

1 **Tree removal as a management strategy for the lady's slipper orchid, a flagship**
2 **species for herb-rich forest conservation**

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26 **Abstract:** In boreal herb-rich forests, the dominance of Norway spruce (*Picea abies*) decreases
27 light availability for understory species, many of which depend on canopy gaps for reproduction.
28 Here, we explored the response of a rare clonal understory herb, the lady's slipper orchid
29 (*Cypripedium calceolus*), to tree removal. We used demographic data spanning 16 years from ten
30 unharvested control sites and ten harvest sites which were divided into three treatments with
31 differing harvest intensity: (1) dense spruce forests, where half of the total tree basal area (TBA)
32 was cut, (2) sparse spruce forests, where one-fourth of the spruce TBA was cut and (3) sparse
33 broadleaf forests, where one-fourth of the total TBA was cut. The effects of harvesting on different
34 demographic rates (ramet density, reproduction, survival, and dormancy) were studied with
35 generalized linear mixed models with harvest intensity, time since harvest and the starting level of
36 the response variable as explanatory variables. Tree removal sites had 2.2 times higher orchid ramet
37 density, 2.4 times higher odds of survival, and 2.1 – 3.1 times higher odds of flowering and fruiting
38 than the control sites, but these effects were not seen at all treatment levels at all times. Tree
39 removal had no effect on dormancy or seedling or flower density. Orchid flowering and fruiting
40 probabilities increased only at the most intensively harvested sites (both spruce forest sites, and
41 dense spruce forest with 50% TBA removal, respectively), while survival and ramet density
42 increased at the moderately harvested broadleaf forest sites. The effects on flowering and fruiting
43 probabilities and survival disappeared quickly (after three years) when the canopy gaps closed,
44 whereas ramet density responded only with a lag of over three years and was maintained to the end
45 of the study. Our results thus demonstrate that for the lady's slipper orchid, selective tree harvest
46 might be a suitable management method that increases population size at the ramet level.

47 **Keywords:** dormancy, flowering, forest gap, forest overgrowth, reproduction, survival

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51 **1. Introduction**

52 The composition of understory vegetation in boreal forests depends on environmental conditions,
53 such as climate, fire, acidification, forest type, and canopy closure (Hart & Chen, 2008; Rydgren,
54 1996; Økland & Eilertsen, 1996). Understory light conditions and associated changes in e.g.
55 temperature and moisture, are considered to be the major limiting components of forest understory
56 cover and species richness in temperate and boreal forests (Barbier, Gosselin, & Balandier, 2008).
57 In addition to light, canopy closure affects many abiotic and biotic factors of the forest understory,
58 which in turn can modify, both directly and indirectly, the growth, survival, and reproduction of
59 understory plants (Fig. 1). Numerous studies have investigated the effect of woody encroachment
60 on grassland ecosystems (e.g. Alford, Hellgren, Limb, & Engle, 2012; Briggs, Blair, & Mccarron,
61 2005) as well as tree gap dynamics and their importance for tree recruitment, particularly in tropical
62 rainforests (Brokaw, 1987; Pascarella, 1998; Svenning, 2002). However, the species-specific
63 responses of herbaceous plants to canopy cover in boreal regions have attracted less attention.

64 In forests, succession is characterized by a transition from an open state dominated by pioneer
65 species to a closed forest with high tree basal area (Clebsch & Busing, 1989; Saldarriaga, West,
66 Tharp, & Uhl, 1988). However, this process may be disrupted by disturbances that change the
67 amount of available resources and affect recruitment. Natural disturbances, such as windthrows or
68 forest fires, are important factors that increase forest biodiversity (Angelstam, 1998; Ulanova,
69 2000). These disturbances typically increase the amount of light available in the understory, which
70 in turn has been observed to increase the reproduction and growth of understory herbs (Brumback,
71 Cairns, Sperduto, & Fyler, 2011; Gill, 1996; Kirchner, Kammermeier, & Bruelheide, 2009;
72 Valverde & Silvertown, 1998).

73 This increased reproduction and growth may be due to improved nutrient availability. As the
74 canopy cover decreases, soil temperature generally increases (Abd Latif & Blackburn, 2010; Norris,

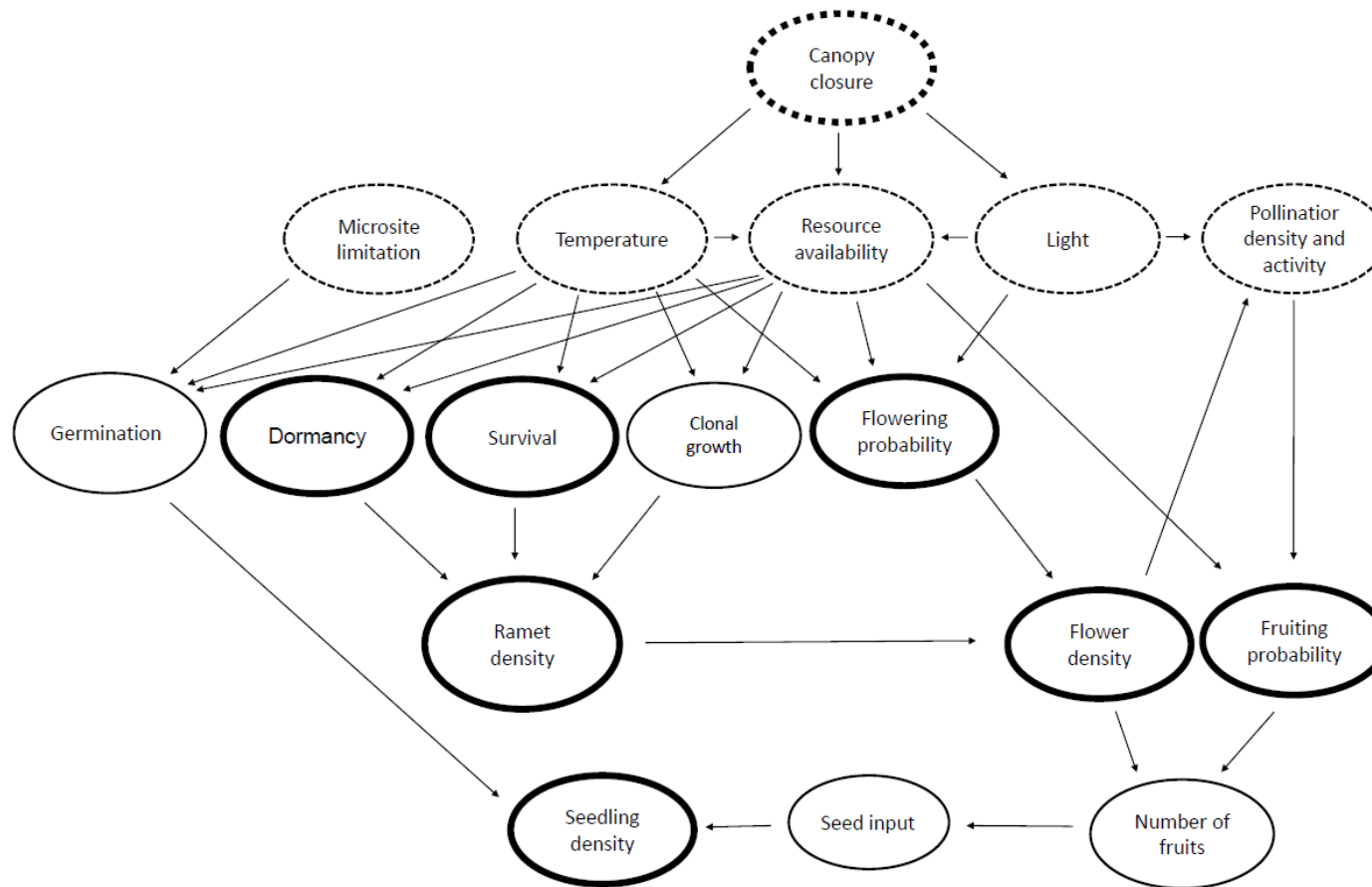
75 Blair, & Johnson, 2001; Seastedt & Adams, 2001; Smith & Johnson, 2004), leading to changes in
76 soil respiration (Smith & Johnson, 2004) and rates of decomposition of organic matter (Canham &
77 Marks, 1985; Seastedt & Adams, 2001). Additionally, decomposition rates and, consequently,
78 nutrient availability can change as a result of altered litter composition (Berg et al., 1993; Ovington,
79 1954). Coniferous forests tend to have slow decomposition rates (D. Zhang, Hui, Luo, & Zhou,
80 2008), with nitrogen and phosphorus availability decreasing in the late, closed, conifer-dominated
81 successional stage (Bormann & Sidle, 1990). In such forests, canopy gaps provide not only
82 increased light, but also a local reduction in acidic leaf litter, with the potential consequence of
83 improved nutrient availability.

84 Canopy cover also affects the soil water balance. On one hand, soil moisture is expected to increase
85 with decreasing canopy cover as plant transpiration decreases and more precipitation reaches the
86 ground (Abd Latif & Blackburn, 2010; Alanen, Leivo, Lindgren, & Piri, 1995; Canham & Marks,
87 1985). On the other hand, though, decreasing canopy cover may increase evaporation as a result of
88 elevated temperatures, thus reducing soil moisture levels. These effects are probably partially
89 dependent on prevailing climatic conditions. In boreal forests that are typically cold and moist,
90 canopy cover has been observed to be negatively correlated with soil moisture and species richness
91 (Rydgren, 1996), while in arid grasslands the opposite is true and soil moisture is highest under tree
92 canopies (D'Odorico, Caylor, Okin, & Scanlon, 2007; De Boever, Gabriels, Ouessar, & Cornelis,
93 2016)

94 The overall net effect of canopy gaps on understory plant performance often depends on gap size
95 and age. For example, slow-growing understory herbs may suffer when canopy gaps are too large
96 because of increased competition from vigorously growing grasses (Sjöberg & Ericson, 1992).

97 Large gaps might also have unfavorable microclimates as wind speed and temperature variations
98 increase (Abd Latif & Blackburn, 2010; Runkle, 1985), which may result in a greater risk of frost

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102 Figure 1. A flow-chart depicting the effects of canopy closure and abiotic factors (dashed line) on different demographic rates (solid lines) of
 103 forest understory herbs. Variables in bold circles are measured in the current study.

104 (Langvall & Ottosson Löfvenius, 2002; Norris et al., 2001) and fruiting failure (Abeli, Jäkäläniemi,
105 Wannas, Mutikainen, & Tuomi, 2013). In general, the effects of canopy gaps on light conditions
106 and vegetation are most pronounced immediately after disturbances and then weaken over time
107 (Beaudet & Messier, 2002), as the gaps close with the lateral growth of surrounding trees and height
108 growth of saplings (Runkle, 1985).

109 The lady's slipper orchid (*Cypripedium calceolus*) is a rare understory herb which prefers half-
110 shaded lime-rich habitats (Rankou & Bilz, 2014). It has intrinsically slow population dynamics,
111 with the long-term population growth rate being close to 1 and very slow convergence to the
112 equilibrium state (Nicolè, Brzosko, & Till-Bottraud, 2005). This suggests that the recent population
113 declines reported in many European countries (Rankou & Bilz, 2014) are due to extrinsic factors.
114 Indeed, previous studies have shown that the viability of lady's slipper orchid populations decreases
115 with increasing canopy closure in boreal and nemoral forests (Bjørndalen, 2015; Brzosko, 2002;
116 but see García, Goñi, & Guzmán, 2010). As noted in extensive field observations of this species,
117 flowering probability, seed set, and seedling establishment are limited under closed-canopy
118 conditions in boreal forests in northern Finland (Laitinen, 2006). Moreover, in a shading
119 experiment, Shefferson et al. (2012) observed that the flower production and survival of shaded
120 plants were lower than those of unshaded plants. These authors also noticed that orchids were able
121 to escape the negative effects of shading through vegetative dormancy (hereafter 'dormancy'), a
122 state in which a plant produces no above-ground shoots for one year or more, and only the below-
123 ground rhizome survives (Shefferson et al., 2012). Dormancy is widely assumed to be a way to
124 escape stress by avoiding unfavorable conditions (Davison, Nicole, Jacquemyn, & Tuljapurkar,
125 2013; Shefferson et al., 2012; Shefferson, Warren, & Pulliam, 2014). In addition, the rate of
126 photosynthesis of understory species in shaded habitats has been observed to be low (Lett &
127 Knapp, 2003; S.-B. Zhang, Hu, Xu, Li, & Yang, 2007), suggesting that the benefits of sprouting

128 would be small and the costs of dormancy would be low. Therefore, we can expect dormancy to be
129 more common in shaded environments than in habitats with more light.

130 Because of its large, showy flowers, the lady's slipper orchid is an ideal flagship species to attract
131 public interest in conservation. Moreover, due to its stable population dynamics, occurrence on rare
132 habitat types, and tendency to co-occur with several other rare orchids, herbs, and mosses, it has
133 been suggested that the lady's slipper orchid could be used as an umbrella species (Bjørndalen,
134 2015; Laitinen, 2006; Nicolè et al., 2005). In other words, the decline of the lady's slipper orchid
135 indicates the degradation of the habitat, and therefore, an improvement in conditions for this orchid
136 might ensure the survival of other species that are dependent on similar habitats (Simberloff, 1998).
137 For example, studies from Sweden and Norway indicate that management favoring half-open
138 forests instead of dense vegetation is recommended to promote the viability of orchid populations
139 (Antonelli, Dahlberg, Carlgren, & Appelqvist, 2009; Bjørndalen, 2015). In this study, we use long-
140 term demographic data from northern Finland to examine whether selective tree harvest could be
141 used as a management method for rare orchids in over-grown herb-rich forests. More specifically,
142 we explored the effects of tree removal treatments of differing intensities on the ramet density,
143 reproduction, survival, and dormancy of the lady's slipper orchid. We hypothesized that the survival
144 and reproduction of the lady's slipper orchid individuals would be highest in the most intensive tree
145 removal treatment, while the proportion of dormant plants would be lowest at the harvested sites.
146 We further predicted that the effects of tree removal treatments would be the most pronounced
147 immediately or shortly after the harvest, and would then slowly decrease over the 16 years of the
148 study as the canopy gaps closed.

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150 **2. Methods**

151 **2.1 The species and study areas**

152 The lady's slipper orchid (*Cypripedium calceolus*) is a nectarless, clonal, long-lived herb with a
153 horizontal rhizome. Ramets form clumps consisting of several clones, in which vegetative
154 propagation dominates over sexual reproduction (Brzosko, 2002; Kull, 1999). Some clones and
155 ramets can remain dormant for several years, although one year is more typical (Brzosko, 2002;
156 Shefferson, Sandercock, Proper, & Beissinger, 2001). One stalk supports one to two, rarely three,
157 yellow slipper-shaped flowers. The average number of minute seeds per capsule is about 6 000–
158 20 000 (Brzosko, 2002; Kull, 1998; Laitinen, 2006). The seedlings live in symbiosis with fungi and
159 spend their first three years as underground protocorms (Kull, 1999). This orchid is mainly boreal,
160 and is widely distributed from Europe to Asia. It grows in moist, half-shaded, herb-rich forests and
161 wooded peatlands with calcium-rich bedrock (Kull, 1999). The species has been declining in
162 several countries, but many populations are now stable or increasing due to the implementation of
163 successful conservation actions (Rankou & Bilz, 2014).

164 As part of the EU Life project in 2001 (details in Laitinen, 2006), all known populations of the
165 lady's slipper orchid in northern Finland were mapped. From these populations, ten sites were
166 chosen for active forest management and ten sites as controls (Table A.1). Three managed and three
167 control sites were located in Oulanka National Park in Kuusamo, northeastern Finland, and the rest
168 of the sites were situated in the municipalities of Tervola and Ylitornio in southwestern Finnish
169 Lapland (Fig. A.1). The habitats consisted of herb-rich forest and were mostly dominated by the
170 Norway spruce (*Picea abies*). In Finland, spruce-dominated old-growth forest represents a natural
171 part of the succession cycle of herb-rich forests. *P. abies* offers shelter and substrate for certain
172 birds and decomposing fungi (Alanen et al., 1995), but also effectively shades the understory and
173 produces acidic litter that decomposes slowly (Alanen et al., 1995; D. Zhang et al., 2008), and the
174 subsequent resource limitation can be detrimental for herbaceous understory species.

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177 **2.2 Field methods and assessment of canopy cover**

178 In the summer of 2001, a randomly located 1×10 m plot was established at each study site. At sites
179 with under 100 ramets, an extra square (up to 8 m^2) was included to obtain a sufficient sample size.
180 The plot size thus varied from 10 m^2 to 18 m^2 (Table A.1). Each isolated ramet or ramet clump was
181 marked using a steel stick with a numbered plastic label, with the number of observed living clumps
182 per plot per year varying from 1 to 299 (mean = 92 clumps). We use a clump as a proxy for a clone,
183 as the ramets grow so closely together that we could not reliably follow them individually, and the
184 identification of actual genetic clones would have required genetic tests or excavation of the plants.
185 Therefore, some clumps may have actually contained multiple overlapping clones and some genetic
186 clones may have been dispersed across several clumps. However, as our analyses primarily focused
187 on population-level variables, we are confident that this did not qualitatively affect our results.

188 In years 2001–2004, 2008–2010, and 2014–2016, we visited all sites once a year during the fruiting
189 time in July and recorded the state of each ramet clump as dormant, vegetative, or flowering. The
190 numbers of flowers and capsules were counted, and newly emerged clumps and seedlings were
191 marked every year. Tree removal was conducted in the winter of 2001 (i.e. after the first summer
192 survey). Three types of forest were represented in the management areas, and each differed in the
193 intensity of selective tree harvest: (1) dense spruce forests, where half of the total tree basal area
194 (TBA) was cut (mean of 48.9% (SD 8.4%)), (2) sparse spruce forests, where one-fourth of the
195 spruce TBA was cut (mean reduction in TBA mean of 26.4% (SD 7.4%)), and (3) sparse broadleaf
196 forests, where one-fourth of the total TBA was cut (mean reduction in TBA mean of 25.7% (SD
197 0.7%)) (Table A.1). Control sites, in which no trees were cut, included the same forest types as the
198 treated sites. Note that due to different initial tree densities, differences in the proportions of
199 removed trees are not directly translatable to differences in the reduction in total amount of wood
200 between habitat types; for example, the total amount of wood removed was smallest in the sparse
201 broadleaf forests because these sites had the lowest initial tree density. The size of the managed

202 areas varied from 600 m² to 1700 m², with the demography plot in the middle. Tree removal was
203 conducted without heavy machinery and all logs and branches were removed from the sites. A thick
204 snow cover protected the plants and ground from mechanical disturbance during cutting.

205 To assess how tree removal affected the light regime, we took photographs during the pre-harvest
206 period and then again in the middle and late post-harvest periods. A camera with a standard zoom
207 lens was oriented straight up toward the sky at 1-m intervals along each plot (10 in total per plot)
208 and from each extra square. The camera was placed at the height of the top of the herbaceous
209 vegetation layer in order to capture the level of canopy openness for trees and shrubs, but not for
210 herbs. Photographs were edited in Adobe Photoshop by filling the open sky with white and canopy
211 with black. We then calculated the canopy cover as the percentage of black in the photographs. The
212 canopy cover percentages calculated from the photographs revealed that the average canopy cover
213 had increased in nearly all sites by the middle post-harvest period, indicating ongoing canopy
214 closure at the control sites and the rapid closure of canopy gaps at the harvest sites (Fig. B.1). The
215 only treatment that resulted in a longer-lasting canopy gap in terms of increased light availability
216 was the most intensive treatment (spruce forest 50% removal). However, none of the statistically
217 tested changes in canopy cover (i.e. differences between treatments or time periods during the pre-
218 harvest and middle and late post-harvest periods) were significant (Fig. B.1, Table B.1).

219 Unfortunately, no comparable photographs were available from the immediate post-harvest period,
220 but according to Laitinen (2006), the tree removal treatments substantially increased light
221 availability during this period, especially the most intensive treatment (spruce forest 50% removal).

222

223 **2.3 Statistical analyses**

224 Clonal growth and sexual reproduction of the lady's slipper orchid were assessed using the
225 following five variables: the densities of ramets (excluding seedlings), flowers, and seedlings (per

226 m²), flowering probability (the proportion of flowering ramets out of mature ramets), and fruiting
227 probability (the proportion of flowers that produced capsules). Moreover, we measured clone-level
228 dormancy as the proportion of dormant clumps out of all clumps known to be alive in a given year.
229 Clone-level survival was measured as the number of clumps that survived to the next year divided
230 by the number of clumps with known fates in the next year. Clumps were assumed dead if they had
231 not been seen aboveground for three or more consecutive visits. Dead plants were further assumed
232 to have died instantly after the last observation. Therefore, final time period (2014 – 2016) had to be
233 excluded from survival analyses due to its spurious perfect survival (i.e. no deaths could be
234 observed). Similarly, we excluded the last year of the study period (2016) from the dormancy
235 analyses because dormancy was inherently defined by observations in subsequent years. Some of
236 the plastic labels were lost during the study, and the fate of these clumps after the last observation
237 of the label is unknown. For these clumps, only the years before the disappearance of the label were
238 used in the analyses. In order to estimate dormancy and survival, knowledge of individual
239 demographic history was needed. Therefore, clumps clearly consisting of more than one clone (e.g.,
240 seedlings and mature plants in the same clump) were either removed from the dataset (91 clumps
241 out of 2304 clumps) or, when possible, were divided into two or more clumps (270 clumps out of
242 2304 clumps) for analytical purposes.

243 We tested differences in demographic rates between managed and control sites using generalized
244 linear mixed models. All models included the starting level (the value of a given response variable
245 in 2001 before treatment), time period (four levels), and treatment (four levels) as fixed explanatory
246 variables. The four levels for time period were: pre-harvest period before logging (summer 2001),
247 immediate post-harvest period (2002 – 2004), middle post-harvest period (2008 – 2010), and late
248 post-harvest period (2014 – 2016). The starting level was used as a covariate to account for initial
249 differences in the response variables among sites. Moreover, the models included geographic region
250 (Kuusamo or SW Lapland) and all possible two-way interactions with time as fixed explanatory

251 variables when these terms were determined to be significant by likelihood-ratio tests. Note that it
252 was not possible to examine other interactions among main factors due to the unbalanced study
253 design. Study site (nested within region) and year were included as random factors in order to take
254 into account the fact that repeated measurements were conducted from the same sites, and that each
255 time period contained three years. Density responses were modeled using a negative binomial
256 distribution with log link, based on the counts and with plot area as an offset, and proportional
257 responses were modeled with a binomial distribution and logit link (function `glmmadmb` from
258 package `glmmADMB`, Fournier et al., 2012). Negative binomial distribution was used instead of
259 Poisson distribution because of its better fit with our overdispersed density data. We assessed model
260 fit based on residual plots (Figure C.1), and evaluated the statistical significance of the fixed factors
261 by comparing the full model to a model without a given factor using likelihood-ratio tests. As the
262 models of dormancy and survival both used different reduced data sets, the original p-values from
263 the likelihood-ratio tests were Bonferroni-corrected only for the models of growth and reproduction.
264 If the treatment term was significant according to the likelihood-ratio tests, each treatment was
265 compared to the control treatment using Dunnett-style contrasts with the exact Dunnett adjustment
266 of the p-values (package `lsmeans`, Lenth 2016). If the treatment \times time interaction was significant,
267 contrasts were calculated separately for each time period. All statistical tests were performed using
268 the statistical program R (Team, 2015).

269

270 **3. Results**

271 Based on the likelihood-ratio tests, there were differences between the four tree removal intensities
272 in all the studied demographic rates, except seedling density (Table 1). However, contrasts
273 comparing the treated and control showed significant differences only for the ramet density, clump
274 survival, flowering probability, and fruiting probability of the lady's slipper orchid (Table D.1,

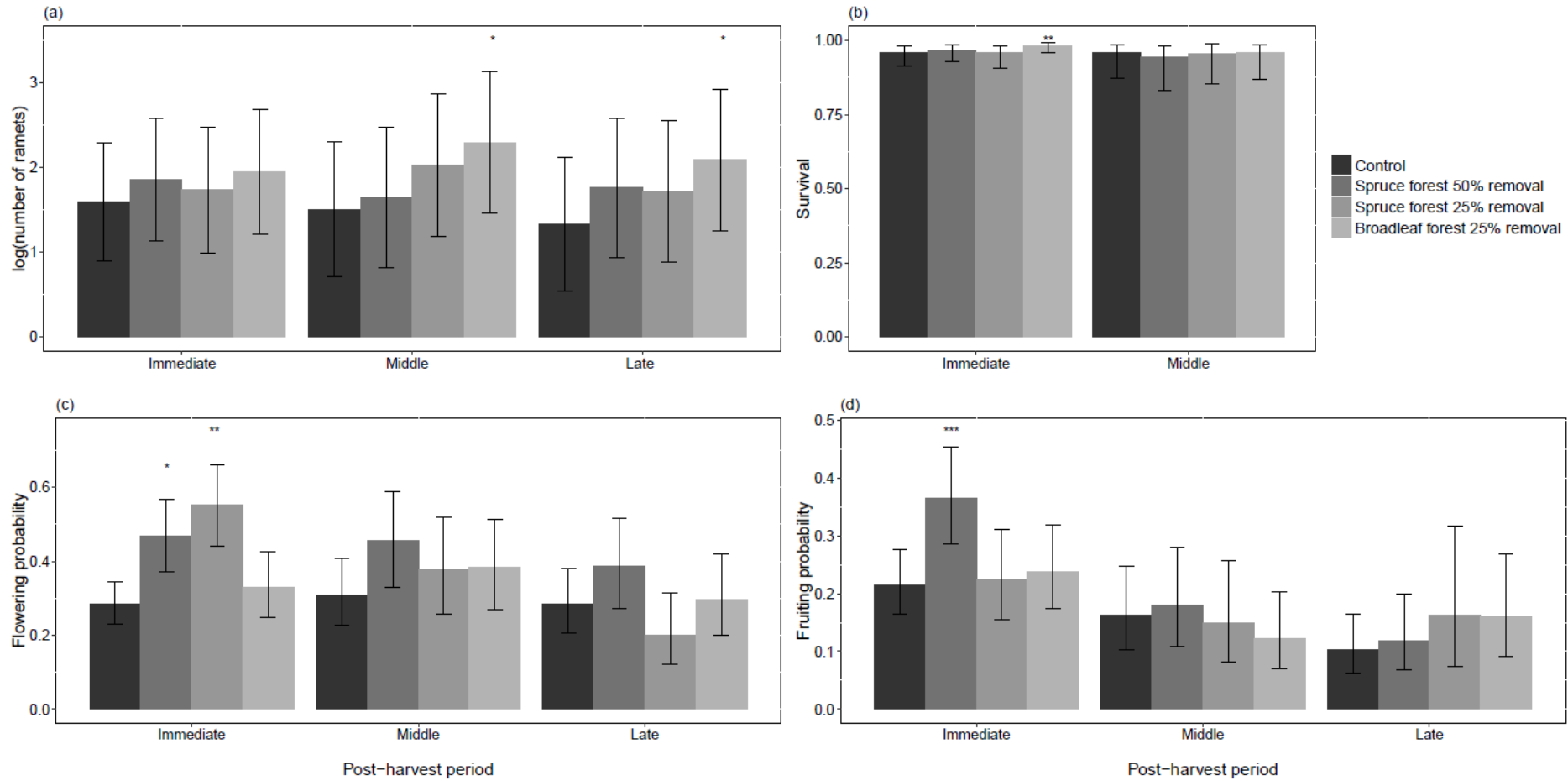
275 Fig.2A). Ramet density was higher in the broadleaf forest 25% removal treatment compared to the
276 control treatment, but this difference was significant only during the middle and late post-harvest
277 periods, with the ramet density being 2.2 times higher at the harvested sites than at the control sites
278 (Fig. 2A, Table D.1). Additionally, the lady's slipper orchid clumps had 2.4 times higher odds of
279 surviving in the broadleaf forest 25% removal treatment in the immediate post-harvest period
280 compared to control (Fig. 2B, Table D.1). Compared to the control sites, flowering probability was
281 higher at both types of treated spruce forest sites (2.2 higher odds in dense spruce forest with 50%
282 total TBA removal and 3.1 higher odds in sparse spruce forest with 25% spruce TBA removal; Fig.
283 2C, Table D.1), while the fruiting probability was higher only in the spruce forest 50% removal
284 treatment sites (2.1 times higher odds of fruiting, Fig. 2D, Table D.1). However, these increases in
285 the probabilities of flowering and fruiting were seen only during the immediate post-harvest period
286 (up to 3 years after the harvest; Fig. 2). There were no regional differences in the overall means of
287 most of the measured demographic variables (Table 1). A posteriori contrasts revealed statistically
288 significant differences between regions for ramet density and survival only (Table D.1). Both these
289 variables were higher in the Kuusamo region than in SW Lapland, with ramet density being 1.8 fold
290 during the middle harvest period and 2.0 fold for the late post-harvest period, and with survival
291 being 2.5 fold in the immediate post-harvest period (Table D.1).

292

293 **4. Discussion**

294 **4.1 Effect of tree removal on the lady's slipper orchid**

295 Ramet density, survival, and probabilities of flowering and fruiting of the lady's slipper orchid
296 responded positively to the tree removal treatments, though not at all sites during all time periods.
297 Our results are consistent with previous studies that have reported the positive effect of light on
298 forest understory herbs (Brumback et al., 2011; Gill, 1996; Kirchner et al., 2009; Valverde &



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300 Figure 2. a) Ramet density, b) survival, c) flowering probability, and d) fruiting probability of *Cypripedium calceolus* by treatment and time
 301 period. Bar heights represent the model prediction, and error bars denote standard errors. Asterisks indicate a significant difference between the
 302 treatment and the control of the same time period. Predictions are averaged over geographic regions and starting level covariates. Count
 303 responses are on a logarithmic scale and proportional responses are back-transformed to the original proportion scale.

Table 1. Results of likelihood-ratio tests of explanatory factors in linear mixed models used to examine the effect of tree removal on the demographic rates of ramet clumps of the lady's slipper orchid over time (significant results in bolded).

	<i>Ramet density</i>	<i>Proportion of dormant ramets</i>	<i>Clump survival</i>	<i>Flower density</i>	<i>Seedling density</i>	<i>Flowering probability</i>	<i>Fruiting probability</i>
Starting level	NT	NT	NT	20.8 _{1, <0.001}	13.0 _{1, 0.002}	NT	6.70 _{1, 0.048}
Treatment	NT	NT	NT	NT	7.19 _{3, 1.000}	NT	NT
Time	NT	NT	NT	NT	8.64 _{2, 0.067}	NT	NT
Region	NT	0.99 _{1, 0.320}	NT	NT	0.558 _{1, 0.331}	6.14 _{1, 0.066}	0.068 _{1, 1.000}
Starting level × Time	10.4 _{2, 0.027}	34.4 _{2, <0.001}	4.02 _{1, 0.045}	2.43 _{2, 1.000}	2.61 _{2, 1.000}	25.0 _{2, <0.001}	3.75 _{2, 0.766}
Treatment × Time	25.5 _{6, 0.001}	48.4 _{6, <0.001}	9.20 _{3, 0.003}	19.4 _{6, 0.018}	0.856 _{6, 1.000}	77.2 _{6, <0.001}	18.9 _{6, 0.022}
Region × Time	47.1 _{2, <0.001}	1.12 _{2, 0.571}	13.7 _{1, 0.002}	13.2 _{2, 0.007}	3.63 _{2, 0.815}	4.88 _{2, 0.436}	1.46 _{2, 1.000}

Flowering probability is estimated as the proportion of flowering ramets out of mature ramets, and fruiting probability is the proportion of flowers that produced capsules. Starting level was used as a continuous covariate, and treatment, time, and region were used as fixed factors. All models included site-nested-within-region and year as random factors. Presented are the deviances, their degrees of freedom and p-values (degrees of freedom and p-values in subscript). *p*-values are Bonferroni-corrected when applicable (see the methods for details). NT = not tested due to significant interactions

305 Silvertown, 1998). For the lady's slipper orchid, the positive effect of forest harvest on flowering
306 and fruiting probabilities during the immediate post-harvest period was probably due to increased
307 nutrient availability and increased pollinator density and activity which resulted in improved
308 pollination success (Fig. 1) as the species is mostly pollinated by solitary bees of the genus *Andrena*
309 that prefer open or half-open habitats (Antonelli et al., 2009; Erneberg & Holm, 1999; Kull, 1999).
310 A similar increase in pollination success due to improved light conditions has also been observed
311 for other forest understory species (Gill, 1996; Pascarella, 1998). However, the positive effects on
312 flowering and fruiting observed here were seen only in the most intensive treatments, where the
313 amounts of removed trees were the highest and only during the first few years after tree removal,
314 before the canopy gaps quickly closed.

315 In general, as flowering and fruiting probabilities increase, seedling production can also be expected
316 to increase (Fig. 1). However, even though the density of seedlings was higher in the treatment
317 sites, these differences were not statistically significant. In other words, the increased capsule
318 production observed at the treated dense spruce forest sites did not translate into a significant
319 increase in seedling production nor did tree removal release the sprouting potential of a potentially
320 preexisting seedling bank. While it is possible that some seedlings may have established during the
321 years the sites were not visited, we can assume that these seedlings would have been observed
322 during some of the subsequent visits. Because the lady's slipper orchid has a long protocorm period
323 (Kull, 1999), the effect of seed input (if any) on recruitment will be seen with a time lag, but a study
324 period of 16 years should have been long enough to detect such lagged responses. Assuming that
325 tree removal did not significantly affect the number of seeds per capsule or their quality, the lack of
326 response in seedling numbers suggests that seedling production of the lady's slipper orchid is
327 constrained by the number of favorable microsites rather than by the number of seeds (Fig. 1), as
328 was observed by Kull (1998) in Estonia. It is possible that tree removal enhanced the growth of
329 other forest herbs that had a stifling effect on the seedlings of the lady's slipper orchid. The fact that

330 increased flowering and capsule-formation probabilities due to selective tree removal did not affect
331 the population size of the lady's slipper orchid calls into question the usefulness of tree harvest as a
332 management method. However, we did observe an increase in the survival of established
333 individuals, which is likely to increase population size at the harvested sites in the long run.

334 Elasticity analyses on both animals and plants have shown that in long-lived species, such as the
335 lady's slipper orchid, the most important demographic component for population growth rate is
336 survival (Franco & Silvertown, 2004; Heppell, Hal, Crowder, Caswell, & Crowder, 2000), making
337 it an ideal target for management efforts. Nevertheless, there may be practical limitations to such an
338 approach: survival is often high in long-lived species and thus difficult to increase sufficiently to
339 halt the population decline. For example, the high clump survival observed in this study (83-99% of
340 clumps survived from year to year) is in line with values reported previously for terrestrial orchids
341 (Gill, 1996; Kéry & Gregg, 2004; Shefferson, 2006; Sletvold & Ågren, 2015). The practical
342 constraints related to high survival values may make demographic rates with lower elasticities (e.g.,
343 fecundity) more feasible targets for conservation (see e.g. Lehtilä, Syrjänen, Leimu, Begona Garcia,
344 & Ehrlén, 2006).

345 It should be noted, though, that in this study we only compared treated sites to the control sites and
346 did not test changes in reproduction, dormancy, and survival between pre-harvest and post-harvest
347 periods. Furthermore, we could not confidently estimate population sizes at the clone level, as many
348 clones could have been intermingled or were lost during the study and possibly marked with
349 another label later on. However, at the ramet level, population size was significantly higher at the
350 broadleaf 25% removal treatment sites than at the control sites during the later years. This higher
351 ramet density seems to be due to increased clonal growth (greater number of ramets per clone)
352 resulting from improved light and nutrient availabilities, and not, instead, the consequence of
353 increased clump sprouting, as the treatments had no effects on the proportion of dormant clumps.

354 Alternatively, the higher ramet density could also potentially be explained by the improved survival
355 of existing clones immediately after the harvest (Fig. 1).

356

357 **4.2 Management implications and conclusions**

358 As has been found with many other rare orchids, the main threats to the lady's slipper orchid
359 include increased shading due to succession, the abandonment of traditional grazing activities and
360 the replacement of natural forests with spruce plantations (Bjørndalen, 2015; Rankou & Bilz, 2014).
361 Therefore, ensuring sufficient light conditions on the forest floor is important for maintaining lady's
362 slipper orchid populations (Antonelli et al., 2009; Bjørndalen, 2015; Rankou & Bilz, 2014) and
363 species richness in herb-rich forests, even if it requires interfering with natural succession through
364 management actions (Alanen et al., 1995).

365 Previous observations from Scandinavia (Antonelli et al., 2009; Bjørndalen, 2015) and our findings
366 show that selective tree harvest might be a suitable management method for the rare lady's slipper
367 orchid. In our study, a 25 – 50% reduction in tree basal area increased population size at the ramet-
368 level by enhancing survival and clonal growth at sparse broadleaf forest sites, and increased the
369 probabilities of flowering and fruiting at spruce forest sites, although these positive effects were not
370 seen during all years. While we can expect responses to change in canopy cover to be species- and
371 habitat-specific, it is likely that tree removal could be used as a management method for other
372 understory species whose reproduction benefits from canopy gaps. For example, Kirchner et al.
373 (2009) observed that the forest herb *Trientalis europaea* produced a higher number of flowers and
374 fruits in canopy gaps than in the shade, and that ramet density increased with increasing light
375 availability, and in primrose (*Primula vulgaris*) populations, brighter patches have been observed to
376 have higher reproduction and lower mortality (Valverde & Silvertown, 1998). Moreover, in the
377 orchid *Isotria medeoloides*, selective removal of 25% TBA more than doubled the number of stems

378 during a ten-year study period (Brumback et al., 2011), showing that tree removal has indeed the
379 potential to increase shoot density also in other orchid species.

380 None of the tree removal treatments considered here significantly increased seedling production,
381 even though there were large differences between the years and study sites in seedling density. The
382 differences between treatments were, however, inconsistent, meaning that rather than being affected
383 by the tree removal treatments, seedling density was dependent on site-specific factors such as
384 microsite limitation (Kull, 1998). Kull (1998) also observed that in Estonia the germination of the
385 lady's slipper orchid was highest at sites with high amounts of light, small total herb coverage, and
386 a thick moss layer that provided stable and moist conditions. Therefore, the germination of the
387 lady's slipper orchid could possibly be enhanced by sowing seeds to small plots where herbs have
388 also been removed. Furthermore, our treatments resulted in only a transient increase in light
389 availability, so it is possible that a repeated or more intensive treatment (e.g., 75% TBA removal)
390 would have resulted in larger and longer-lasting responses. While the positive effects of forest
391 management on survival and flowering probability were seen only for a maximum of three years
392 after tree removal, suggesting a need for repeated treatments, ramet density responded with a lag of
393 several years and lasted until the end of the study period (15 years after harvest). More experiments
394 are needed to determine the optimal intensity and frequency of tree removal to maximize benefits
395 for the orchid populations. Although clear-cuts have been observed to significantly increase the
396 number of plant species in spruce dominated herb-rich forests in Finland, this increase is
397 accompanied by a considerable shift in species composition benefitting early-successional species
398 (Pykälä, 2004). Further, in Sweden (Sjöberg & Ericson, 1992) and Norway (Bjørndalen, 2015)
399 clear-cuts have been observed to have negative effects on lady's slipper orchid populations,
400 presumably due to the increased risk of frost and competition with graminoids and other herbs
401 (Sjöberg & Ericson, 1992). Irrespective of the extent of tree removal, intensive disturbance of the
402 soil surface should be avoided because the rhizomes of the lady's slipper orchid grow near the

403 ground surface (Kull, 1999; Laitinen, 2006) and are thus easily damaged. Moreover, when
404 removing spruce, the highly acidic logging waste (e.g., twigs and needles) must also be removed
405 from the site to avoid negative effect on soil quality (Alanen et al., 1995) and, consequently, on the
406 lady's slipper orchid. Overall, we recommend selective tree removal, together with sowing seeds in
407 plots where the herbaceous layer has been removed, to manage this rare flagship species in
408 overgrown forests.

409

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418

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