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1 Managing conservation values of protected sites: how to maintain deciduous trees in white-backed
2 woodpecker territories

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12

13 Abstract

14 Successional and other temporal habitat changes may also affect conservation areas and reduce their
15 conservation value. Active management to promote vulnerable habitat features may be an effective,
16 but controversial, solution. Old deciduous trees and deciduous dead wood in boreal forest reserves
17 are examples of habitat features that may be lost during succession, yet several threatened species,
18 including the white-backed woodpecker (*Dendrocopos leucotos*), are dependent on them.

19 Encroaching spruce have been removed from white-backed woodpecker territories to promote the
20 regeneration of deciduous trees and to preserve habitat quality, although the efficiency of this
21 treatment is unclear. In this study, we measured the canopy tree potential (integrating the number,
22 height and condition) of aspen, birch and spruce saplings, and the number and basal area of mature
23 trees in control and treatment sites 2–12 years after spruce removal. The canopy tree potential of
24 aspen saplings increased on treated sites, along with a decrease in the number of spruce saplings
25 and mature spruce trees. We found no evidence that spruce removal would benefit birch saplings.

26 For both aspen and birch saplings, the abundance of mature trees of the same species increased their
27 canopy tree potential more than spruce removal. Overall, our results indicate that spruce removal
28 facilitates aspen regeneration, particularly in areas where large mature aspen trees are present. The
29 lack of birch regeneration, however, indicates that maintaining a full array of important habitat
30 characteristics in white-backed woodpecker territories may require a more comprehensive set of
31 management tools than simply removal of spruce.

32 Keywords: Habitat management; Regeneration; Recruitment; Herbivory; Restoration; Umbrella
33 species

34 1 Introduction

35 Ecosystems in boreal forests have been subject to habitat loss, fragmentation and degradation;
36 consequently, a large proportion of habitats and a vast number of forest-dwelling species are now
37 red-listed (Kouki et al. 2018, Hyvärinen et al. 2019). One of the most widely applied tools to
38 maintain these species and their habitats is the establishment of strictly protected conservation
39 areas. However, some features of high conservation value are closely associated with certain phases
40 of forest succession, and the initial biodiversity value of protected areas may change as succession
41 proceeds. Particularly, the retention of species dependent on forests with a high proportion of old
42 deciduous trees and deciduous dead wood may require active management and restoration in
43 protected sites, as these elements are typically transient in boreal forests.

44 In boreal forests, deciduous trees are most abundant after stand-replacing disturbances (Hellberg et
45 al. 2003), such as high-severity fire and wind. Light-demanding pioneer species, including birch
46 (*Betula* spp. L.) and European aspen (*Populus tremula* L.), prevail in the early and intermediate
47 successional phases (Angelstam & Mikusinski 2004), but are slowly outcompeted by shade-tolerant
48 Norway spruce (*Picea abies* L. Karst). Although the proportion of deciduous trees gradually
49 decreases as the stand ages, gap dynamics can also facilitate the regeneration of deciduous trees and

50 maintain a mixed tree species composition in old-growth forests (Lilja et al. 2006). Thus, boreal
51 forests form a dynamic landscape in which coniferous trees dominate the late successional stands,
52 and deciduous trees create spatial and temporal patches. Naturally, these main successional trends
53 also affect protected areas and may change their ecological properties. This is of particular concern
54 as many protected areas are established to save the species associated with old and dead deciduous
55 trees (Kouki et al. 2004, 2018), and because many species dependent on old deciduous trees and
56 deciduous dead wood are now threatened (Hyvärinen et al. 2019).

57 A key conservation-dependent species that specializes on utilizing old and dead deciduous trees is
58 the white-backed woodpecker (*Dendrocopos leucotos* L.), which excavates nesting cavities in large
59 trees, and feeds primarily on the larvae of saproxylic beetles and moths that live in deciduous dead
60 wood (Angelstam & Mikusiński 1993). Degradation and loss of habitat, driven by intensive forestry
61 and fire suppression measures, have led to a dramatic decline in white-backed woodpecker numbers
62 in Fennoscandia in the last century, and the species became critically endangered (Virkkala 1993).
63 Large-scale conservation efforts, including the protection of the remaining breeding sites and the
64 provision of winter-time feeding, have been implemented to save the species in Finland, and the
65 population has now recovered to around 320-360 breeding pairs (Timo Laine, personal
66 communication, 2020).

67 Although most of the breeding sites are protected, it is uncertain how long these sites will remain
68 suitable for the white-backed woodpecker. The successional change in tree-species composition
69 from light-demanding pioneer tree species to shade-tolerant spruce will lead to a gradual decline in
70 the suitability of these sites for the white-backed woodpecker. The current forests rich in old
71 deciduous trees are likely legacies from historical disturbances (Eriksson et al. 2010), and in the
72 absence of these disturbances, especially fire, regeneration of new deciduous trees is low.
73 Furthermore, deciduous saplings are preferentially browsed by many herbivores, such as moose

74 (*Alces alces* L.). Although frequent browsing does not necessarily increase deciduous sapling
75 mortality, it can effectively restrict recruitment rate of mature trees (Edenius et al. 2011).

76 In addition to the woodpecker, the successional change towards conifer-dominance can affect a
77 range of other species that are also dependent on the old-growth deciduous forests. For instance,
78 forests suitable for the white-backed woodpecker can contain a large number of threatened
79 saproxylic beetles (Martikainen et al. 1998), and the presence of the woodpecker has been found to
80 indicate high species richness of forest birds and red-listed cryptogams (Mikusiński et al. 2001,
81 Roberge et al. 2008). Managing biodiversity values crucial to the white-backed woodpecker could
82 benefit the other species that have similar habitat requirements (Roberge et al. 2008), and
83 accordingly, the white-backed woodpecker could be used as a management umbrella species (Caro
84 2010) for communities in old-growth deciduous forests.

85 In an attempt to prolong the deciduous phase, spruce has been selectively harvested in protected
86 white-backed woodpecker territories (Laine & Heikkilä 2012). Yet, the efficiency of this
87 management action is debatable. Bell et al. (2015) found that dead-wood creation combined with
88 conifer removal can benefit saproxylic beetles in forests originally restored for the white-backed
89 woodpecker, and in North America, removal of conifers has facilitated the vegetative reproduction
90 of trembling aspen (*Populus tremuloides* Michx.) (Jones et al. 2005, Krasnow et al. 2012).

91 However, whether conifer removal facilitates the regeneration of deciduous trees, therefore
92 affecting future forest structure and succession, in white-backed woodpecker territories has not been
93 assessed.

94 In this study, we studied whether the removal of spruce from white-backed woodpecker territories
95 can maintain deciduous trees on conservation sites. We hypothesize that spruce removal promotes
96 the regeneration of deciduous trees and postpones successional change in tree-species composition.
97 Among deciduous trees, our focus was on European aspen and birch (*Betula pendula* Roth and
98 *Betula pubescens* Ehrh.), which are important tree species for white-backed woodpecker breeding

99 (Angelstam & Mikusiński 1993) and foraging (Löhmus et al. 2010). We examined the number and
100 height of tree saplings in white-backed woodpecker territories, comparing untreated stands (control)
101 with stands where spruce had been removed as a management treatment. Our specific questions
102 were:

103 1) Is the canopy tree potential (a metric integrating the number, height and condition) of aspen,
104 birch and spruce saplings affected by spruce removal?

105 2) Are the saplings affected by the species composition of mature trees or by herbivory?

106 3) Do the treated stands change with time since the treatment?

107 Since there are several other threatened species that are associated with patchily occurring
108 deciduous trees in boreal forests and that share habitat preferences with the white-backed
109 woodpecker, we anticipate that our results will also have interest and application beyond the
110 implications for the white-backed woodpecker.

111

112 2. Material and Methods

113 2.1 Study area and sampling

114 The study sites are protected mature herb-rich or mesic heath forests dominated by deciduous trees
115 and with an abundant supply of deciduous dead-wood. All sites are located in eastern Finland,
116 within 80 km radius of the location 62°36'N, 29°6'E. We selected the study sites based on data
117 obtained from the Metsähallitus Parks & Wildlife Finland in regard to white-backed woodpecker
118 territories and breeding sites in 2016–2017. From these territories, we selected protected forests
119 where Parks & Wildlife Finland had carried out spruce removal as habitat management action
120 between 2006 and 2016; typically, these management cuttings focus on areas where spruce
121 undergrowth is high. Our aim was to include woodpecker territories where spruce had been

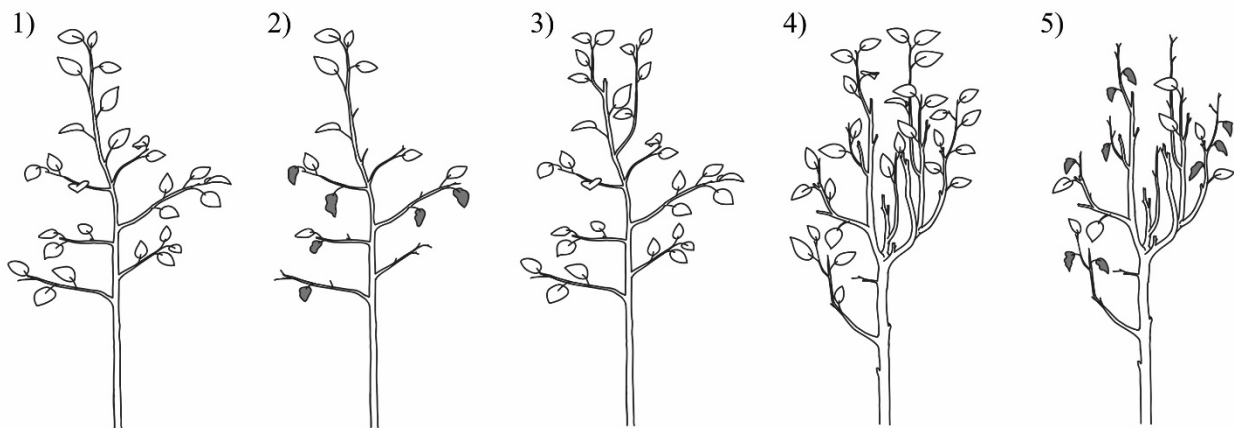
122 removed only in part of the forest area, so that both control and treatment plots could be located
123 within the same forest. However, this was not possible in two stands; therefore, we placed the
124 control plots in the in the closest white-backed woodpecker territor with similar forest site type and
125 overstorey composition.

126 The inventories of saplings were carried out in July and August 2018. For the inventories, we
127 located three circular sample plots, each with a radius of 5.64 m (area = 100 m²), to random
128 compass directions at 10, 25 and 50 m distance from the center of the stands. However, in the
129 treatment stands where groups of spruce had been removed (as opposed to complete removal), a
130 truly random placement of plots was not a feasible option. In these cases, we located cut spruce
131 stumps closest to the initial location of the plot and moved the plot center accordingly. In addition,
132 we moved the initial plot location if it was placed in a stream or outside of the forest. In two control
133 stands and one treatment stand, we could fit only two control and treatment plots, respectively.

134 In both treatment and control plots, we measured the number of tree saplings, and for each sapling,
135 we recorded the species, height and condition. Only saplings with a minimum height of 50 cm and
136 maximum height of 700 cm were measured. We assigned saplings to five classes according to their
137 condition (Fig. 1). The condition classes were later used to calculate the amount of herbivory as a
138 percentage of saplings browsed. For groups of saplings sprouting from the same spot, we measured
139 only the tallest sapling and recorded the number of suckers. We measured the number of mature
140 trees (> 7 m high), and their diameter at breast height (1.3 m) within a radius of 10 m (area = 314
141 m²) around each sample plot center. In addition, to calculate canopy cover, we took a photograph of
142 the canopy (using a 17 mm lens on a camera body with a crop factor of 1.6) from the center of each
143 plot, approximately 30 cm from the ground level. We converted the canopy photographs into black-
144 and-white images in Adobe Photoshop CS 6. In R, applying packages raster (Hijmans 2018) and
145 dplyr (Wickham et al. 2018), we built a function which calculates the canopy cover as the

146 percentage of black pixels from all pixels. Example photos of both treatment and control stands, as
147 well as black-and-white converted canopy photographs, are provided in Appendix A.1.

148 Unfortunately, Metsähallitus Parks & Wildlife Finland does not collect data on the spruce removal
149 intensity. To estimate the intensity of spruce removal in management cuttings, we recorded the
150 number and basal area of cut spruce stumps within each plot.



151

152 Figure 1. Sapling condition classes; grey leaves indicate dead leaves: 1) sapling top is alive and the
153 sapling is healthy; 2) sapling top is alive, but otherwise the sapling is in poor condition; 3) the top
154 has been browsed but otherwise the sapling is healthy; 4) the top has been browsed repeatedly over
155 several years and the sapling has branched, but is still healthy; 5) the top has been browsed
156 repeatedly and the sapling is in poor condition.

157

158 2.2 Canopy tree potential: a metric integrating the number, height and condition of tree saplings

159 To estimate the effect of spruce removal at the plot-level, we built a summarizing metric to indicate
160 longer-term growth and the canopy tree potential of the saplings. The metric combines sapling
161 height and condition with sapling density for two reasons. First, shade-intolerant, pioneer tree
162 species exhibit slow growth rates under closed canopies with little light, which is associated with
163 high mortality rates (Kneeshaw et al. 2005). Second, the sapling condition relates to herbivory

164 pressure and general weakened condition that are likely to influence the survival of a sapling, and
 165 mortality caused by, for example, herbivory, competition, or environmental stressors is especially
 166 high when tree saplings are small (den Herder et al. 2009, Franklin et al. 1987). When examining
 167 regeneration of trees, it is therefore relevant to assess not only the number of tree saplings present,
 168 but also give more weighting to healthy saplings that have already escaped both herbivory pressure
 169 and the size classes of greatest mortality rates. We defined this metric W (hereafter “canopy tree
 170 potential”) as

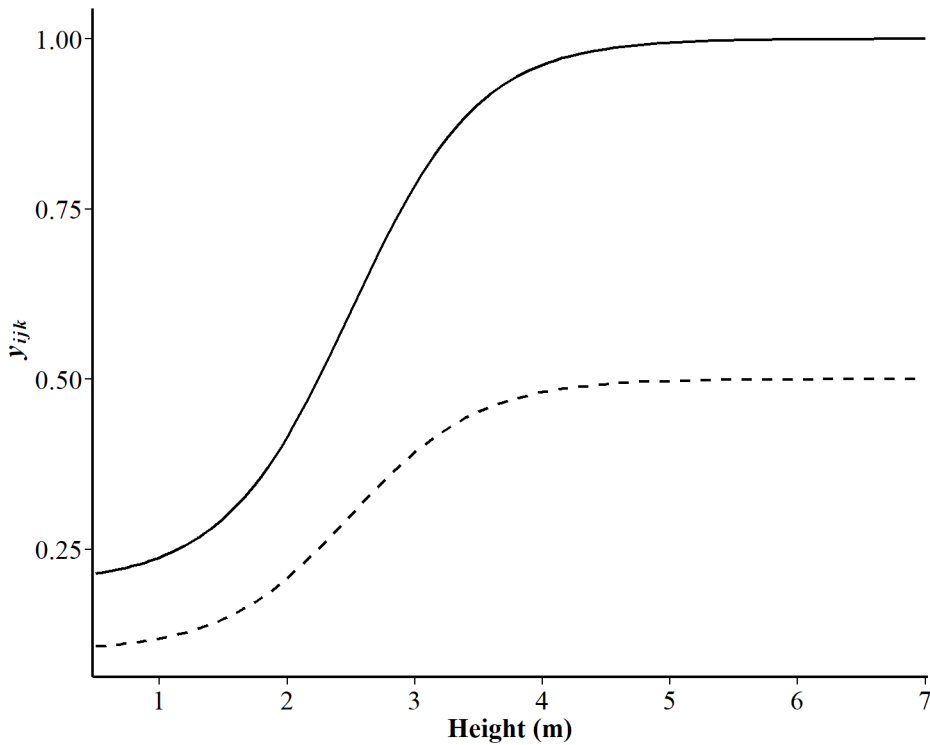
$$171 \quad W = \sum_{k=1}^n y_{ijk} ,$$

172 where y_{ijk} is the value of y in plot i , for tree species j and sapling individual k , further defined as:

$$173 \quad y_{ijk} = c + \frac{d}{1 + e^{b(h-a)}}$$

174 in which h is the height of the sapling in meters, and a and b are constants that define the slope of
 175 the function y (Fig. 2). We assumed these constants to take the values of 2.5 and -2, respectively.
 176 With these values of a and b , the increase in y is greatest when the height of the sapling is between
 177 2 and 3 m. This is a critical height class after which apical parts of a sapling are out of reach for
 178 moose (Ericsson et al. 2001). Parameters c and d are related to the theoretical minimum and
 179 maximum value of y that a sapling can obtain in each condition class. As we assumed these limiting
 180 values to be 0.2 and 1, respectively, the parameters take the form of $c = \frac{0.2}{z}$, and $d = \left(\frac{1}{z}\right) - c$,
 181 where z is the simplified condition class with a value of 1 (healthy or near-healthy; initial condition
 182 classes 1 and 3) or 2 (severely browsed or in poor condition; initial classes 2, 4 and 5). With the
 183 aforementioned limiting values, for a sapling in poor condition, the value of y is approximately half
 184 of the value a healthy sapling of the same size would acquire.

185 Using this definition, the value of y approaches 1 for healthy saplings > 3 m in height, whereas
186 small saplings in poor condition exhibit values close to 0.1 (Fig. 2).



187

188 Figure 2. Values of y_{ijk} as a function of the height of the sapling and simplified condition class,
189 describing the canopy tree potential of a sapling. Solid line = simplified condition class 1 (healthy
190 unbrowsed saplings), dashed line = simplified condition class 2 (saplings that have been severely
191 browsed and/or are in poor condition).

192

193 2.3 Statistical analyses

194 We used multivariate analysis of variance (MANOVA) to examine whether the variables differed
195 between the control and treatment plots. Linear mixed model (LMM), using restricted maximum
196 likelihood (REML), was used to analyze the effect of plot-level variables on aspen, birch and spruce
197 saplings. We log-transformed the species-specific canopy tree potential W via $\log(1+W)$, to
198 normalize the heteroscedastic residuals. The explanatory variables included in the models were

199 treatment, basal area of spruce stumps, number of spruce stumps, percentage of saplings browsed,
200 canopy cover (%), and number and basal area (cm²) of overstory (> 7 m high) aspen, birch and
201 spruce. Basal area values of overstory trees were also log-transformed because of their extremely
202 wide range, and because we assumed that a change in small values to be more important than the
203 same absolute change in the larger values.

204 The linear mixed models were constructed by forward stepwise selection via Akaike's Information
205 Criteria (AIC). First, we entered each explanatory variable independently into the model as a fixed
206 factor and chose the one that had the lowest AIC value. Then, we included each of the remaining
207 variables individually as a second variable in the model from the previous step, and again chose the
208 model with the lowest AIC value. We repeated these steps until no further improvements in AIC
209 could be achieved. As the data is hierarchical by nature, we included forest stand as a random factor
210 in each model. In final models, we used marginal R² to calculate the variance explained by fixed
211 factors, and conditional R² to calculate the variance explained by both random and fixed factors
212 (Nagakawa & Schielzeth 2013).

213 To explore whether time since treatment affected the log-transformed canopy tree potential W of
214 each sapling species, we built linear mixed models for treatment plots only. Linear mixed models
215 for the treatment plots were constructed using the same procedure of forward stepwise selection via
216 AIC as employed for the whole dataset, but we also included time since treatment as an explanatory
217 variable. In addition, to explore the effect of each explanatory variable independently on the whole
218 dataset and on the treatment plots only, we used linear mixed models with only one variable at a
219 time as a fixed factor, and forest stand as a random factor.

220 All statistical analyses were performed using statistical programming environment R version 3.5.3
221 (R Core Team 2019), applying packages car (Fox & Weisberg 2011), lme4 (Douglas et al. 2015)
222 and MASS (Venables & Ripley 2002).

223

224 3. Results

225 3.1 Characteristics of control and treatment plots

226 The data included a total of 1669 aspen, spruce and birch saplings in 49 control and 50 treatment
227 plots from altogether 19 forest stands (Appendices A.1 and A.2). The majority (53 %) of the
228 saplings had a height of 0.5-0.99 m, and the sapling numbers decreased exponentially with
229 increasing height (Appendix A.4).

230 The average number and canopy tree potential of spruce saplings (4.2 ± 0.8 saplings and 1.0 ± 0.2
231 W) were significantly lower in treatment plots than in control plots (10.8 ± 1.8 saplings and $4.7 \pm$
232 $0.6 W$) (Table 1). For aspen, both sapling count (11.7 ± 2.4 saplings) and canopy tree potential (2.3
233 ± 0.5) were greater in treatment plots than in the controls (4.6 ± 0.9 and 1.1 ± 0.3 , respectively),
234 whereas there were no significant differences in the corresponding values of birch saplings. Number
235 of overstory trees and their basal area did not differ between controls and treatments, with the
236 exception of spruce which was more numerous in control plots (5.3 ± 1.0) compared to treatment
237 plots (1.8 ± 0.4).

238

239 Table 1. Average (\pm Standard Error) of characteristics in the control and treatment plots, and results
240 of multivariate analysis of variance, which was used to test the significance of differences between
241 control and treatment plots. Statistically significant ($P < 0.05$) results are in bold. W = canopy tree
242 potential (see chapter 2.2).

Plot characteristic	Control	Treatment	$F_{1,97}$	P
Spruce saplings, number	10.8 (± 1.8)	4.2 (± 0.8)	10.86	0.001
Aspen saplings, number	4.6 (± 0.9)	11.7 (± 2.4)	7.80	0.006
Birch saplings, number	1.4 (± 0.3)	1.1 (± 0.3)	0.42	0.52

Spruce saplings, <i>W</i>	4.7 (± 0.6)	1.0 (± 0.2)	29.74	<0.001
Aspen saplings, <i>W</i>	1.1 (± 0.3)	2.3 (± 0.5)	5.02	0.027
Birch saplings, <i>W</i>	0.9 (± 0.2)	0.8 (± 0.2)	0.11	0.74
Spruce stumps, number	0.06 (± 0.06)	22.3 (± 4.1)	28.4	<0.001
Spruce stump area (cm ²)	1.1 (± 1.1)	736 (± 179)	16.51	<0.001
Mature spruce, number	5.3 (± 1.0)	1.8 (± 0.4)	11.91	<0.001
Mature aspen, number	2.8 (± 0.6)	5.1 (± 1.4)	2.16	0.145
Mature birch, number	11.0 (± 0.9)	12.6 (± 1.4)	0.95	0.33
BA of mature spruce (cm ²)	1668 (± 349)	1655 (± 365)	0.00	0.98
BA of mature aspen (cm ²)	2454 (± 488)	2597 (± 583)	0.03	0.85
BA of mature birch (cm ²)	7031 (± 1766)	5982 (± 399)	0.34	0.56
Herbivory (%)	19.8 (± 2.4)	22.5 (± 3.1)	0.48	0.49
Canopy cover (%)	74.9 (± 1.2)	72.1 (± 1.0)	3.32	0.07

243

244 3.2 Effects of spruce removal and plot characteristics on saplings

245 In the final linear mixed models, the effect and relative importance of plot variables and spruce-
 246 removal treatment varied greatly by sapling species (Table 2). In all models, however, the canopy
 247 tree potential of deciduous saplings increased with either basal area or number of mature trees of the
 248 same species. The model fits and scatter plots of continuous variables used as fixed effects are
 249 illustrated in Fig. 3.

250 The canopy tree potential of aspen saplings increased with basal area of mature aspen (df = 84.39, *t*
 251 = 4.1, *P* < 0.001) and percentage of saplings browsed (df = 75.29, *t* = 3.5, *P* < 0.001) in the plots,
 252 whereas the increasing basal area of living spruce affected aspen saplings negatively (df = 92.96, *t* =
 253 -2.1, *P* = 0.036). In addition, spruce removal treatment had positive influence on the canopy tree
 254 potential of aspen saplings (df = 86.54, *t* = 2.1, *P* = 0.043).

255 Table 2. The effects of spruce removal (treatment) and plot characteristics on the canopy tree
 256 potential (log-transformed measure *W* integrating the number, height and condition of saplings in
 257 each plot; see text) of saplings, according to the final linear mixed models (LMM). Mature tree
 258 basal areas (BA) have been log-transformed prior to model construction. d.f is the approximated

259 denominator degree of freedom. For the full models, conditional R^2 values are given; for fixed
 260 effects, marginal R^2 values are given.

Species	Explanatory variable	Coeff. (S.E.)	d.f.	<i>t</i>	<i>P</i>	Var. (Std. Dev)	R^2
Aspen	Full model						0.45
	Random effects						
	Forest site					0.036 (0.191)	
	Residual					0.315 (0.562)	
	Fixed effects						0.38
	(Intercept)	0.188 (0.170)	70.82	1.11	0.271		
	BA of mature aspen	0.069 (0.017)	84.39	4.14	< 0.001		
	Herbivory	0.012 (0.004)	75.29	3.50	< 0.001		
	BA of mature spruce	-0.041 (0.019)	92.96	-2.13	0.036		
	Treatment	0.241 (0.117)	86.54	2.05	0.043		
Birch	Full model						0.40
	Random effects						
	Forest site					0.007 (0.085)	
	Residual					0.185 (0.430)	
	Fixed effects						0.37
	(Intercept)	2.926 (0.540)	81.16	5.41	< 0.001		
	No. of mature birch	0.035 (0.005)	91.67	6.41	< 0.001		
BA of mature birch	-0.345 (0.064)	82.10	-5.36	< 0.001			
Spruce	Full model						0.61
	Random effects						
	Forest site					0.154 (0.39)	
	Residual					0.252 (0.502)	
	Fixed effects						0.37
	(Intercept)	2.77 (0.602)	93.70	4.60	< 0.001		
	Treatment	-0.894 (0.113)	84.46	-7.89	< 0.001		
Canopy cover	-0.019 (0.008)	92.11	-2.33	0.022			
No. of mature spruce	-0.022 (0.013)	95.00	1.623	0.108			

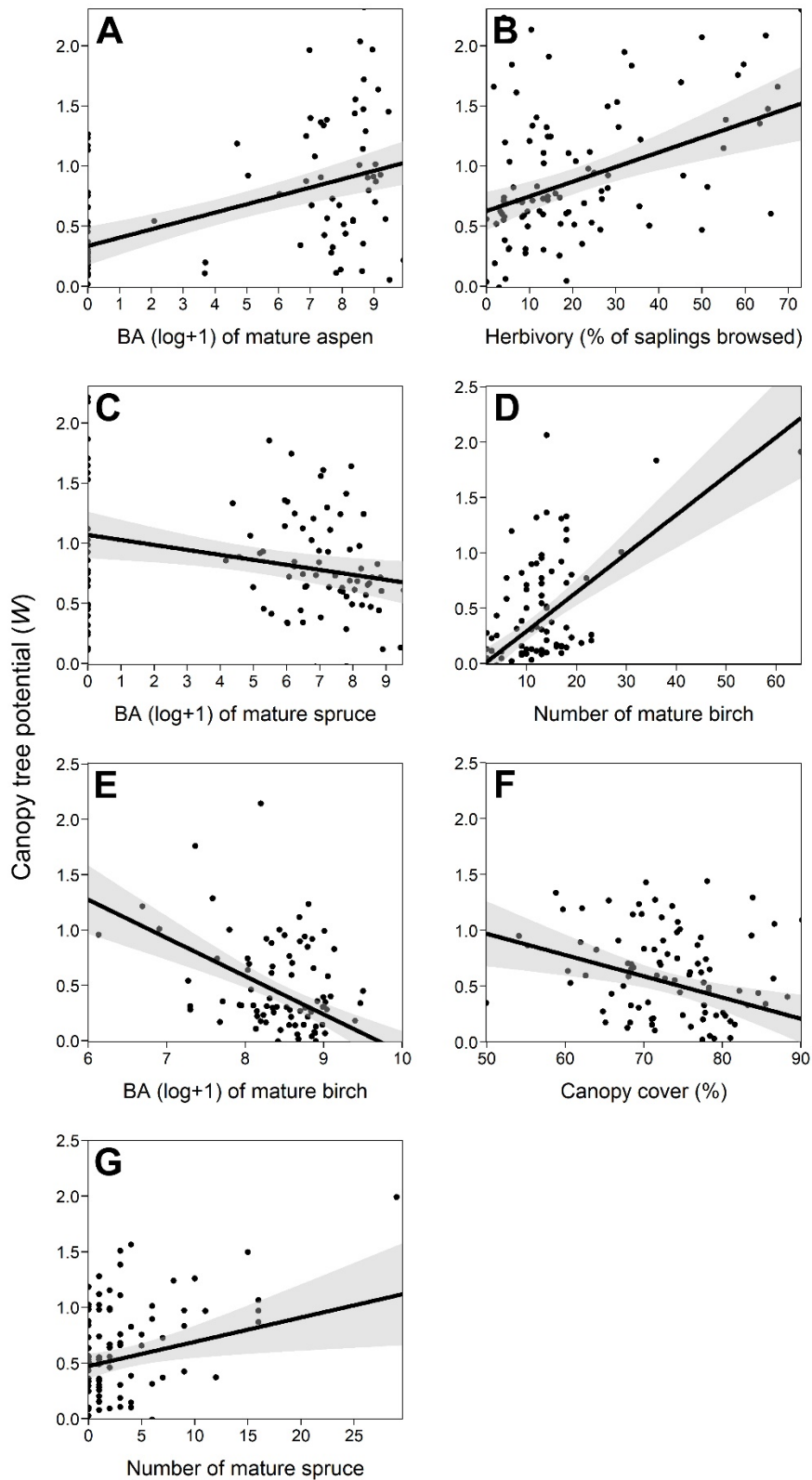
261

262 For birch saplings, the number and basal area of mature birch were the only variables included in
 263 the final linear mixed model. The canopy tree potential of birch saplings increased with the number
 264 of mature birch (df = 91.7, $t = 6.4$, $P < 0.001$), while the increasing basal area of living birch (df =
 265 82.1, $t = -5.4$, $P < 0.001$) affected the canopy tree potential negatively. In addition, when each

266 explanatory variable were assessed on their own (Appendix A.7), increasing mature spruce number
267 ($t = -2.32, P = 0.023$) and basal area ($t = -3.52, P < 0.001$) had negative effects on birch saplings.

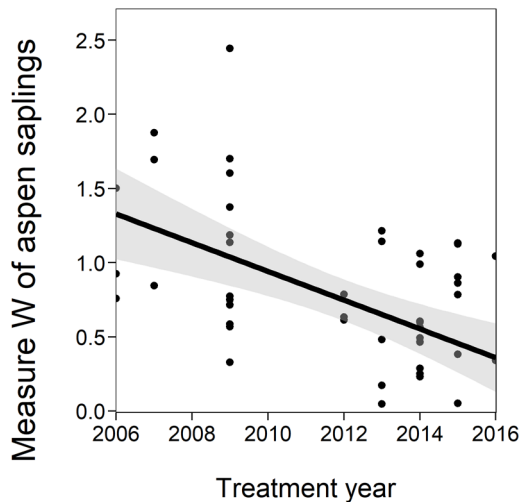
268 Treatment had the most notable effect on spruce ($df = 84.5, t = -7.9, P < 0.001$), with spruce
269 saplings displaying less canopy tree potential in the treatment plots. The estimates of treatment
270 intensity did not increase the model fit for spruce saplings and were therefore excluded from the
271 model. In the linear mixed model constructed for treatment plots only (Appendix A.6), however, the
272 increasing number of cut stumps ($df = 22.2, t = 4.1, P < 0.001$) had positive effect on the canopy
273 tree potential of spruce saplings, whereas the effect of increasing stump basal area ($df = 32.1, t = -$
274 $2.4, P = 0.021$) was negative.

275 Notably, treatment year only affected aspen saplings ($df = 17.6, t = -2.9, P = 0.003$), with lower
276 canopy tree potential values observed in recently treated sites (Fig 4; Appendix A.6). In addition,
277 the number and basal area of cut spruce stumps had no effect on aspen and birch saplings when only
278 treatment plots were considered (LMM models with only one fixed factor, $P > 0.05$; Appendix
279 A.8).



280

281 Figure 3. The fitted values from the final linear mixed models, showing the effect of fixed effects
 282 on the canopy tree potential (W) of aspen (A–C), birch (D–E) and spruce (F–G) saplings. Only
 283 continuous variables are shown.



284

285 Figure 4. The fitted values from the final linear mixed model for treatment plots only, showing the
 286 effect of time since treatment on the canopy tree potential of aspen saplings. The whole model is
 287 provided in Appendix 6.

288

289 4 Discussion

290 4.1 Effect of spruce removal on saplings

291 Our results show that spruce removal can restrict spruce encroachment. The impact of spruce
 292 removal on the canopy tree potential of deciduous saplings, however, was weak and varied with tree
 293 species. The canopy tree potential of aspen saplings displayed a weak positive response to spruce
 294 removal, whereas there was no effect for birch saplings. Additionally, for aspen saplings, the
 295 canopy tree potential increased along time since treatment. All species, especially deciduous
 296 saplings, benefited from an increasing abundance of mature trees of the same species.

297 Several studies have found that conifer removal facilitates growth and regeneration of trembling
 298 aspen (Shepperd 2001, Jones et al. 2005, Krasnow et al. 2012, Berrill et al. 2017), a North
 299 American species ecologically similar to European aspen. Both these are light-demanding pioneer
 300 species that, typically, are slowly outcompeted by conifers during forest succession. In addition, the

301 sexual reproduction of both aspen species is strongly tied to forest fires, in the absence of which the
302 primary form of reproduction is via suckering (Myking et al. 2011).

303 The enhanced growth and regeneration of trembling aspen after conifer removal likely results from
304 two primary factors. First, removing conifers increases the amount of sunlight transmitted to the
305 understory (Shepperd 2001, Berrill et al. 2017), creating a favorable environment for the
306 regeneration and growth of shade-intolerant aspen. Second, conifer removal can act as a slight
307 disturbance mechanism inducing hormonal stimulation in trembling aspen, initiating vegetative
308 regeneration via suckering (Jones et al. 2005). Given the similar ecologies of trembling and
309 European aspen, it is probable that both these factors benefited the aspen saplings in the spruce
310 removal sites in our study. Moreover, after release from competition with conifers, aspen can
311 allocate resources to radial growth rather than increased sucker production (Bretfeld et al. 2015);
312 this allocation could have contributed to the rather weak response of aspen saplings in our models.

313 The canopy tree potential of aspen saplings increased with time since spruce removal, indicating
314 that aspen benefits from the treatment with a time lag. For instance, Jones et al. (2005) suggested
315 that aspen can take several years to recover from the initial disturbance of conifer removal,
316 stimulate sucker production, and allocate energy to growth.

317 In contrast to aspen, the canopy tree potential of birch saplings showed no response to spruce
318 removal in our study. If spruce removal benefits aspen regeneration by inducing sucker production,
319 the lack of a response in birch could stem from the different vegetative reproduction strategies
320 between these two deciduous tree species. The primary form of vegetative reproduction in both *B.*
321 *pubescens* and *B. pendula* is sprouting from basal buds, which typically occurs as a response to
322 damage, such as fire or cutting (Atkinson 1992). Moreover, of the 1669 saplings in our sample
323 plots, only 125 birch, decreasing the reliability of the models for this species.

324 Previous studies have shown that the intensity of conifer removal affects the response magnitude in
325 trembling aspen. For example, Berrill et al. (2017) found that growth of young aspen increased
326 more when a large number of conifers were removed, although Krasnow et al. (2012) suggested that
327 there may be a threshold of optimum treatment intensity. In our study, however, the intensity of
328 spruce removal had no effect on deciduous saplings. In the case of spruce saplings in treatment
329 plots, the canopy tree potential increased with the number of stumps present, but decreased with the
330 increasing basal area of stumps. Heavily encroached plots where a large number of spruce trees had
331 been removed may be areas with a large spruce seed bank and optimal environmental conditions for
332 seed germination. Thus, these areas are quickly recolonized. On the other hand, removing larger
333 spruce specimens can reduce the number of mature trees that produce seed, likely prolonging the
334 time spruce takes to recolonize the area.

335 4.2 Mature tree species composition and canopy cover

336 The influence of mature trees on deciduous saplings was greater than that of spruce removal. In the
337 case of aspen, the basal area of mature parental trees was the most important variable increasing the
338 canopy tree potential of aspen saplings. The large basal area of parental trees has been found to
339 correlate with a greater root sucker potential in trembling aspen (Perrette et al. 2014), likely caused
340 by high root density (Frey et al. 2003). However, increasing basal area is also associated with
341 increasing canopy cover, and thus, lower levels of understory light (Comeau et al. 2006), which
342 could restrict aspen regeneration. Therefore, it is somewhat surprising that increasing canopy cover
343 had a positive effect on aspen saplings in our spruce removal sites. These results suggest that in
344 stands with a large basal area of mature aspen, the greater potential for sucker production outweighs
345 the negative effects of increased canopy cover.

346 For birch saplings, the canopy tree potential increased with the number of mature birch trees
347 present, but decreased in comparison to their basal area. As the basal area generally increases as
348 trees grow taller, this is consistent with the findings of Götmark et al. (2005), who reported that

349 birch saplings were more numerous in young forests than in mature forests. Birch does not seem to
350 benefit from the increasing basal area of parental trees to the same extent as aspen, probably
351 because of the different vegetative reproduction strategy.

352 The increasing basal area of mature spruce had a negative effect on the canopy tree potential of
353 aspen saplings. This suggests that the increasing abundance of spruce limits the regeneration of
354 aspen, supporting the findings of Eerikäinen et al. (2005) and Clement et al. (2019). In addition to
355 decreased light availability (Shepperd 2001, Berrill et al. 2017) and increased competition, conifers
356 have been hypothesized to alter soil chemistry unfavorable to deciduous species (Calder et al.
357 2011). While the responses to spruce removal were weak or lacking in our data, the negative
358 influence of increasing spruce basal area indicates that removing mature spruce will benefit the
359 regeneration of both birch and aspen.

360 4.3 Herbivory pressure

361 Aspen is a favorite food source for moose, and while recurrent browsing does not necessarily cause
362 increased mortality rates in aspen saplings (Edenius et al. 2011), high moose populations can
363 severely restrict or even halt aspen from reaching a height safe from browsing (de Chantal et al.
364 2009). Surprisingly, our results indicated a positive association between the proportion of saplings
365 browsed and the canopy tree potential of aspen saplings. Moose are more likely to utilize stands
366 with a high density of aspen saplings (Ericsson et al. 2001, de Chantal et al. 2009) and accordingly,
367 it is probable that browsing was more frequent in our plots with greater aspen sapling densities
368 where the canopy tree potential resulted from the very high abundance of saplings instead of their
369 height or condition. Although our results do not directly demonstrate the negative impact of
370 herbivores on deciduous potential, regulating herbivore pressure close to protected areas might be
371 worth consideration.

372 5 Conclusions

373 Our results suggest that spruce removal is an effective management tool to delay spruce
374 encroachment and facilitate aspen regeneration, and thereby ensure the future presence of aspen
375 trees in white-backed woodpecker territories. Spruce removal can be highly applicable in areas
376 where large mature aspen trees are present, and where mature spruce trees are removed in addition
377 to spruce saplings.

378 Aspen is one of the most preferred nesting cavity tree species of the white-backed woodpecker
379 (Angelstam & Mikusiński 1993) and is frequently used for foraging (Stenberg & Hogstad 2004).
380 However, compared to aspen, birch may be a more crucial component of white-backed woodpecker
381 territories. Yet, in our study, birch saplings did not benefit from spruce removal. Birch snags, logs,
382 and dead branches are the most commonly used foraging substrates for the white-backed
383 woodpecker (Stenberg & Hogstad 2004); typically, birch comprises more than half of the living tree
384 composition in the breeding sites (Virkkala 1993). Aspen and birch have been found to differ in
385 their saproxylic beetle composition (Jonsell et al. 2004); one of the most important prey items to the
386 white-backed woodpecker. Therefore, the habitat suitability of white-backed woodpecker territories
387 may change not only with spruce encroachment, but also if there is a change in the dominant
388 deciduous tree species.

389 We anticipate that the greater canopy potential of aspen saplings after spruce removal will
390 eventually result in a continuous supply of mature aspen trees, especially in areas where
391 herbivorous pressure by moose is low or moderate. However, the lack of an observed response by
392 birch to spruce removal indicates that tree layer composition and, therefore, the habitat quality of
393 the white-backed woodpecker territories may nevertheless change, even when spruce removal is
394 successfully applied to promote aspen. Thus, the importance of birch for the white-backed
395 woodpecker, and for many other birch-associated species, highlights a need for additional measures
396 that are more specifically targeted at maintaining birch trees.

397

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