultural fields are
322 small and often situated nearby settlements, which could further contribute to the observed
323 pattern. Roe deer and hares may also benefit from agricultural land, since they forage for grasses in
324 summer. Other ungulate species, however, may respond differently to landscape structure; for
325 example, in southern Sweden red deer browsing on spruce was positively related to farmland area
326 (Jarnemo et al. 2014).

327 Our results contradict some previous studies (Ericsson et al. 2001), in which browsing pressure was
328 higher in stands surrounded by younger forests. Moose does prefer young forests in winter and
329 feeds especially on pine saplings, so large proportion younger forests near the conservation areas
330 could have increased browsing within conservation areas. In our study, however, the proportion of
331 young forests varied quite little among the conservation areas; thus it is not surprising that the
332 proportion of saplings and younger forest did not influence browsing pressure. Furthermore,
333 farmland is also a spatially and temporally rather permanent landscape feature, so its influence on
334 browsing pressure accumulates over years. The negative effect of the proportion of mature forest
335 within 1 km radius can indicate that moose actually prefers landscapes with younger forests,
336 although the effect was not very strong. The positive effect of human impact at the 3 km radius is
337 harder to explain but can indicate that at a larger 3 km scale human activities are not that important
338 for moose foraging.

339 Although we did include conservation area size and local aspen density in the landscape models, our
340 study focused on landscape factors. The separate model, which included only the local
341 characteristics, indicated that increasing pine volume increases also browsing damage. Although this
342 result is intuitive since moose prefers pine saplings as food in winter, total pine volume does not
343 indicate the availability of pine saplings. Indeed, including pine volume in the landscape models
344 increased the model performance only slightly, and the farmland area remained the most significant
345 factor. Furthermore, local factors should have been measured in each conservation area, had our
346 focus been on the local factors. Because many other ecological factors (e.g. alternative food sources)
347 within conservation areas can also influence browsing pressure (Nikula et al. 2004, de Chantal &
348 Granström 2007, Jarnemo et al. 2014), the interplay between local and landscape factors in
349 determining browsing pressure deserves further research attention.

350 **4.3 Conclusions**

351 Our study showed that the size structure of aspen population varies among conservation areas. In
352 most conservation areas, there was only few large aspens and very few large, dead aspens. Despite
353 rather high density of aspen saplings in some areas, there was a clear gap in the middle-sized
354 aspens, indicating intense past browsing pressure. Overall, it seems that the number of young
355 aspens is not enough to replace older trees in the long term with current browsing pressure, and
356 therefore local aspen persistence is not assured. This may jeopardize many threatened aspen-
357 associated species. Our study demonstrated that landscape structure can influence browsing
358 pressure in conservation areas. More specifically, small conservation areas that have a large
359 proportion of farmland in the surroundings may face higher browsing pressure; thus, landscape
360 structure should be considered when planning management measures in conservation areas.

361 **ACKNOWLEDGEMENTS**

362 We thank Suomen Biologian Seura Vanamo ry, Societas pro Fauna et Flora Fennica and University of
363 Jyväskylä for the financial support.

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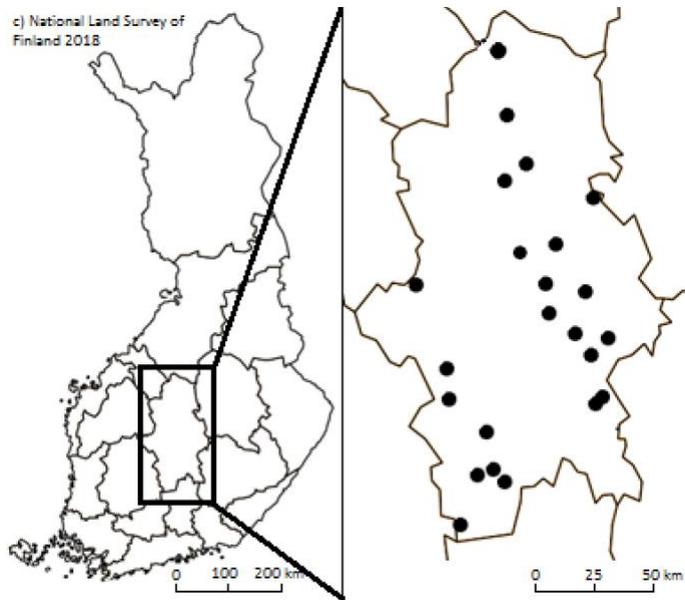
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Appendix 1. The studied conservation areas in Central Finland.



Appendix 2. Characteristics of the studied conservation areas.

Site	Area (ha)	Tree age (max. yrs)	Tree volume (mean m ³ ha ⁻¹)					Forests types (% of area)			
			Total	Spruce	Pine	Birch	Other broad-leaved	Herb-rich*	Mesic heath	Sub-xeric heath	Dry heath
Hallalähde	1	105	163	68	60	28	7	3	83	15	0
Hintonniemi	23	174	140	32	90	15	3	3	53	37	8
Hirvijärvi	60	158	239	135	87	15	2	12	67	17	4
Hitonhaukanvuori	121	148	164	43	105	12	4	4	59	35	2
Hopeaharju	25	114	232	161	37	30	3	23	72	5	0
Ilvesjoen lehto	2	96	221	101	23	85	11	77	23	0	0
Isolähteenpuro	6	154	153	25	111	17	1	1	43	50	6
Kaitajärvi	206	122	186	91	64	24	7	17	65	14	3
Kanavuori	105	155	189	42	120	23	4	11	65	23	0
Limpinginrotko	101	143	209	111	69	24	4	26	63	10	0
Listonniemi	203	128	178	58	83	30	6	19	58	22	0
Louhivuori	103	133	116	5	101	9	1	0	17	67	16
Matolammi	76	138	245	64	172	8	1	7	68	23	2
Metsokangas	25	121	193	58	110	21	5	4	82	14	0
Myllykolun lehto	2	87	180	77	31	60	13	61	39	0	0
Palosenranta	4	109	136	46	50	35	6	14	80	5	1
Rajala	91	122	286	199	44	34	9	46	53	2	0
Ristinien lähteikkö	14	123	163	63	33	55	12	46	52	2	0
Ruokomäki	77	126	128	26	82	15	4	3	45	43	9
Ryönien lehto	7	106	229	110	73	35	11	19	77	4	0
Teerikangas	24	117	289	191	72	22	4	16	83	1	0
Tervajärvi	24	83	93	30	10	34	18	51	47	2	0
Vuorilammen alue	157	128	248	150	60	31	6	20	77	3	0

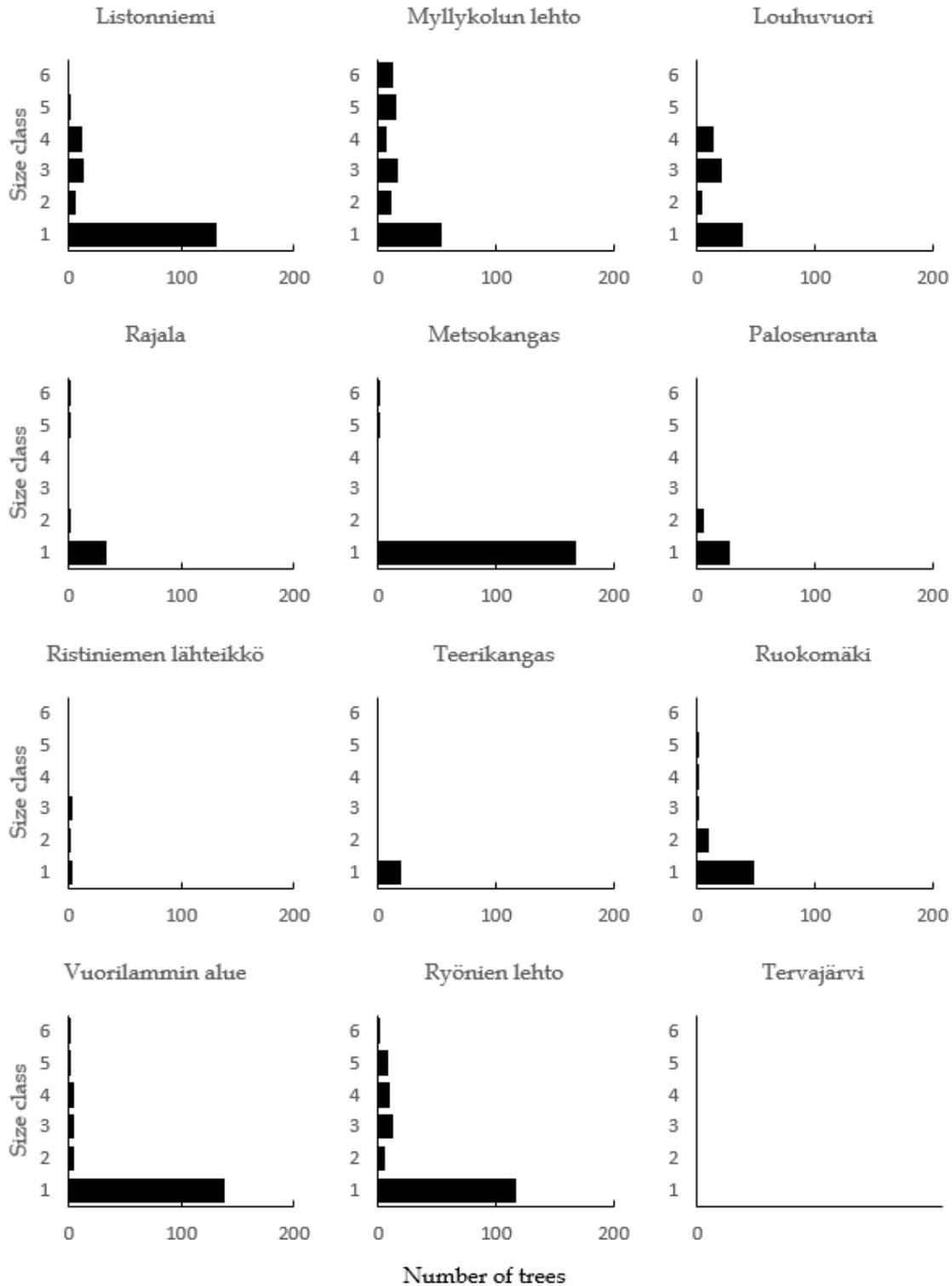
* Includes herb-rich heath forests

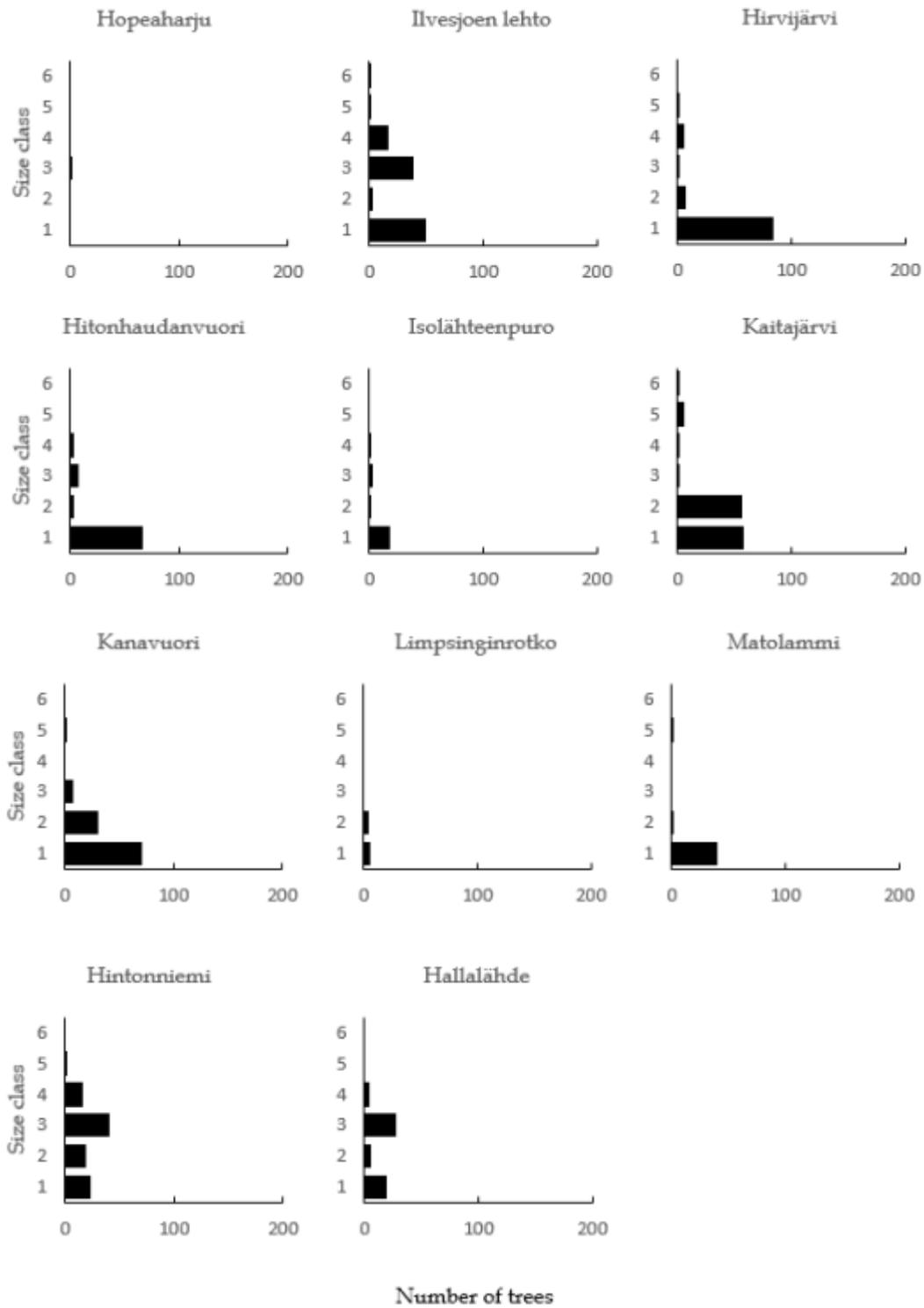
Land use types	Land use variable
Continuous urban fabric Discontinuous urban fabric Commercial units Industrial units Road and rail networks Airports Mineral extraction sites Construction sites Leisure facilities Other sport and leisure facilities Peat production site	Areas of human impact
Arable land Fruit trees and berry plantations Pastures Natural pastures Land principally occupied by agriculture	Farmland
Broad-leaved forest on mineral land Broad-leaved forest on peat land Mixed forest on mineral land Mixed forest on peat land Mixed forest on solid mineral land Coniferous forest on mineral land Coniferous forest on peat land Coniferous forest on solid mineral land	Mature forest (> 20 yrs old)
Broad-leaved forest on mineral land Broad-leaved forest on peat land Mixed forest on mineral land Mixed forest on peat land Mixed forest on solid mineral land Coniferous forest on mineral land Coniferous forest on peat land Coniferous forest on solid mineral land Transitional woodland, cc (crown cover) < 10% Transitional woodland, cc 10-30%, on mineral land Transitional woodland, cc 10-30%, on solid mineral land Transitional woodland, under power line Bare rock	Young forests (\leq 20 yrs old)
Inland marshes on land Inland marshes on water Transitional woodland, cc 10-30%, on peat land Beaches, dunes and sand plains Treeless bogs Rivers Lakes	Water bodies and wetland

Appendix 4. Summary of the explanatory variables in GIS analyses.

Variables	N	Minimum	Maximum	Mean	SD
Area of conservation areas (ha)	21	1	206	67	66
Aspen density (dbh < 5 cm)	21	16	525	208	150
1000 m scale					
Urban areas (%)	21	0	52	5	11
Farmland (%)	21	0	21	4	6
Mature forest (%)	21	11	81	59	17
Young forest (%)	21	9	40	23	9
Water bodies and wetland (%)	21	1	52	10	12
3000 m scale					
Urban areas (%)	21	0	24	4	6
Farmland (%)	21	0	27	5	7
Mature forest (%)	21	19	71	51	16
Young forest (%)	21	16	38	26	5
Water bodies and wetland (%)	21	2	51	14	15

Appendix 5. The number of living aspens in different size classes in the studied conservation areas. Size classes in the y-axel are following: 1) ≤ 130 cm, 2) > 130 cm but dbh (diameter at breast height) < 5 cm, 3) = dbh 5–15 cm, 4) dbh 15–25 cm, 5) dbh 25–35 cm, 6) dbh ≥ 35 cm.





Appendix 6. The relationship between browsing (≤ 130 cm aspens browsed) and landscape variables within a 1 km buffer. Mature forests were not included, because their area correlated strongly negatively with the area of young forests. Only models with delta value < 3 are shown. R^2m is the explained variation without random variables, R^2c without random variables.

Model	Intercept	Area	Density	Farmland	Human impact	Young forest	Waters	df	logLik	AICc	delta	weight	R^2m	R^2c
5	0.53			-0.42				3	-803.1	1612.3	0.00	0.12	0.05	0.07
21	0.52			-0.44		0.11		4	-802.5	1613.1	0.77	0.08	0.05	0.07
13	0.53			-0.42	0.11			4	-802.6	1613.3	1.02	0.07	0.05	0.07
7	0.50		-0.09	-0.45				4	-802.8	1613.6	1.32	0.06	0.05	0.07
53	0.51			-0.45		0.17	0.11	5	-801.9	1613.9	1.62	0.05	0.05	0.07
15	0.50		-0.11	-0.46	0.13			5	-802.1	1614.2	1.89	0.05	0.05	0.07
37	0.53			-0.42			0.02	4	-803.1	1614.2	1.95	0.04	0.05	0.07
6	0.53	0.01		-0.41				4	-803.1	1614.3	2.00	0.04	0.05	0.07
29	0.53			-0.44	0.07	0.08		5	-802.3	1614.6	2.35	0.04	0.05	0.07
23	0.51		-0.07	-0.47		0.09		5	-802.3	1614.7	2.37	0.04	0.05	0.07
22	0.52	0.07		-0.43		0.13		5	-802.3	1614.7	2.44	0.04	0.05	0.08
14	0.53	0.06		-0.40	0.13			5	-802.5	1615.1	2.77	0.03	0.05	0.07
54	0.51	0.11		-0.42		0.22	0.13	6	-801.5	1615.1	2.77	0.03	0.06	0.07
45	0.53			-0.41	0.11		0.04	5	-802.5	1615.1	2.84	0.03	0.05	0.07