Author(s): Komonen, Atte; Tuominen, Laura; Purhonen, Jenna; Halme, Panu

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

Atte Komonen[1], Laura Tuominen[1,2], Jenna Purhonen[1] & Panu Halme[1]

[1]University of Jyväskylä, Department of Biological and Environmental Science, School of Resource Wisdom, P.O. Box 35, FI-40014 University of Jyväskylä, Finland.

[2]Current address: University of Turku, Department of Biology, FI-20014 University of Turku, Finland

Corresponding author: atte.komonen@jyu.fi; +358-40-8053894

Abstract

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

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

Introduction

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

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

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

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

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

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

2 MATERIALS AND METHODS

2.1 Study areas

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

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

2.2 Field methods

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

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

2.3 GIS analyses

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

In the GIS analysis, we calculated the proportion of each land use class within 1 and 3 km radii from the center point of each conservation area, using the coordinate center point of each conservation area as the center point for the buffers; the conservation areas were included within the buffers. These radii were chosen because they reflect both the size of roe deer (0.5-1 km^2; Kjellander et al. 2004) and moose territories (10-20 km^2; Cederlund & Sand 1994), respectively. The home range size of mountain hare is similar to roe deer (Dahl & Willebrand 2005, Kauhala et al. 2005). All pixels that had their center point inside the buffers were included. With a 1000 m radius, the circles of Palosenranta and Vuorilammi were overlapping 9%, and with a 3000 m radius 50%. Because the overlap was minor, the overlapping areas were included in the analyses. The estimations were conducted with ArcGIS program.

2.4 Statistical analysis

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

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

Spatial autocorrelation in the proportion of browsed aspens between the study sites (for all aspens, as well as < 130 cm and > 130 cm aspens separately) was analysed using Moran’s I statistic standard deviate with one, two and four nearest neighbours. Because there was no indication of autocorrelation (Moran’s I = -0.77-0.86, p > 0.24), final statistical analyses were done without autocorrelation. The statistical analyses were done with R software version 3.5.1 (R core team 2018). The relationship between the size of the conservation area and the density of living aspens was analysed with linear regression, and the relationship between the density of middle-sized aspens and the proportion of browsed aspens with Pearson correlation. These analyses were conducted with SPSS Statistics 24.0

3 RESULTS

3.1 Aspen population structure

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

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

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

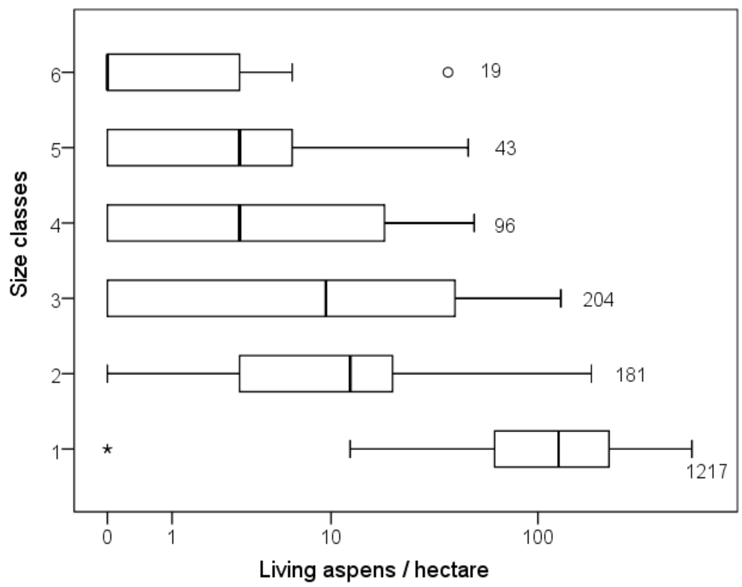

Figure 1. Median density of living aspens in different size classes in the studied conservation areas. The boxes indicate 25% to 75% percentiles. Whiskers extend to 1.5 times the interquartile range or to the minimum or maximum values, if there were no outliers. The numbers in the panel indicate the

total numbers of trees in different size classes. Size classes: 1) height ≤ 130 cm, 2) height > 130 cm 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 ≥ 35 cm.

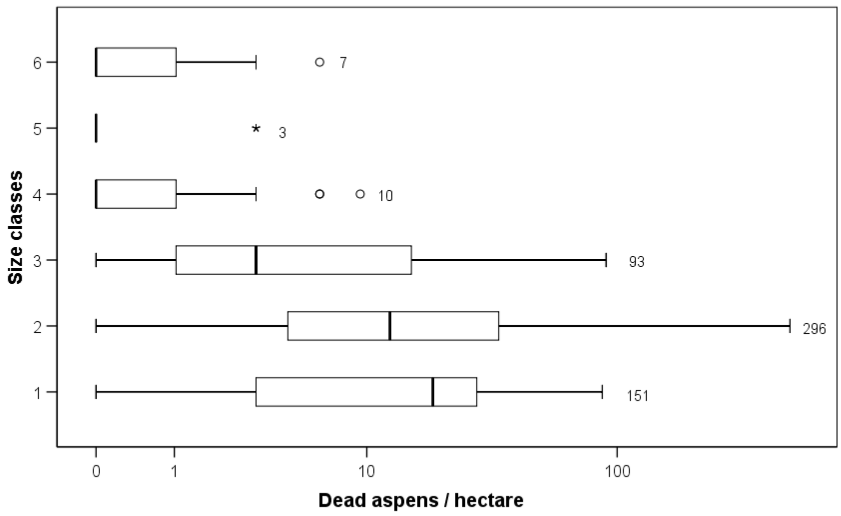

Figure 2. Median density of dead aspens in different size classes in the studied conservation areas. The boxes indicate 25% to 75% percentiles. Whiskers extend to 1.5 times the interquartile range or to the minimum or maximum values, if there were no outliers. The numbers in the panel indicate the total numbers of trees in different size classes. Size classes: 1) height ≤ 130 cm, 2) height > 130 cm 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 ≥ 35 cm.

3.2 Browsing and landscape structure

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

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

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

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

Table 3. The relationship between browsing (≤ 130 cm aspens browsed) and landscape variables within a 3 km buffer. R^2m is the explained variation without random variables, R^2c without random 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

4 DISCUSSION

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

4.1 Aspen population structure

The overall size structure of aspen, combining all studied conservation areas, resembled a reverse J-curve. This is typical for trees, which face high mortality in youngest cohorts and increasing survival in older cohorts (Hett & Loucks 1976). In old-growth forests, however, the size structure of aspen often resembles Gaussian curve (Latva-Karjanmaa et al. 2007), but this depends greatly on the disturbance regime. Indeed, the size distribution was very variable among the studied conservation areas (see also Kouki et al. 2004).

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

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

The positive relationship between the size of the conservation area and the density of living aspens (dbh < 5 cm) suggests that browsing pressure is smaller and, consequently, aspen regeneration better in larger conservation areas. In extreme cases, habitat management, such as enhancing aspen regeneration by gap fellings to create a continuum, may be necessary (see also Latva-Karjanmaa et al. 2007). However, the effect of such measures is likely to be transient, unless ungulate populations are regulated simultaneously. Fencing may provide best protection against browsing but is probably too expensive.

4.2 Browsing damage

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

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

4.3. Influence of landscape structure

Landscape structure influenced browsing probability. At both 1 km and 3 km scales, the proportion of the farmland had a negative relationship with the browsing of living aspen saplings (height ≤ 130 cm or dbh < 5 cm). At 1 km scale also the proportion of mature forest (negative effect), and at the 3 km scale, the proportion of human impacted area (positive effect), were included in the best models. In summer, moose prefers mature forests and avoids human settlements, and in winter, it avoids agricultural areas and human settlements (Nikula et al. 2004). This may well explain the observed negative relationship between farmland area and browsing. In Central Finland, agricultural fields are small and often situated nearby settlements, which could further contribute to the observed pattern. Roe deer and hares may also benefit from agricultural land, since they forage for grasses in summer. Other ungulate species, however, may respond differently to landscape structure; for example, in southern Sweden red deer browsing on spruce was positively related to farmland area (Jarnemo et al. 2014).

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

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

4.3 Conclusions

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

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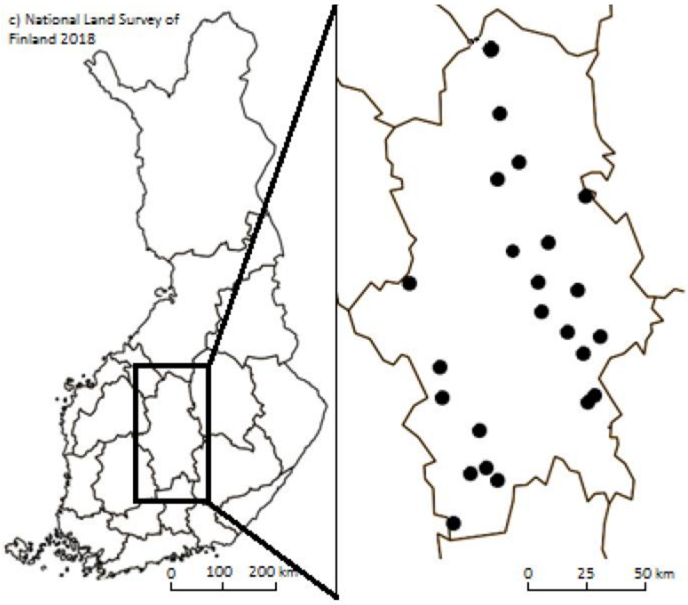
Appendix 1. The studied conservation areas in Central Finland.



Appendix 2. Characteristics of the studied conservation areas.

			Tree volume (mean m^3ha^{-1})					Forests types (% of area)			
Site	Area (ha)	Tree age (max. yrs)	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
Hitonhaudanvuori	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
Limpsinginrotko	101	143	209	111	69	24	4	26	63	10	0
Listonniemi	203	128	178	58	83	30	6	19	58	22	0
Louhuvuori	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
Ristiniemen 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

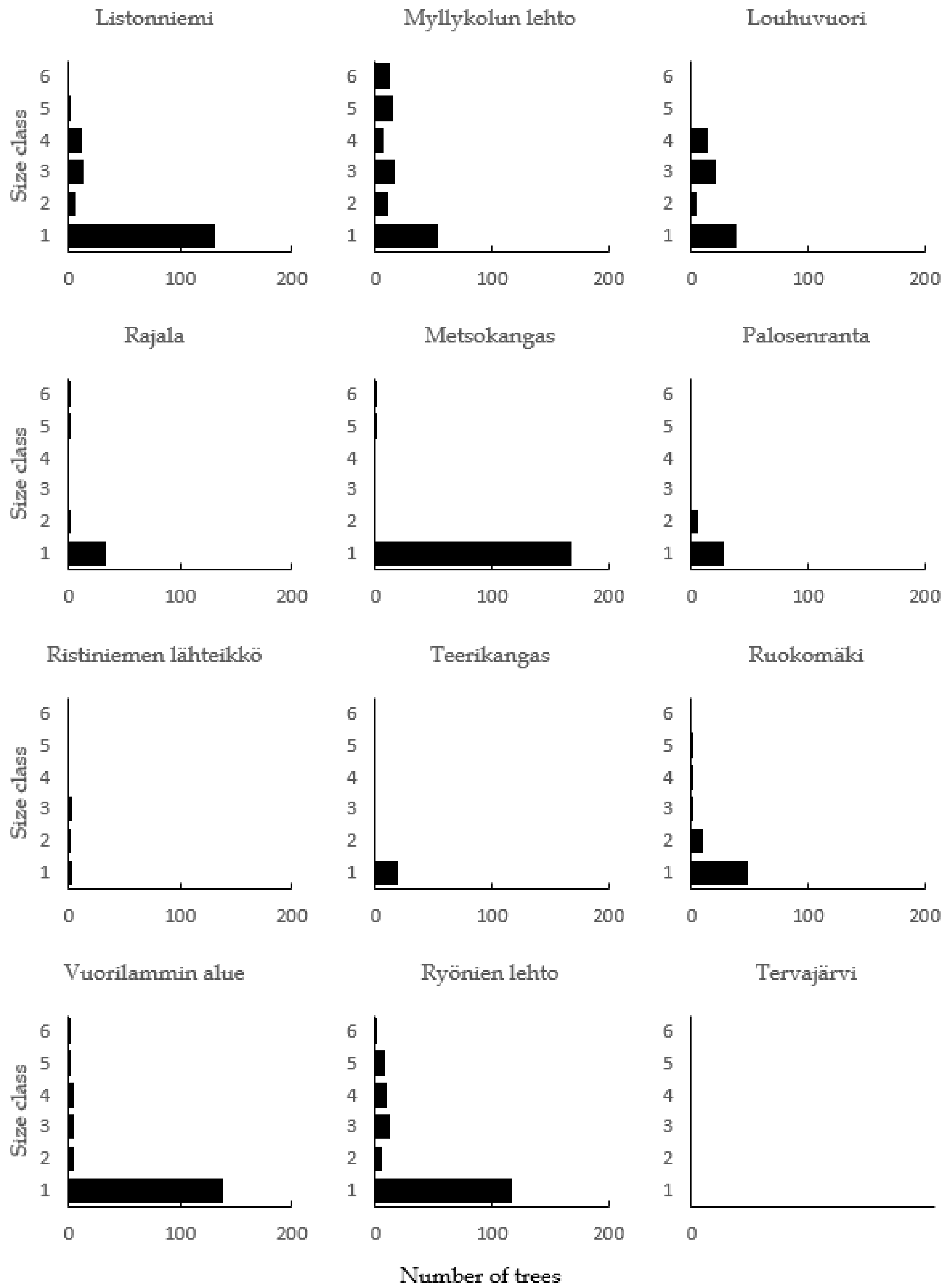
* Includes herb-rich heath forests

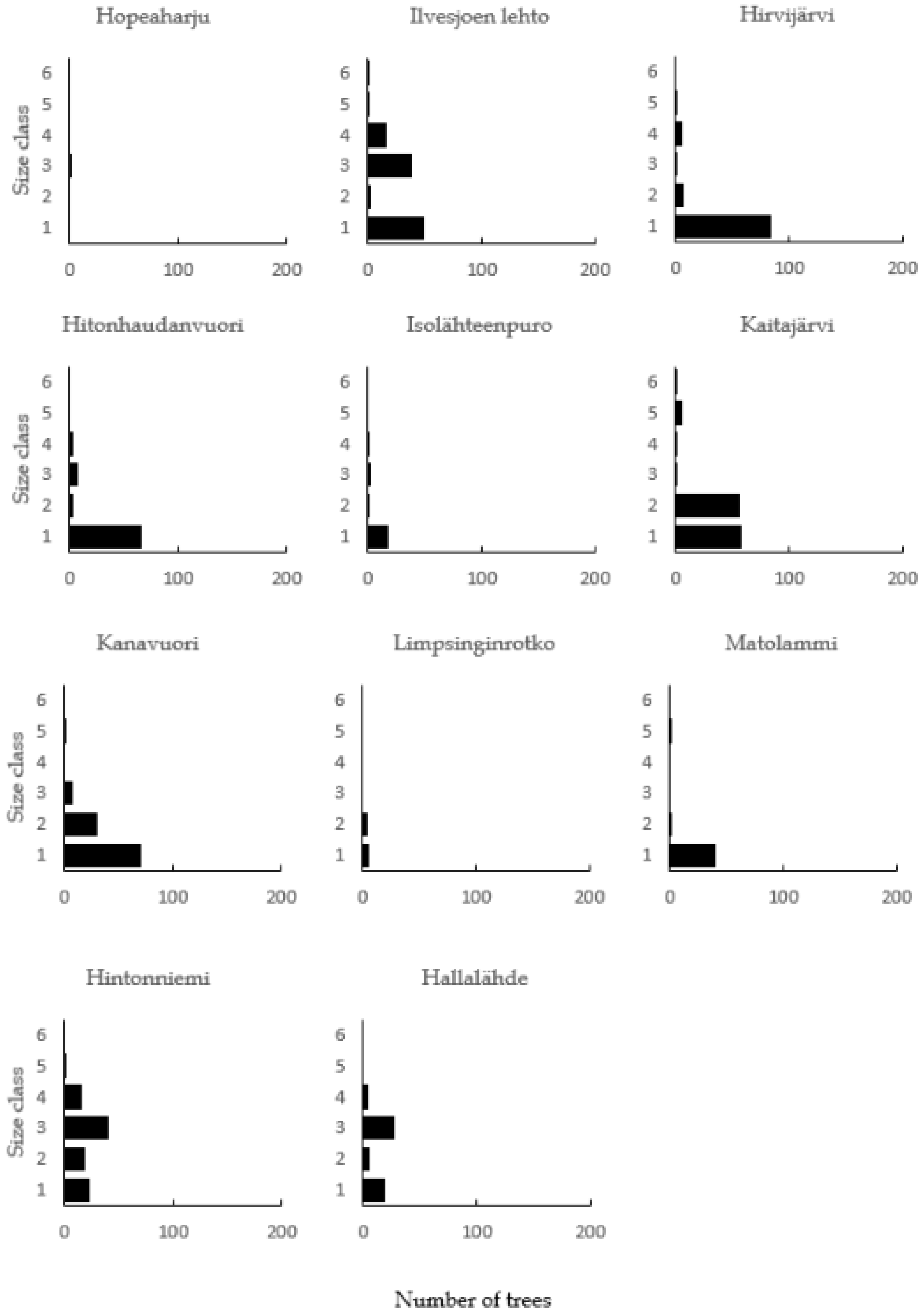
Land use types	Land use variable
Continuous urban fabric Discontinuous urban fabric Commercial units Industrial units Road and rail networks Airports Mineral extraction sites Construction sites Leisure facilities Other sport and leisure facilities Peat production site	Areas of human impact
Arable land 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 (≤ 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.




Hopeaharju
Ilvesjoen lehto
Hirvijärvi
Hitonhaudanvuori
Isolähteenpuro
Kaitajärvi
Kanavuori
Limpsinginrotko
Matolammi
Hintonniemi
Hallalähde
Size class
1
2
3
4
5
6
0
100
200
Number of trees

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