Author(s): Hämäläinen, Karoliina; Junninen, Kaisa; Halme, Panu; Kouki, Jari

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Year: 2020

Version: Accepted version (Final draft)

Please cite the original version:

Hämäläinen, K., Junninen, K., Halme, P., & Kouki, J. (2020). Managing conservation values of protected sites : How to maintain deciduous trees in white-backed woodpecker territories. Forest Ecology and Management, 461, Article 117946. https://doi.org/10.1016/j.foreco.2020.117946

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

Karoliina Hämäläinen[1], Kaisa Junninen[1,2], Panu Halme[3,4], Jari Kouki[1]

[1] School of Forest Sciences, University of Eastern Finland, P.O. Box 111, FI-80101 Joensuu, Finland

[2] Metsähallitus Parks & Wildlife Finland, c/o UEF/Borealis, P.O. Box 111, FI-80101 Joensuu, Finland

[3] Department of Biological and Environmental Science, University of Jyväskylä, P.O. Box 35, FIN-40014, Jyväskylä, Finland

[4] School of Resource Wisdom, University of Jyväskylä, P.O. Box 35, FIN-40014, Jyväskylä, Finland

Abstract

Successional and other temporal habitat changes may also affect conservation areas and reduce their conservation value. Active management to promote vulnerable habitat features may be an effective, but controversial, solution. Old deciduous trees and deciduous dead wood in boreal forest reserves are examples of habitat features that may be lost during succession, yet several threatened species, including the white-backed woodpecker (*Dendrocopos leucotos*), are dependent on them. Encroaching spruce have been removed from white-backed woodpecker territories to promote the regeneration of deciduous trees and to preserve habitat quality, although the efficiency of this treatment is unclear. In this study, we measured the canopy tree potential (integrating the number, height and condition) of aspen, birch and spruce saplings, and the number and basal area of mature trees in control and treatment sites 2–12 years after spruce removal. The canopy tree potential of aspen saplings increased on treated sites, along with a decrease in the number of spruce saplings and mature spruce trees. We found no evidence that spruce removal would benefit birch saplings.

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

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

1 Introduction

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

In boreal forests, deciduous trees are most abundant after stand-replacing disturbances (Hellberg et al. 2003), such as high-severity fire and wind. Light-demanding pioneer species, including birch (*Betula* spp. L.) and European aspen (*Populus tremula* L.), prevail in the early and intermediate successional phases (Angelstam & Mikusinski 2004), but are slowly outcompeted by shade-tolerant Norway spruce (*Picea abies* L. Karst). Although the proportion of deciduous trees gradually decreases as the stand ages, gap dynamics can also facilitate the regeneration of deciduous trees and maintain a mixed tree species composition in old-growth forests (Lilja et al. 2006). Thus, boreal forests form a dynamic landscape in which coniferous trees dominate the late successional stands, and deciduous trees create spatial and temporal patches. Naturally, these main successional trends also affect protected areas and may change their ecological properties. This is of particular concern as many protected areas are established to save the species associated with old and dead deciduous trees (Kouki et al. 2004, 2018), and because many species dependent on old deciduous trees and deciduous dead wood are now threatened (Hyvärinen et al. 2019).

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

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

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

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

In an attempt to prolong the deciduous phase, spruce has been selectively harvested in protected white-backed woodpecker territories (Laine & Heikkilä 2012). Yet, the efficiency of this management action is debatable. Bell et al. (2015) found that dead-wood creation combined with conifer removal can benefit saproxylic beetles in forests originally restored for the white-backed woodpecker, and in North America, removal of conifers has facilitated the vegetative reproduction of trembling aspen (*Populus tremuloides* Michx.) (Jones et al. 2005, Krasnow et al. 2012). However, whether conifer removal facilitates the regeneration of deciduous trees, therefore affecting future forest structure and succession, in white-backed woodpecker territories has not been assessed.

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

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

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

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

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

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

2. Material and Methods

2.1 Study area and sampling

The study sites are protected mature herb-rich or mesic heath forests dominated by deciduous trees and with an abundant supply of deciduous dead-wood. All sites are located in eastern Finland, within 80 km radius of the location 62°36′N, 29°6′E. We selected the study sites based on data obtained from the Metsähallitus Parks & Wildlife Finland in regard to white-backed woodpecker territories and breeding sites in 2016–2017. From these territories, we selected protected forests where Parks & Wildlife Finland had carried out spruce removal as habitat management action between 2006 and 2016; typically, these management cuttings focus on areas where spruce undergrowth is high. Our aim was to include woodpecker territories where spruce had been removed only in part of the forest area, so that both control and treatment plots could be located within the same forest. However, this was not possible in two stands; therefore, we placed the control plots in the in the closest white-backed woodpecker territor with similar forest site type and overstorey composition.

The inventories of saplings were carried out in July and August 2018. For the inventories, we located three circular sample plots, each with a radius of 5.64 m (area = 100 m^2), to random compass directions at 10, 25 and 50 m distance from the center of the stands. However, in the treatment stands where groups of spruce had been removed (as opposed to complete removal), a truly random placement of plots was not a feasible option. In these cases, we located cut spruce stumps closest to the initial location of the plot and moved the plot center accordingly. In addition, we moved the initial plot location if it was placed in a stream or outside of the forest. In two control stands and one treatment stand, we could fit only two control and treatment plots, respectively.

In both treatment and control plots, we measured the number of tree saplings, and for each sapling, we recorded the species, height and condition. Only saplings with a minimum height of 50 cm and maximum height of 700 cm were measured. We assigned saplings to five classes according to their condition (Fig. 1). The condition classes were later used to calculate the amount of herbivory as a percentage of saplings browsed. For groups of saplings sprouting from the same spot, we measured only the tallest sapling and recorded the number of suckers. We measured the number of mature trees (> 7 m high), and their diameter at breast height (1.3 m) within a radius of 10 m (area = 314 m^2) around each sample plot center. In addition, to calculate canopy cover, we took a photograph of the canopy (using a 17 mm lens on a camera body with a crop factor of 1.6) from the center of each plot, approximately 30 cm from the ground level. We converted the canopy photographs into black-and-white images in Adobe Photoshop CS 6. In R, applying packages raster (Hijmans 2018) and dplyr (Wickham et al. 2018), we built a function which calculates the canopy cover as the percentage of black pixels from all pixels. Example photos of both treatment and control stands, as well as black-and-white converted canopy photographs, are provided in Appendix A.1.

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

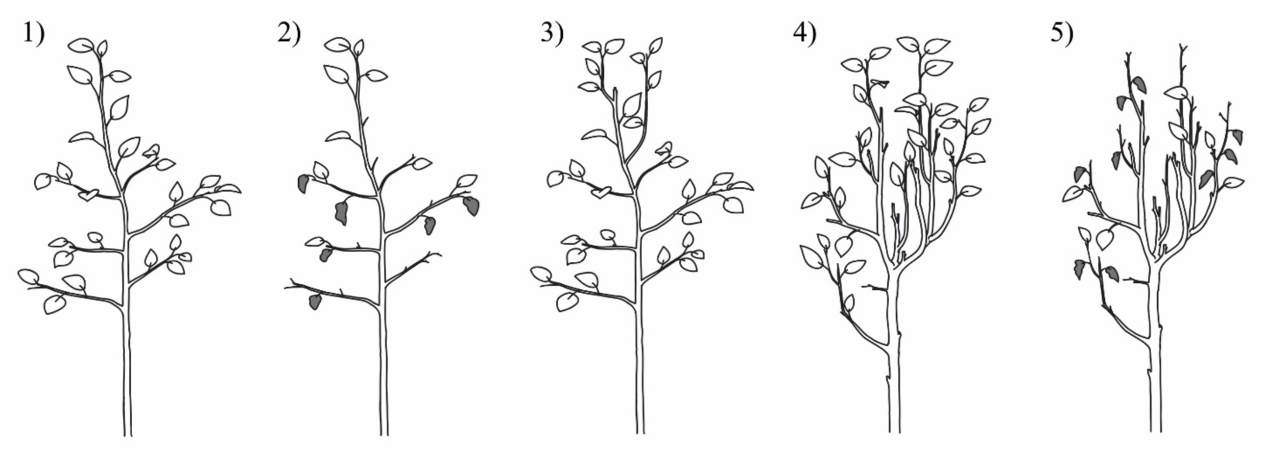

Figure 1. Sapling condition classes; grey leaves indicate dead leaves: 1) sapling top is alive and the sapling is healthy; 2) sapling top is alive, but otherwise the sapling is in poor condition; 3) the top has been browsed but otherwise the sapling is healthy; 4) the top has been browsed repeatedly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

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

To estimate the effect of spruce removal at the plot-level, we built a summarizing metric to indicate longer-term growth and the canopy tree potential of the saplings. The metric combines sapling height and condition with sapling density for two reasons. First, shade-intolerant, pioneer tree species exhibit slow growth rates under closed canopies with little light, which is associated with high mortality rates (Kneeshaw et al. 2005). Second, the sapling condition relates to herbivory pressure and general weakened condition that are likely to influence the survival of a sapling, and mortality caused by, for example, herbivory, competition, or environmental stressors is especially high when tree saplings are small (den Herder et al. 2009, Franklin et al. 1987). When examining regeneration of trees, it is therefore relevant to assess not only the number of tree saplings present, but also give more weighting to healthy saplings that have already escaped both herbivory pressure and the size classes of greatest mortality rates. We defined this metric *W* (hereafter "canopy tree potential") as

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

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

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

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

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

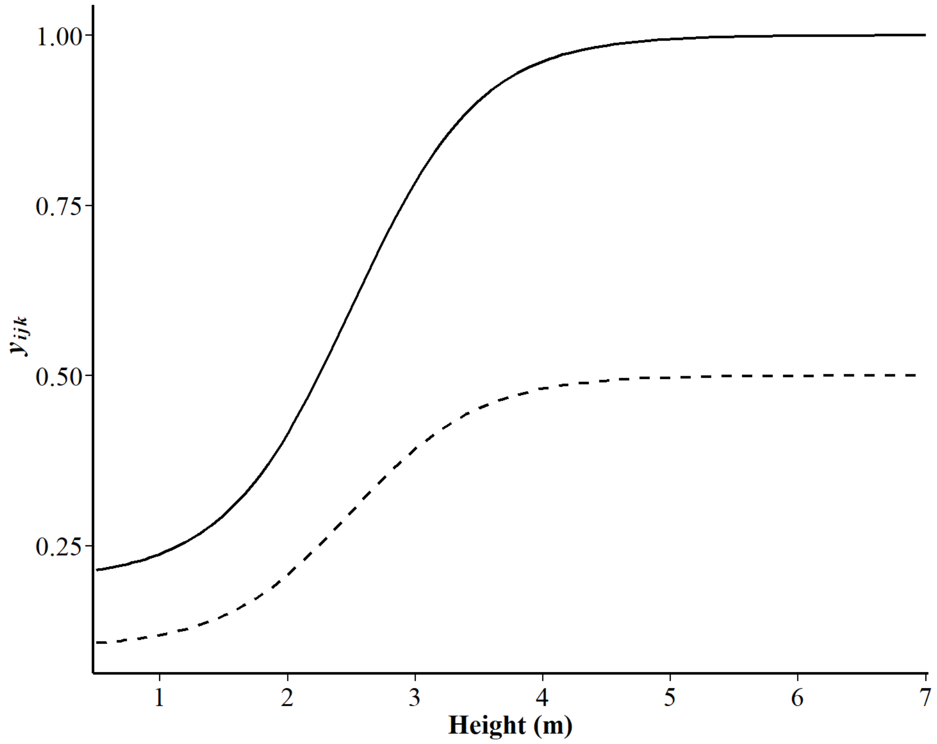

Figure 2. Values of y_{ijk} as a function of the height of the sapling and simplified condition class, describing the canopy tree potential of a sapling. Solid line = simplified condition class 1 (healthy unbrowsed saplings), dashed line = simplified condition class 2 (saplings that have been severely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

2.3 Statistical analyses

We used multivariate analysis of variance (MANOVA) to examine whether the variables differed between the control and treatment plots. Linear mixed model (LMM), using restricted maximum likelihood (REML), was used to analyze the effect of plot-level variables on aspen, birch and spruce saplings. We log-transformed the species-specific canopy tree potential W via log(1+W), to normalize the heteroscedastic residuals. The explanatory variables included in the models were treatment, basal area of spruce stumps, number of spruce stumps, percentage of saplings browsed, canopy cover (%), and number and basal area (cm^2) of overstory (> 7 m high) aspen, birch and spruce. Basal area values of overstory trees were also log-transformed because of their extremely wide range, and because we assumed that a change in small values to be more important than the same absolute change in the larger values.

The linear mixed models were constructed by forward stepwise selection via Akaike's Information Criteria (AIC). First, we entered each explanatory variable independently into the model as a fixed factor and chose the one that had the lowest AIC value. Then, we included each of the remaining variables individually as a second variable in the model from the previous step, and again chose the model with the lowest AIC value. We repeated these steps until no further improvements in AIC could be achieved. As the data is hierarchical by nature, we included forest stand as a random factor in each model. In final models, we used marginal R^2 to calculate the variance explained by fixed factors, and conditional R^2 to calculate the variance explained by both random and fixed factors (Nagakawa & Schielzeth 2013).

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

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

3. Results

3.1 Characteristics of control and treatment plots

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

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

Table 1. Average (± Standard Error) of characteristics in the control and treatment plots, and results of multivariate analysis of variance, which was used to test the significance of differences between control and treatment plots. Statistically significant (P < 0.05) results are in bold. *W* = canopy tree 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, *W*	4.7 (± 0.6)	1.0 (± 0.2)	29.74	**<0.001**
Aspen saplings, *W*	1.1 (± 0.3)	2.3 (± 0.5)	5.02	**0.027**
Birch saplings, *W*	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

3.2 Effects of spruce removal and plot characteristics on saplings

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

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

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

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

Species	Explanatory variable	Coeff. (*S.E.*)	d.f.	*t*	*P*	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		

For birch saplings, the number and basal area of mature birch were the only variables included in the final linear mixed model. The canopy tree potential of birch saplings increased with the number of mature birch (df = 91.7, t = 6.4, P < 0.001), while the increasing basal area of living birch (df = 82.1, t = -5.4, P < 0.001) affected the canopy tree potential negatively. In addition, when each explanatory variable were assessed on their own (Appendix A.7), increasing mature spruce number (t = -2.32, P = 0.023) and basal area (t = -3.52, P < 0.001) had negative effects on birch saplings.

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

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

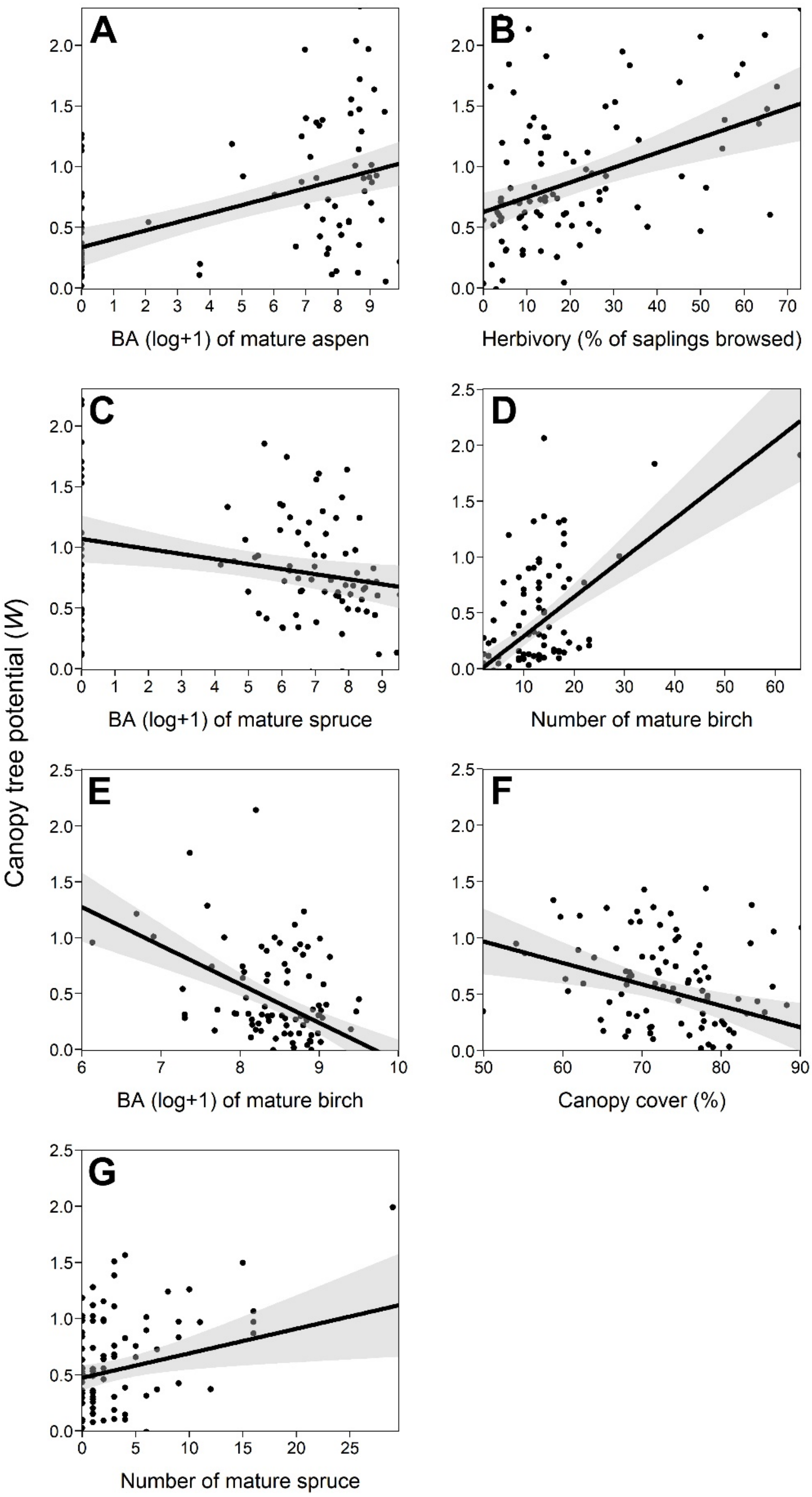

Figure 3. The fitted values from the final linear mixed models, showing the effect of fixed effects on the canopy tree potential (*W*) of aspen (A–C), birch (D-E) and spruce (F–G) saplings. Only continuous variables are shown.

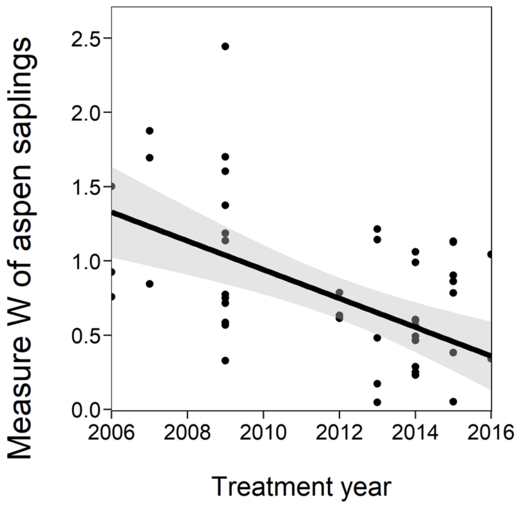

Figure 4. The fitted values from the final linear mixed model for treatment plots only, showing the effect of time since treatment on the canopy tree potential of aspen saplings. The whole model is provided in Appendix 6.

4 Discussion

4.1 Effect of spruce removal on saplings

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

Several studies have found that conifer removal facilitates growth and regeneration of trembling aspen (Shepperd 2001, Jones et al. 2005, Krasnow et al. 2012, Berrill et al. 2017), a North American species ecologically similar to European aspen. Both these are light-demanding pioneer species that, typically, are slowly outcompeted by conifers during forest succession. In addition, the sexual reproduction of both aspen species is strongly tied to forest fires, in the absence of which the primary form of reproduction is via suckering (Myking et al. 2011).

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

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

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

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

4.2 Mature tree species composition and canopy cover

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

For birch saplings, the canopy tree potential increased with the number of mature birch trees present, but decreased in comparison to their basal area. As the basal area generally increases as trees grow taller, this is consistent with the findings of Götmark et al. (2005), who reported that birch saplings were more numerous in young forests than in mature forests. Birch does not seem to benefit from the increasing basal area of parental trees to the same extent as aspen, probably because of the different vegetative reproduction strategy.

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

4.3 Herbivory pressure

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

5 Conclusions

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

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

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

Acknowledgements

The field work was funded by the Jenny and Antti Wihuri foundation (grant number 00170109). We thank Malla Pulkkinen for her indispensable contribution to the field work, Otso Ovaskainen for his great insight in statistical analyses, and Timo Laine and Rauli Perkiö for providing data of the white-backed woodpecker territories and the locations of the spruce removal areas.

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