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Browsing hinders the regeneration of broadleaved trees in uneven-aged forest management in southern Finland

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Abstract

Uneven-aged forest management has attained increasing popularity. It may benefit biodiversity, buffer against pests and abiotic damages, decrease runoff from clearcuts and improve recreational values. We studied how gap cuttings and single-tree selection cuttings influence browsing damage in spruce-dominated forests in south-central Finland. Overall, browsing damage was especially frequent in aspen and rowan, but also in birch. The larger the basal area left in harvesting, the lower the browsing pressure on birch and rowan; neither the harvesting method nor the seedling density had an independent effect on browsing damage. Although larger tree retention levels may reduce browsing damage, the regeneration and recruitment of shade-intolerant broadleaved trees may be compromised.

Key words: browsing damage, gap cutting, moose, selection silviculture, single-tree selection, tree recruitment

Introduction

Forest management requires new methods not only to better balance between wood production, biodiversity protection and recreational values, but also to mitigate climate change and related biotic and abiotic risks. Uneven-aged forest management is one alternative to even-aged that is currently overwhelmingly dominant in forest management in the Nordic countries (Kuuluvainen et al. 2012). In coniferous forests, uneven-aged management can diversify stand structure by retaining broadleaved trees, which enhance biodiversity (Tikkanen et al. 2006), improve soil conditions (Sariyildiz et al. 2005) and mitigate biotic and abiotic risks (Nevalainen 2017).

Selection is a forest management system based on uneven stand structures, such as variable tree ages and sizes mixed at small spatial scales (Lundqvist 2017). Trees are removed as single trees or small groups, which enhances continuous recruitment of seedlings into the tree strata. Shade tolerant Norway spruce (*Picea abies* Karst.) is generally considered the only suitable tree as the main stand species for selection systems in boreal Fennoscandia (Eerikäinen et al. 2014, Lundqvist 2017), unless a low stand density is maintained (Eerikäinen et al. 2014). Gap cutting is one harvesting methods used in selection systems. In gap cutting, all trees growing in a small area within a forest stand are removed to harvest timber and to promote tree regeneration in the gap. In spruce forests, gap cutting is mainly used as complementary to single-tree selection management to speed up regeneration and to help to maintain shade-intolerant species.

There are still relatively few studies on silvicultural pros and cons concerning uneven-aged forest management, especially with regards to biotic damages. Recently, forest experts assessed the overall risk of forest damage to be smaller in uneven-aged than in even-aged management in Finland (Nevalainen 2017). However, considering broadleaved trees, ungulate browsing may hinder their regeneration and recruitment, i.e. entering the tree strata. Moose is the most important browser that damages seedlings in boreal forests (McInnes et al. 1992, Hörnberg, 2001). Moose diet varies seasonally. Over 90% of summer food comprises willows (*Salix* spp.), birches (*Betula* spp.), European aspen (*Populus tremula* L.) and rowan (*Sorbus aucuparia* L.) (Wam & Hjeljord 2010). In winter, over 75% of food comprises pine (*Pinus sylvestris* L.) and willows (Shipley et al. 1998). Even in pine plantations moose may preferably browse broadleaved trees (Heikkilä 1991), which can alter tree species

composition and reduce litter production (McInnes et al. 1992). In pine plantations, the increasing area of small, grassy openings increases browsing damage (Heikkilä 1990). Similarly in mature spruce forests, single-tree selection and gap cutting create openings of variable sizes, which may increase browsing damage.

The regeneration and recruitment of broadleaved trees may be compromised in uneven-aged forest management in boreal Fennoscandia, mainly due to the poor survival of the shade intolerant species, further exacerbated by browsing. We studied how the management method (single-tree selection or gap cutting), shading (basal area of retained trees) and density of broadleaved seedlings influence browsing damage. Tree-species specific browsing damage was quantified as the proportion of browsed seedlings. Because gaps have smaller basal areas and higher seedling densities, and high seedling densities can attract moose, we predicted that browsing damage is greater in gaps than in single-tree selection stands. Because moose is a selective forager, we predicted that browsing damage varies among broadleaved tree species.

2 MATERIALS AND METHODS

1.1 Study sites

The study was conducted in south-central Finland that belongs to the southern boreal zone (see Ahti et al. 1968). The research stands representing single-tree selection had been established in 1991–1992 for studies on tree and stand development in uneven-aged Norway spruce forests (ERIKA research project at the Natural Resources Institute Finland; Eerikäinen et al., 2007, 2014, Saksa and Valkonen, 2011). The single-tree selection stands were in Vesijako (n = 11) and Evo (n = 3), and the gap cutting stands in Isojärvi (n = 17). The distance between the most distant areas was 50 km (Appendix 1).

The forest stands represent mesic *Oxalis-Myrtillus* type (20% of stands) and submesic *Myrtillus* type (80%) (Cajander 1926), which are the most common spruce site types in southern and central Finland. The average portion of Norway spruce on experimental plots was about 75% of the total stand volume. Other abundant tree species were Scots pine, silver birch (*Betula pendula* Roth), downy birch (*Betula pubescens* Ehrh.) and European aspen. All

stands were truly multi-aged (with trees up to 170 years old) and full-storied (in the sense of Ahlström and Lundqvist 2015). The experimental design and measurements are described in detail in Eerikäinen et al. (2007, 2014), and Saksa and Valkonen (2011).

The research stands representing gap cutting were in the Isojärvi experimental forest area, which has been designated for research and development of uneven-aged management under the DISTDYN project (Koivula et al. 2014). The Isojärvi experimental area covers an area of 689 ha. The predominant forest site types are the submesic *Myrtillus* type and the mesic *Oxalis–Myrtillus* type (Cajander 1926). The dominant tree species are Norway spruce and Scots pine, with substantial proportions of silver and pubescent birch, occasionally mixed with European aspen, rowan, common alder (*Alnus glutinosa* (L.) Gaertn.) and grey alder (*Alnus incana* (L.) Moench). Forests in both research areas are managed according to the principles of natural disturbance emulation (Attiwill 1994; Bergeron et al. 2002; Long 2009); see Kuuluvainen and Aakala (2011) for typical natural forest dynamics in this region and Koivula et al. (2014) for their application in the DISTDYN project.

The gap cutting treatments involved harvesting small irregular clearcut gaps with areas of 0.1–0.5 ha (diameter 30–80 m) with 10–50 m wide unharvested (residual) forest buffers between the gaps. Stand areas varied between 0.5 and 8.9 ha, and each harvested stand contained one to seven gaps, making up 20–33% of the total stand area. The sites were harvested between January 2010 and February 2011.

1.2 Sampling

Browsing damage was surveyed in June 2018. Nine circular plots were systematically placed at each site (Appendix 2). At sites with single-tree selection, larger plots (diameter 8 m; 5 m in gaps) were used, because we expected lower seedling density. To cover the entire gap or harvested area, the outermost plots were placed 4 m from the gap or stand borders. In some single-tree selection stands, the borders of the harvested area were vague, and study plots were placed 30 m and 15 m from the center. Browsing damage was recorded for all trees that were 0.5–3.0 m tall, which corresponds to the typical browsing height of moose (Suominen et al. 1999, Ball & Dahlgren 2002). Extensive branching is common in broadleaved seedlings. If seedlings branched above-ground, or clearly from the same stump, they were counted as a

single individual; otherwise they were counted as separate individuals. It was not unambiguous to distinguish the damage caused by different browsers; however, we only observed feces and hoof prints of moose during the survey. At some sites, we observed hare pellets, and some damage in smaller seedlings was probably caused by hare.

Basal area (m^2ha^{-1}) of retained trees was estimated with an angle count (relascope) at the center plot. We also estimated the height of the dominant canopy story and the height of spruce, pine and birch seedlings. In 2017, moose density in the study regions was 3.3–3.5 animals 1000 ha^{-1} (Luke 2018).

1.3 Statistical analyses

Data from the nine circular plots were pooled for each gap and single-tree selection stand; spruce was excluded because it was not browsed. The proportion of browsed seedlings was used as the response variable. Only birch and rowan were abundant enough for tree-species specific analyses. Beta regression models with a logit link were applied to model the relationship between the proportion of browsed seedlings and explanatory variables. Beta regression is commonly used when the dependent variable can only take values between zero and one, and is beta-distributed (Cribari-Neto & Zeileis 2010). For birch, rowan and all broadleaved trees separately, we built a set with eight models: 1) intercept only, 2) forest management method, 3) basal area of the trees, 4) density of broadleaved seedlings, and 5-8) all combinations of the variables. The main difference between the management methods was the basal area of trees (gaps have smaller basal area of retained trees than single-tree selection stands), but management method could also have additional effects on seedling density and browsing damage. Akaike Information Criterion for small sample sizes (AICc) was used to compare models within a set. The model with the smallest AICc was the best with respect to expected Kullback-Leibler information loss (Burnham & Anderson 2002). Beta regressions were conducted with the constrained nonlinear regression in IBM SPSS statistics version 26. Standard errors and confidence intervals were estimated with bootstrapping (n = 1000). The basal area and density of broadleaved seedlings correlated only moderately (VIF = 1.6), so both were included in the modelling. Relationships between the basal area and seedling densities were analysed with linear regression, and the relationships between seedling densities of different tree species with Pearson correlation (r_p) with 2-tailed p-values.

3 RESULTS

Seedling densities and the proportion of browsed seedlings varied greatly between tree species, as well as between gaps and single-tree selection areas (Table 1). Rowan, birch and spruce were the most frequent and abundant seedling species. The proportion of browsed rowan seedlings was 75% and that of birch 36%; none of the spruce seedlings had been browsed. The proportion of browsed rowan and birch seedlings correlated positively among the sites (r_p = 0.51, p = 0.004, n = 31).

Basal area of retained trees was smaller in the gaps than in the single-tree selection areas. The median (min-max) basal area in the gaps was 3.5 (0-13) m^2ha^{-1} and that in the single-tree selection areas 16.0 (11-22) m^2ha^{-1}. The median density of seedlings was higher in the gaps than in the single-tree selection areas: 6451 (1867-17599) vs. 2343 (398-7869) ha^{-1} for all broadleaves, 2546 (679-16524) vs. 409 (133-4421) ha^{-1} for birch, and 1924 (679-6112) vs. 1437 (155-4355) ha^{-1} for rowan.

Seedling density was related to the basal area, but not for all tree species. The larger the basal area, the lower the density of broadleaved seedlings (linear regression: $F_{1,29}$ = 18.3, p < 0.001, r^2 = 0.39; Fig. 1). Similar decrease was documented for birch but not for rowan ($F_{1,29}$ = 7.1, p = 0.012, r^2 = 0.20; $F_{1,29}$ = 2.73, p = 0.11, r^2 = 0.09, respectively). For birch, the negative relationship was mainly caused by the very low density of seedlings at basal areas ≥ 15 m^2ha^{-1}, while at smaller basal areas birch density was highly variable and there was no relationship between density and basal area ($F_{1,20}$ = 0.87, p = 0.36, r^2 = 0.04).

Browsing damage was related to the basal area. Based on the AICc values, the best models within the model sets included always the basal area as an independent variable, and the most parsimonious model (ΔAICc < 1.23) included only the basal area (Table 2, Appendix 3). The larger the basal area, the smaller the proportion of browsed seedlings. This relationship was rather weak when considering all tree species (Fig. 2a), but stronger for rowan and birch (Fig. 2b,c). There was no relationship between the density of seedlings and the proportion of browsed seedlings (Appendix 3).

4 DISCUSSION

Rowan and aspen had the highest proportion of browsing damage (ca. 75%), which corroborates previous studies on the food preference of moose (Heikkilä 1990, Shipley et al. 1998, Wam & Hjeljord 2010). The browsing damage on birch (36%) was similar to the documented browsing damage in summer (Wam & Hjeljord 2010), but higher compared to damage in winter (Shipley et al. 1998, Wam & Hjeljord 2010). Spruce was frequent in the study plots but it was not browsed at all. A rather low proportion of the pine seedlings had been browsed, but the species was too infrequent to be analysed in detail. Although we cannot be fully certain that moose was the sole cause of damage, the observed pellets and hoof prints in the plots suggest that this was likely.

Gaps had almost exclusively smaller basal areas of retained trees than single-tree selection areas. Basal areas were negatively related to the density of broadleaved and birch seedlings: the larger the basal area, the lower the density of seedlings. We hypothesized that higher seedling density might attract more moose, and consequently increase browsing damage (Ball & Dahlgren 2002; but see Heikkilä 1990), but this was not observed. Yet, our results indicate that selective logged sites do attract moose, which may then cause considerable damage to broadleaved seedlings. Because the documented browsing damage combined feeding from all seasons, more research is needed to establish whether there is between-season variation in browsing pressure in differently managed uneven-aged forests.

The larger the basal area of retained trees, the smaller the proportion of browsed birch and rowan seedlings. The effect of basal area was rather weak for all tree species but stronger for rowan and birch, whereas management type did not have an independent effect. When basal area was small ($< 10 \ m^2ha^{-1}$), browsing damage on birch was rather variable (11–84%), whereas the damage on rowan was uniformly higher (67-96%). This suggests that for birch some additional factors than basal area influence browsing pressure. Furthermore, the result also suggests that browsing damage, especially on rowan seedlings, can be mitigated by retaining larger basal areas in management. Although rowan tolerates shade better than birch and aspen (summarized in Götmark et al. 2005), cutting intensity must be carefully adjusted to balance between regeneration, recruitment and browsing damage. Rowan is an economically unimportant tree species and does not host very unique biota (Jüriado et al.

2003, Tikkanen et al. 2006), yet rowan litter is beneficial for soil quality (Carnol & Bazgir 2013). Birch in turn is more abundant, economically important and hosts more specialist species, so its successful regeneration and recruitment has broader implications. Aspen was infrequent among the studied stands, but its importance for biodiversity is overwhelming (Koivula et al. 1999, Tikkanen et al. 2006).

Because the original experimental set-up was designed for studying forest growth, it was not optimal for studying moose browsing: all the gap cuttings were in the same area and the single-tree selection stands in three separate areas. However, moose density in all areas was rather similar (3.3–3.5 1000 ha^{-1}; Luke 2018). Furthermore, moose foraging pattern varies greatly even among adjacent stands, so only some direct gap- or stand-specific estimates of moose density would have enabled us to disentangle fully the browsing pressure from the management type and other environmental factors. Although the variable moose density, even within study areas, was likely to increase variability in browsing damage, the overall pattern in relation to basal area was consistent.

Selection is one management method to better balance between wood production, biodiversity protection and recreational values, as well as to mitigate climate change and related biotic and abiotic risk. We found that broadleaved trees do regenerate in gap cutting and single-tree selection sites, but their recruitment to the tree strata may be reduced due to intense browsing pressure. Concerning regeneration and recruitment of broadleaved trees, the basal area of trees retained in uneven-aged management must be balanced with the shade tolerance of the targeted broadleaved trees. As the studied stands were spruce dominated, our study does not tell, how different types of uneven-aged management and browsing damage coincide in pine forests. Thus, more studies are needed on browsing damage in different types of forest and different types of uneven-aged management.

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DECLARATION OF INTEREST STATEMENT

The authors declare no conflict of interest.

REFERENCES

Ahlström, M.A. & Lundqvist, L. 2015. Stand development during 16-57 years in partially harvested sub-alpine uneven-aged Norway spruce stands reconstructed from increment cores. Forest Ecology and Management 350, 81–86.

Ahti, T., Hämet-Ahti, L. & Jalas, J. 1968. Vegetation zones and their sections in northwestern Europe. Annales Botanici Fennici 5, 169–211.

Attiwill, P. 1994. The disturbance of forest ecosystems: The ecological basis for conservative management. Forest Ecology and Management 63, 247–300.

Ball, J. & Dahlgren, J. 2002. Browsing damage on pine (*Pinus sylvestris* and *P. contorta*) by a migrating moose (*Alces alces*) population in winter: relation to habitat composition and road barriers. Scandinavian Journal of Forest Research 17, 427–435.

Bergeron, Y., Leduc, A., Harvey, B.D. & Gauthier, S. 2002. Natural fire regime: A guide for sustainable forest management of the Canadian boreal forest. Silva Fennica 36, 81–95.

Burnham, K.P. & Anderson, D.R. 2002. Model selection and multimodel inference: A practical information-theoretic approach. New York: Springer-Verlag.

Cajander, A.1926. The theory of forest types. Acta Forestalia Fennica 29(3). 108 p.

Carnol, M. & Bazgir, M. 2013. Nutrient return to the forest floor through litter and throughfall under 7 forest species after conversion from Norway spruce. Forest Ecology and Management 309, 66–75.

Cribari-Neto, F. & Zeileis, A. 2010. Beta Regression in R. Journal of Statistical Software 34(2), 1-24. URL http://www.jstatsoft.org/v34/i02/.

Eerikäinen, K., Miina, J. & Valkonen, S. 2007. Models for the regeneration establishment and the development of established seedlings in uneven-aged, Norway spruce dominated forest stands of southern Finland. Forest Ecology and Management 242, 444–461.

Götmark, F., Fridman, J., Kempe, G. & Nordén, B. 2005.Broadleaved tree species in conifer-dominated forestry: regeneration and limitation of saplings in southern Sweden. Forest Ecology and Management 214, 142–157.

Heikkilä, R. 1990. Effect of plantation characteristics on moose browsing on Scots pine. Silva Fennica 24, 341–351.

Heikkilä, R. 1991. Moose browsing in a Scots pine plantation mixed with deciduous tree species. Acta Forestalia Fennica 224, 1–13.

Hörnberg, S. 2001. Changes in population density of Moose (Alces alces) and damage to forests in Sweden. Forest Ecology and Management 149, 141–151.

Jüriado, I., Paal, J. & Liira, J. 2003. Epiphytic and epixylic lichen species diversity in Estonian natural forests. Biodiversity and Conservation 12, 1587–1607.

Koivula, M., Punttila, P., Haila, Y. & Niemela, J. 1999. Leaf litter and small-scale distribution of carabid beetles (Coleoptera, Carabidae) in the boreal forest. Ecography 22, 424–435.

Koivula, M., Kuuluvainen, T., Hallman, E., Kouki, J., Siitonen, J. & Valkonen, S. 2014. Forest management inspired by natural disturbance dynamics (DISTDYN) – a long-term research and development project in Finland. Scandinavian Journal of Forest Research 29, 579–592.

Kuuluvainen, T. & Aakala, T. 2011. Natural forest dynamics in boreal Fennoscandia: a review and classification. Silva Fennica 45, 823–841.

Kuuluvainen, T., Tahvonen, O. & Aakala, T. 2012. Even-Aged and Uneven-Aged Forest Management in Boreal Fennoscandia: A Review. AMBIO 41, 720–737.

Long, J. 2009. Emulating natural disturbance regimes as a basis for forest management: a North American view. Forest Ecology and Management 257, 1868–1873.

Luke (Natural Resources Institute Finland) 2018. Riistahavainnot [Game statistics].
http://riistahavainnot.fi/hirvielaimet/hirvitiheys (accessed 16 July 2018)

Lundqvist, L.2017. Tamm Review: Selection system reduces long-term volume growth in
Fennoscandic uneven-aged Norway spruce forests. Forest Ecology and Management 391,
362–375.

McInnes, P.F., Naiman, R.J., Pastor, J. & Cohen Y. 1992. Effects of moose browsing on
vegetation and litter of the boreal forest, Isle Royale, Michigan USA. Ecology 73, 2059–
2075.

Nevalainen, S. 2017. Comparison of damage risks in even- and uneven-aged forestry in
Finland. Silva Fennica 51(3), article id 1741.

Saksa, T. & Valkonen, S. 2011. Dynamics of seedling establishment and survival in uneven-
aged boreal forests. Forest Ecology and Management 261, 1409–1414.

Sariyildiz, T., Anderson, J.M. & Kucuk, M. 2005. Effects of tree species and topography on
soil chemistry, litter quality, and decomposition in Northeast Turkey. Soil Biology and
Biochemistry 37, 1695–1706.

Shipley, L.A., Blomquist, S. & Danell, K. 1998. Diet choices made by free-ranging moose in
northern Sweden in relation to plant distribution, chemistry, and morphology. Canadian
Journal of Zoology 76, 1722–1733.

Suominen, O., Danell, K. & Bergström, R. 1999. Moose, Trees, and Ground-Living
Invertebrates: Indirect Interactions in Swedish Pine Forests. Oikos 84, 215–226.

Tikkanen, O.-P., Martikainen, P., Hyvärinen, E., Junninen, K. & Kouki, J. 2006. Red-listed
boreal forest species of Finland: associations with forest structure, tree species, and decaying
wood. Annales Zoologici Fennici 43, 373–383.

Wam, H. & Hjeljord, O. 2010. Moose summer diet from feces and field surveys: a
comparative study. Rangeland Ecology and Management 63, 387–395.

Figure legends

Figure 1. The relationship between the basal area (m^2ha^{-1}) of trees and the $\log_{10}$-transformed seedling density (ha^{-1}) for rowan, birch and all broadleaved trees.

Figure 2. The relationship between the basal area of retained trees (m^2ha^{-1}) and the proportion of browsed seedlings of all broadleaved species (a), birch (b) and rowan (c). The lines represent fitted beta regression models containing both the basal area of trees and the management method.

Table 1. The total number observed and mean density (ha^{-1}) of seedlings by tree species. 'Sites' indicates the number of gaps and stands (max = 31), in which there were at least five seedlings of the given species.

	Sites	Number	Density		Browsed	
			Mean	(min-max)	Mean	(min-max)
Spruce (*Picea abies*)	28	1417	1514	(57–8488)	0	(0–0)
Pine (*Pinus sylvestris*)	4	34	59	(0–509)	4	(0–33)
Birch (*Betula* spp.)	31	1665	2396	(133–16524)	36	(9–84)
Aspen (*Populus tremula*)	5	82	149	(0–1698)	76	(0–100)
Rowan (*Sorbus aucuparia*)	31	1884	2181	(155–6112)	75	(30–96)
Willows (*Salix* spp.)	1	31	45	(0–283)	73	(0–100)
Juniper (*Juniperus communis*)	3	50	46	(0–287)	43	(0–100)
Alder (*Alnus* spp.)	9	145	187	(0–1075)	14	(0–100)

Table 2. Beta regression models for the relationship between the proportion of the browsed seedlings of all broadleaved species, birch and rowan. For each model, degrees of freedom (df), loglikelihood (logLik), AICc value, delta (AICc$_i$-AICc$_{min}$) and Akaike weight are shown. BA = basal area of trees (m^{2}ha^{-1}), Seedlings = seedling density, and Management = gap cutting or single-tree selection. Parameter estimates are in Appendix 3.

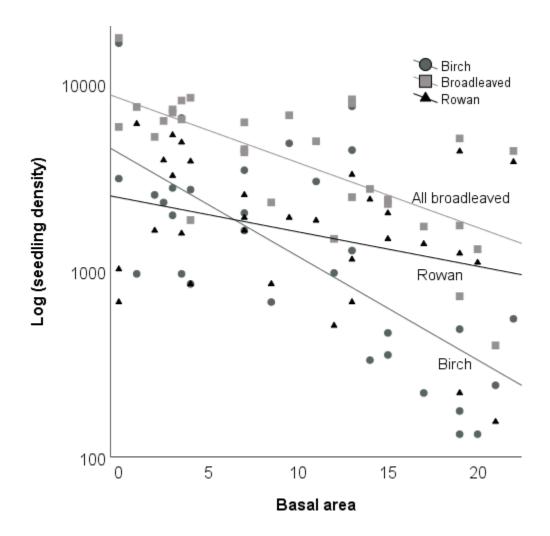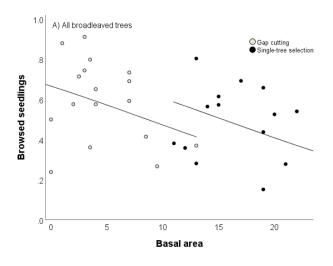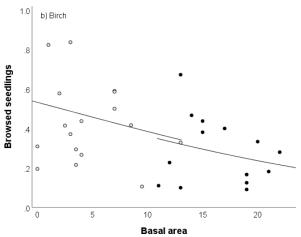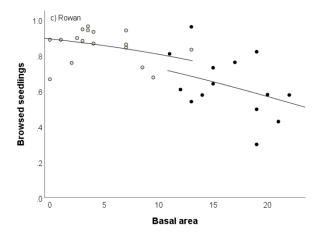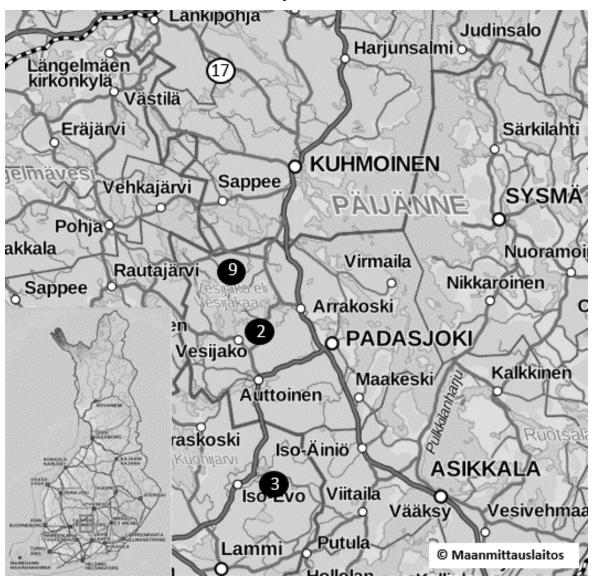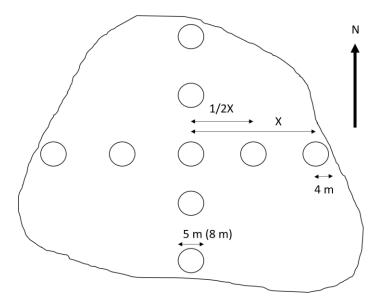|	df	logLik	AICc	delta	weight
All broadleaved species					
BA + Seedlings	4	11.97	-14.40	0.00	1.00
BA	3	10.07	-13.25	1.15	0.56
Management + Seedlings	4	11.26	-12.98	1.42	0.49
Management + BA	4	10.67	-11.80	2.60	0.27
Management + BA + Seedlings	5	11.96	-11.52	2.88	0.24
Management	3	9.14	-11.39	3.01	0.22
Intercept	2	7.80	-11.17	3.23	0.20
Seedlings	3	8.54	-10.19	4.21	0.12
Birch					
BA + Seedlings	4	13.74	-17.94	0.00	1.00
BA	3	12.18	-17.47	0.47	0.79
Management + BA	4	13.14	-16.74	1.20	0.55
Management + BA + Seedlings	5	14.17	-15.94	2.00	0.37
Management	3	10.92	-14.95	2.99	0.22
Management + Seedlings	4	11.82	-14.10	3.84	0.15
Intercept	2	8.49	-12.55	5.39	0.07
Seedlings	3	9.38	-11.87	6.07	0.05
Rowan					
Management + BA + Seedlings	5	28.61	-44.82	0.00	1.00
BA + Seedlings	4	26.78	-44.02	0.80	0.67
BA	3	25.24	-43.59	1.23	0.54
Management + BA	4	26.55	-43.56	1.26	0.53
Management	3	24.25	-41.61	3.21	0.20
Management + Seedlings	4	25.57	-41.60	3.22	0.20
Seedlings	3	19.28	-31.67	13.15	0.00
Intercept	2	15.76	-27.09	17.73	0.00

Figure 1.

Figure 2.

Appendix 1. Study areas in south-central Finland. The white circle represents the gap cutting stands in Isojärvi (n = 17 gaps), and the black circles the single-tree selection stands in Vesijako (n = 9 + 2 stands) and Evo (n = 3 stands). The direct distance between the southernmost Evo and the northernmost Isojärvi is ca. 50 km.

Appendix 2. Sampling design. The outer irregular line represents a single gap or a single-tree selection stand. Browsing damage was recorded from nine circular plots (5 m diameter in gaps and 8 m in single-tree selection stands). Plots were placed systematically such that the outermost plots were to the main compass directions from the center plot and 4 m from the gap or stand edge. The middle plots were half the distance (1/2X) between the center and the outermost plots.

Appendix 3. Beta regression models for the relationship between the proportion of the browsed seedlings of all broadleaved species, birch and rowan. For each model, estimates, standard error (SE), 95% confidence intervals, degrees of freedom (df), loglikelihood (logLik), AICc value, delta (AICc$_i$-AICc$_{min}$) and Akaike weight are shown. The 95% CIs for significant parameter estimates (in bold) do not include zero. BA = basal area of trees (m^{2}ha^{-1}), Seedlings = seedling density, and Management = gap cutting or single-tree selection. For 'Management' gap cutting was used as a baseline.

Model	Intercept Estim.	SE	95% CI		Management Estim.	SE	95% CI		Basal area (BA) Estim.	SE	95% CI		Seedling density Estim.	SE	95% CI		df	logLik	AICc	delta	weight
All broadleaved species																					
BA + Seedlings	1.82	0.93	0.00	3.63					**-0.08**	**0.04**	**-0.16**	**-0.00**	-0.16	0.13	-0.41	0.09	4	11.97	-14.40	0.00	1.00
BA	**0.56**	**0.28**	**0.01**	**1.10**					-0.04	0.02	-0.08	0.01					3	10.07	-13.25	1.15	0.56
Management + Seedlings	1.47	0.91	-0.30	3.25	**-1.04**	**0.52**	**-2.07**	**-0.01**					-0.15	0.14	-0.43	0.13	4	11.26	-12.98	1.42	0.49
Management + BA	0.69	0.36	-0.02	1.40	0.54	0.75	-0.93	2.01	-0.08	0.06	-0.19	0.04					4	10.67	-11.80	2.60	0.27
Management + BA + Seedlings	**1.83**	**0.9**	**0.07**	**3.58**	-0.75	0.76	-2.23	0.74	-0.04	0.04	-0.12	0.05	-0.17	0.14	-0.45	0.11	5	11.96	-11.52	2.88	0.24
Management	0.36	0.20	-0.02	0.75	-0.41	0.28	-0.96	0.14									3	9.14	-11.39	3.01	0.22
Intercept	0.18	0.14	-0.09	0.45													2	7.80	-11.17	3.23	0.20
Seedlings	-0.02	0.35	-0.71	0.66									0.04	0.08	-0.10	0.19	3	8.54	-10.19	4.21	0.12
Birch																					
BA + Seedlings	0.87	0.80	-0.70	2.44					**-0.09**	**0.04**	**-0.17**	**-0.01**	-0.11	0.10	-0.31	0.08	4	13.74	-17.94	0.00	1.00
BA	-0.02	0.27	-0.56	0.51					**-0.06**	**0.02**	**-0.10**	**-0.02**					3	12.18	-17.47	0.47	0.79
Management + BA	0.03	0.35	-0.67	0.72	0.10	0.68	-1.12	1.43	-0.06	0.05	-0.16	0.03					4	13.14	-16.74	1.20	0.55
Management + BA + Seedlings	0.73	0.85	-0.92	2.42	-0.26	0.88	-1.97	1.46	-0.07	0.07	-0.21	0.07	-0.11	0.11	-0.33	0.12	5	14.17	-15.94	2.00	0.37
Management	-0.27	0.20	-0.66	0.13	**-0.65**	**0.30**	**-1.23**	**-0.06**									3	10.92	-14.95	2.99	0.22
Management + Seedlings	0.39	0.79	-1.15	1.93	-1.06	0.58	-2.21	0.09					-0.10	0.13	-0.34	0.15	4	11.82	-14.10	3.84	0.15
Intercept	**-0.54**	**0.15**	**-0.84**	**-0.24**													2	8.49	-12.55	5.39	0.07
Seedlings	**-0.83**	**0.33**	**-1.47**	**-1.18**									0.06	0.07	-0.08	0.20	3	9.38	-11.87	6.07	0.05
Rowan																					
Management + BA + Seedlings	**2.16**	**0.75**	**0.68**	**3.63**	-0.75	0.69	-2.11	0.60	-0.06	0.06	-0.17	0.06	-0.01	0.08	-0.17	0.16	5	28.61	-44.82	0.00	1.00
BA + Seedlings	**2.27**	**0.64**	**1.02**	**3.51**					**-0.10**	**0.03**	**-0.16**	**-0.04**	-0.01	0.07	-0.14	0.12	4	26.78	-44.02	0.80	0.67
BA	**2.15**	**0.26**	**1.63**	**2.66**					**-0.09**	**0.02**	**-0.14**	**-0.05**					3	25.24	-43.59	1.23	0.54
Management + BA	**2.13**	**0.29**	**1.56**	**2.70**	-0.45	0.61	-1.64	0.74	-0.07	0.04	-0.16	0.02					4	26.55	-43.56	1.26	0.53
Management	**1.77**	**0.18**	**1.42**	**2.12**	**-1.21**	**0.27**	**-1.73**	**-0.68**									3	24.25	-41.61	3.21	0.20
Management + Seedlings	**1.66**	**0.52**	**0.64**	**2.68**	**-1.20**	**0.41**	**-1.99**	**-0.40**					0.02	0.07	-0.12	0.16	4	25.57	-41.60	3.22	0.20
Seedlings	**0.66**	**0.33**	**0.01**	**1.32**									0.11	0.06	-0.01	0.22	3	19.28	-31.67	13.15	0.00
Intercept	**1.11**	**0.16**	**0.80**	**1.42**													2	15.76	-27.09	17.73	0.00