

1 **Trade-offs in berry production and biodiversity under prescribed burning**
2 **and retention regimes in Boreal forests**

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19 Abstract

- 20 1. Green tree retention and prescribed burning are practices used to mitigate negative effects
21 of boreal forestry. Beside their effects on biodiversity, these practices should also
22 promote non-timber forest products (NTFPs). We assessed: (1) how prescribed burning
23 and tree retention influence NTFPs by examining production of bilberry *Vaccinium*
24 *myrtillus* and cowberry; *Vaccinium vitis-idaea* (2) if there are synergies or trade-offs in
25 the delivery of these NTFPs in relation to delivery of species richness, focusing on five
26 groups of forest dwelling species.
- 27 1. We used a long-term experiment located in eastern Finland with three different
28 harvesting treatments: clearcut-logging, logging with retention patches and unlogged,
29 which were combined with or without prescribed burning. Eleven years after the
30 treatment application, we scored plant cover and berry production in different
31 microhabitats within these treatments, while species richness data for five species groups
32 (ground-layer lichens and bryophytes, vascular plants, saproxylic beetles, pollinators –
33 here bees and hoverflies) were collected at the stand level.
- 34 2. Logging favoured cowberry production, particularly for plants growing in the vicinity of
35 stumps. Logging was detrimental for cover and berry production of bilberry. Retention
36 mitigated these negative effects slightly, but cover and berry production were still
37 substantially lower compared to unlogged forests. Prescribed burning increased cowberry
38 production in retention patches and in unlogged forest. Bilberry production decreased
39 with burning, except in unlogged forest where the effect was neutral.

40 3. No single management treatment simultaneously favoured all values - NTFPs and
41 richness - and trade-offs among values were common. Only bilberry production and
42 beetle diversity were higher under retention forestry, or in unlogged stands, compared to
43 logged stands. Prescribed burning favoured many values when performed in combination
44 with retention forestry, or in unlogged stands, but different treatment combinations
45 favoured different species groups.

46 4. *Synthesis and applications.* Our results demonstrate that widely-applied conservation
47 practices in managed boreal forests are unlikely to benefit all ecosystem values
48 everywhere. If high multi-functionality is desired, managing at a landscape scale,
49 countering the local trade-offs among values, may be more appropriate than the stand
50 scale conservation practices commonly practiced today.

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54 **Key words:** Ecosystem service Forestry; Landscape management; Multi-functionality;
55 Non-timber forest products; Retention forestry, Species richness, landscape scale, boreal
56 forests, berry production, prescribed burns

57 Introduction

58 Up until the 1990s, forestry was characterized by a single service approach, i.e. maximizing
59 production of biomass. However, increased appreciation for the additional values that forests can
60 deliver has since then led to the development of new types of forest management systems,
61 including retaining groups of trees during clearcut harvest and applying prescribed burning, with
62 the aim to support a broader set of ecosystem services and values (Gustafsson et al. 2012;
63 Lindenmayer et al. 2012). However, to what extent these conservational measures promote
64 services and additional values such as berry production and species richness, are rarely evaluated
65 together. Therefore, we set out to explore the impact of the aforementioned conservation
66 measures on delivery of multiple values (ecosystem services and biodiversity) in boreal Finland.

67

68 Leaving trees and snags during clearcut timber harvest, known as retention forestry, is employed
69 to preserve legacies from previous generations of trees, and believed to be fundamental for
70 maintaining biodiversity and function of forests (Franklin et al. 1997). Nowadays, practices that
71 preserve or restore such legacies are used worldwide to facilitate multifunctional objectives in
72 forestry (Gustafsson et al. 2012; Lindenmayer et al. 2012), and considered standard practice in
73 Scandinavia (Gustafsson et al. 2010). Prescribed burning, although less widely used as a
74 conservation measure, also aims at maintaining or emulating natural legacies lost during harvest
75 operations in boreal forests (Heikkala et al. 2016). Efficient fire suppression has led to a lack of
76 wildfires in parts of the boreal biome (Niklasson & Granström 2000; Wallenius et al. 2007), and
77 prescribed burning is therefore, used to promote biodiversity by restoring the legacies from
78 wildfires (Halme et al. 2013). In Fennoscandia, prescribed burning is part of the national forest

79 conservational strategies and included in certification schemes such as Forest Steward Council
80 (FSC) (Annon 2012, 2014). Although these two conservation measures are intended to promote a
81 broad set of ecosystem services, including delivery of non-timber forest products (NTFPs) such
82 as production of wild berries and mushrooms (Gustafsson et al. 2012), they have primarily been
83 applied to support biodiversity (Gustafsson et al. 2010). This is also reflected in the literature on
84 effects of retention forestry and prescribed burning, which is heavily biased towards the
85 relationship between timber production and conservation of biodiversity (e.g. Halpern et al.
86 2012; Johnson et al. 2014; Fedrowitz et al. 2014). Only a few studies have examined effects
87 related to ecosystem services (Lazaruk et al. 2005; Rodríguez & Kouki 2015, 2017), and to our
88 knowledge, there are no previous studies examining the effects on NTFPs, or studies that have
89 explored synergies and trade-offs among the different values that these conservation measures
90 are expected to deliver.

91

92 Wild berries of boreal forests in Eurasia, mainly produced by the two ericaceous dwarf-shrubs
93 bilberry (*Vaccinium myrtillus* L.) and cowberry (*Vaccinium vitis-idaea* L.), are highly valued
94 NTFPs (Kangas 2001). In Finland, which has a forest cover of about 23 million ha, the annual
95 yields can be as high as 312 million kg for bilberry and 386 million kg for cowberry (Turtiainen
96 et al. 2011). Although the proportion of berries picked is rather low, 5-6% for bilberries and 8-
97 10% for cowberries (Turtiainen et al. 2011), berry production still represents a large value.

98 Estimating the economic value of these berries is complicated, as it will vary greatly depending
99 on the proportion of berries picked and on the current market price. However, if forest

100 management is adjusted to improve bilberry production, the revenue from bilberry production
101 may exceed that of timber production, and the profitability of stand management may potentially

102 be doubled (Miina et al. 2010). In addition to this provisioning service, berry picking also
103 constitutes a highly-valued cultural ecosystem service (Pouta et al. 2006). Finally, these dwarf
104 shrubs are also essential for many herbivores and omnivores (e.g. birds, voles, cervids, and
105 invertebrates) and these species often form the basis of complex trophic networks in forests (e.g.
106 Lakka & Kouki 2009). Despite the multitude of values that berry production represents, its
107 response to forest management has so far received surprisingly little attention (Pohjanmies et al.
108 2017).

109

110 Developing management schemes that simultaneously deliver multiple values is challenging, as
111 the delivery of one type of value often results in lowered revenue from other values (Bennett et
112 al. 2009; Strengbom et al. in press). Despite these trade-offs, it is often possible to find
113 management options that balance the output between different values, and thus improve multi-
114 functionality (Bradford & D'Amato 2012). The possibilities to develop such balanced
115 management strategies are, however, often limited by a lack of knowledge on the relationship
116 among different services, and how changed revenue from one service influences revenue from
117 others (Raudsepp-Hearne et al. 2010). Hence, if the aim is to increase or preserve multi-
118 functionality, there is a need for a better understanding of how different management practices,
119 such as those primarily applied for preservation of biodiversity, influence the revenue from other
120 services such as production of NTFPs.

121

122 The aim of our study was two-fold: **firstly**, we wanted to investigate how two common
123 conservational practices, prescribed burning and green tree retention, influence production of

124 wild berries, and if the effects differ depending on type of microhabitat (near trees or on flat
125 ground between trees). **Secondly**, we wanted to explore how these two measures influence multi-
126 functionality by examining potential synergies and trade-offs between how these practices
127 influence berry production (a NTFP) and biodiversity.

128

129 Materials and Methods

130 Study area

131 The study was conducted in the mid-boreal vegetation zone of Eastern Finland (approx. 63°10'N,
132 30°40'E, 165 m asl, see Supplementary information Figure SA1 for map over the experimental
133 sites). The area has an annual mean temperature of +2°C (-12°C in January and +15.8°C in July)
134 and the annual mean precipitation is in the range of 500-800 mm (about half as snow)
135 (Ilmatieteen laitos 1991).

136

137 Prior to the experimental manipulations, all sites were covered with about 150 year-old
138 coniferous forest of dry *Vaccinium–Empetrum* heath type. Scots pine (*Pinus sylvestris* L.)
139 dominated the tree layer, with Norway spruce (*Picea abies* L. H. Karst) and birch species (*Betula*
140 *pendula* R. and *B. pubescens* Ehrh.) as co-dominants. Pre-harvest living volume in the stands
141 was on average 288 m³ ha⁻¹. All sites had similar vegetational composition (Johnson et al. 2014)
142 and overall high cover of bilberry (range among sites=32 to 64%) and cowberry (range among
143 sites=18 to 51%). The experimental area has historically only been exposed to very low-
144 intensity selective logging during the late 1800s and early 1900s, but no intensive modern

145 forestry had been conducted at the experimental sites prior to the experiment (Hyvärinen et al.
146 2006).

147
148 The experiment consisted of 18 forest stands, each 3-4 ha in size (see Fig. SA1), and subjected to
149 6 treatments in a two-factor factorial design (n=3 for each treatment combination). Prescribed
150 burning (two levels: unburned or burned) and harvest intensity (management treatment with
151 three levels of retention: 1) logged, i.e. no retention and 0% of the pre-harvest tree volume
152 retained, 2) retention forestry with 17.4% retained, $\sim 50 \text{ m}^3 \text{ ha}^{-1}$, and 3) unlogged, i.e. 100%
153 retained) were the main factors. The stands assigned to be harvested were logged during the
154 winter of 2000-2001. In the retention treatment, the retained trees were aggregated into at least
155 five evenly sized circular groups. The prescribed burnings were performed during two
156 consecutive days at the end of June 2001. Humus layer consumption was higher in logged stands
157 (change in average humus depth -27%) than in unlogged stands (-8 %), and average flame
158 height, was on average 2.2m and 3.9m in unlogged stands and retention groups, respectively
159 (Hyvärinen et al. 2006).

160

161 **Data collection**

162 Density of berries and plant cover of the two species were scored in mid-July 2012 (for 2012
163 weather data see Table SA1). In 2012, berry yields were above the average in Finland (Kauko
164 Salo, Natural Resources Institute Finland, Pers. Comm.). In our inventory, which coincided with
165 the peak of berry production, we counted all berries growing on plants rooted within inventory
166 frames sized 0.4 by 0.4 m. The frame was divided into 100 four by four cm grid cells, and cover

167 was scored as the number of cells with the species present. Cover and berries were counted in
168 two types of microhabitat, on flat ground and in the vicinity of a stump or a tree base (north and
169 south-facing sides to make sampling consistent). In the treatments with full and no retention, we
170 scored cover and berry density at 72 locations in each stand. We used a semi-systematic
171 sampling design, with four transects evenly spaced and positioned in the central area of the
172 stand, with nine randomly selected locations along each transect (see Fig. SA2 for an illustration
173 and details). At each location, the nearest stump/tree base with a diameter greater than 20 cm
174 (stumps/trees large enough to potentially create differences in microhabitat) was selected
175 together with the corresponding flat ground that fulfilled the criteria of being a potential growth
176 location for the species, i.e. wet micro sites and sites with bare rock were excluded. In the
177 retention forestry treatment, we used a slightly different sampling design, so that both the
178 retention patches and open areas were sampled. Inside the retention patches, we scored cover and
179 berry densities at 20 randomly chosen tree bases and 20 locations with flat ground, fulfilling the
180 same criteria as described above. In a similar way, we scored cover and berry densities in the
181 vicinities of stumps and flat grounds outside the retention patch. We scored 40 stumps and 40
182 locations on flat ground in the area starting from the edge of the retention patch to c. 30 m away
183 from the group, i.e. approximately the area within one tree-length from the retention patch (Fig.
184 SA2).

185

186 Data on species richness were retrieved from previous studies conducted by us in the same
187 experimental sites. We included data on pollinators (bees and hoverflies collected in 2013, from
188 Rodríguez & Kouki 2017), saproxylic beetles (collected 2011, from Heikkala et al. 2016), plants,
189 bryophytes (mosses and liverworts) and ground-layer macrolichens (collected 2011, from

190 Johnson et al. 2014). These species groups were chosen as they were collected around the same
191 time period (2011-2013) and represented a broad range of species groups. These data were
192 collected at the stand level and not for each microhabitat as for berries. Pollinators were sampled
193 four times during the growing season using twenty-one 500-mL colored pan traps with a surface
194 area of 0.47 m². Traps were separated by four meters along two 40 m intersecting transects in
195 each stand. In the retention treatment, 12 were placed on the logged part and 9 in the unlogged
196 part of the stand. Saproxylic beetles were sampled over the growing season (May-September)
197 using flight-interception traps that consisted of two crossed plastic panes (40 cm×60 cm) and a
198 funnel (diameter=40 cm) located under the panes. Ten traps separated by 20 meters were placed
199 in each stand, and in the retention treatment these ten traps were split between the logged and
200 unlogged part. Plant and cryptogram percentage cover at the species level were recorded in each
201 stand by evenly placing 15 plots (2×2 m) along three transects, which were ca. 40 m apart from
202 each other. These transects intersected with unlogged parts in the retention treatment.

203

204 **Data analysis**

205 Effects of the treatments (management: logging, retention, unlogged; fire: unburned, burned;
206 microhabitat: tree/stump, flat ground) on plant cover and berry production were statistically
207 tested by generalized linear mixed models using the MCMCglmm package (ver. 2.22.1, Hadfield
208 2010) in R (ver. 3.3.1, R Development Core Team 2016). Pre-experimental plant cover for each
209 shrub species was first included as a covariate, but as this variable had no impact on cover
210 models (Bilberry: $P = 0.28$, Cowberry: $P = 0.77$) nor on fruit models (Bilberry: $P = 0.80$,
211 Cowberry: $P = 0.60$), it was removed from the final models. Separate models were fitted to (i)
212 test if logged areas in the retention treatment (retention-L) responded differently to the

213 treatments compared to logging (i.e. examined if the effects of tree retention extend out into the
214 logged areas), and (ii) if retention patches (i.e., unlogged, retention-U) responded differently to
215 the treatments compared to unlogged stands (i.e. examining effects on the retention patches from
216 the surrounding logged area). Treatments (management, fire, microhabitat) and their interactions
217 were included in the models as fixed effects and to account for the nested design (microhabitat
218 nested in management treatment), we included site and tree/stump-flat ground pairs as random
219 effects. To test if changes in berry production were explained by changes in plant cover, we
220 fitted an additional model for fruit production where we included plant cover (log-transformed)
221 as an offset term. We used binomial errors for plant cover, and for berry production (number of
222 berries) we fitted a zero-inflated Poisson model (ZIP) to account for the large number of zeros in
223 the data. In a ZIP model, zeros are attributed to either the Poisson process, or to the zero-inflation
224 process.

225

226 Models were run for a minimum of 500 000 MCMC iterations and neither multiple model runs
227 nor different priors affected model estimates. Flat uninformative priors were used for the fixed
228 effects and parameter-expanded priors were used for the random factors. Standard procedures
229 were employed to evaluate the model fit (e.g. trace plots and sampling plots). Treatment effects
230 (i.e. model coefficients) were considered statistically significant if the 95% credible confidence
231 interval did not include zero. We re-ran models with different contrasts to test and quantify
232 specific treatment effects. Model results are illustrated as effect plots where treatment effects (on
233 the log scale) are shown in relation to a reference level. Contrasts between any of the treatments
234 can be evaluated from effect plots, and can be considered statistically significantly different if
235 the 95% credible interval does not include the point estimates of interest.

236

237 To compare the response of berry production with species richness (total number of species) to
238 our treatments, we estimated treatment effects as percent change relative to the standard
239 management practice (i.e., logging without prescribed burning). We did not calculate any
240 multifunctionality measures (Byrnes et al. 2014), as we only have one true function – namely
241 berry production. We first calculated the mean berry production for each replicate, as the species
242 richness studies did not include microhabitat in their sampling design (i.e., $n = 3$ and $N = 18$).
243 The investigated variables varied in data range and distribution, with various degrees of
244 increasing variance with the mean. To model all variables in the same way and to avoid
245 transformations, we employed generalized linear models with a Gamma error distribution and
246 log-link. This approach gave robust results and facilitated comparisons between the response
247 variables. Approximate confidence intervals were achieved by multiplying the standard errors by
248 two.

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253 Results

254 The unburned, unlogged sites in the study area had a similar cover of cowberry and bilberry (on
255 average 28% and 42%, respectively), but berry yield was higher for bilberry than for cowberry (3

256 and 14 per per m², respectively). Mean berry production per site and treatment is presented in
257 Figure 1 and Table SA2, while modeled effects are described below.

258

259 **Cowberry**

260 Logging without subsequent burning increased cover of cowberry in the vicinity of stumps in
261 logged areas (Fig. 2a). Burning generally decreased cover, particularly near stumps, but it had a
262 positive effect on cover on flat ground in unlogged stands.

263 In general, differences between microhabitats and treatments were greater for berry production
264 than for cover, and the effects on berry production were not driven by changes in plant cover
265 (Fig. 2ab). Accounting for plant cover, i.e. estimating the effect on berry production per percent
266 plant cover, barely changed the model coefficients in Fig. 2b. Logging (with and without
267 retention trees) increased cowberry production. For example, logging resulted in 80 times more
268 berries across microhabitats (logged versus unlogged). Furthermore, in logged stands prescribed
269 burning reduced the difference in berry production between stumps and flat ground (from 22
270 times to 2.3 times higher near stumps, Fig. 2a). In contrast, prescribed burning had a small
271 positive effect on berry production in the retention treatment (not statistically significant), and a
272 large positive effect in the unlogged treatment. Thus, 11 years after burning, the retention
273 treatment had the highest berry production across microhabitats (+1100% and +340% compared
274 to unlogged and logged areas, respectively), and logged and unlogged stands showed a similar
275 production on flat ground, but logged stands had higher production in the vicinity of stumps (Fig.
276 2b).

277

278 When comparing berry production and cover in the logged area outside retention patches
279 (retention-L) with cover and production on logged stands (i.e., clearcuts), we found that the
280 response to logging was similar, indicating that the effect of tree retention does not extend
281 beyond the retention patch (Fig. 3a, SA3a). In contrast, burning decreased plant cover and berry
282 production (-31%) on logged stands, while a positive effect on berries (+100%) was observed in
283 the retention treatment (retention-L) (Fig.3a). This contrasting effect of fire on berries was driven
284 by different effects near stumps. Unlogged areas (unlogged stands and retention-U) also showed
285 a similar pattern to the overall analysis (Fig. 3b; SA3b). Cover and production were higher in
286 retention-U, indicating that the effect of logging extended into the retained patches. Moreover,
287 our results demonstrate a much stronger effect of prescribed burning in unlogged forests
288 compared to retention patches (retention-U).

289

290 **Bilberry**

291 Logging reduced plant cover, so that on average it was less than 1% on flat ground in clear cuts,
292 compared to 49% in unlogged stands. Comparing microhabitats, stumps on logged stands had
293 twenty times higher cover than flat ground (absolute cover still low though), while tree bases in
294 the unlogged stands had 63% lower cover than the corresponding flat ground (Fig. 2c).

295 Prescribed burning, however, reduced plant cover in the vicinity of trees/stumps.

296 Differences in berry production between unburned management treatments (logged, retention,
297 unlogged) were largely explained by cover (Fig. 2cd). The effect of prescribed burning on
298 production differed slightly from the effect on plant cover, with burning reducing berry

299 production across microhabitats, in both the logged and retention treatments, but not altering
300 production in the unlogged stands.

301

302 Comparing bilberry cover and berry production between unburned logged stands and logged
303 areas in the retention treatment (i.e. logged vs. retention-L), we observed similar results to the
304 overall analyses for cover (Fig. SA3c), but less so for production (Fig. 3c). Thus, retaining trees
305 increased cover outside the retention patches (11 times higher cover on flat ground), while berry
306 production only increased near stumps. For unlogged and retention-U treatments, the effect of
307 burning and microhabitat on cover were almost identical (Fig. SA3d). However, unlogged forest
308 had an overall higher cover than retention patches (e.g. in unburned stands: 21 times and 16
309 times higher on flat ground and in the vicinity of trees, respectively), suggesting extended effects
310 of logging into the patches (i.e., retention-U). Berry production was also higher in unlogged
311 stands, but production differed in its response to prescribed burning (Fig. 3d). Inside retention-U
312 areas, fire decreased production (-94%), while it had a neutral/positive effect in unlogged stands
313 (+226%, but not statistically different from zero).

314

315 **Non-timber forest products versus species richness**

316 Trade-offs between effects on berry production and biodiversity were common (Table 1, see
317 Supplementary information Table SA2 for species richness treatment means). Only bilberry
318 production and beetle richness increased with tree retention or unlogged conditions, compared to
319 logged stands (Table 1), and most variables indicated lower values compared to logging
320 (cowberry production, pollinator richness, bryophyte richness, lichen richness). Burning

321 combined with logging had no positive effects on the investigated variables, but decreased
322 cowberry production and bryophyte richness. In contrast, burning combined with retention or
323 unlogged treatments increased bilberry production, and richness for pollinators, beetles and
324 lichens. The number of red-listed species were few and only found among pollinators and
325 beetles: pollinators 1% (1 species), beetles 2.4% (7 species).

326

327

328 Discussion

329 Our study shows that berry production (a non-timber forest product, NTFP) is not severely
330 hampered by retention forestry or by prescribed burning, although the effects vary among
331 microhabitats. The conservation measures examined had inconsistent effects on species richness
332 of the taxa included, but combining retention forestry and prescribed burning appeared to
333 provide the best outcome when all values (NTFPs and richness) were considered, while burning
334 of logged stands (i.e., clearcuts) produced the least favourable outcome. Nevertheless, as
335 individual values are maximized under different treatments, there were clear trade-offs in the
336 delivery of different values that are supposed to be favoured by the conservational measures
337 examined.

338

339 **Berry production**

340 *Logging and retention*

341 Logging increased cowberry production, with berry production being about 80 times higher in
342 logged than in unlogged stands 11 years after logging. Thus, our results provide support for the
343 idea that cowberry may recover rather quickly from the disturbance induced by logging, and that
344 logging can favour cowberry production by creating a more open habitat (Kardell 1980;
345 Raatikainen et al. 1984). We also showed that the positive effect of logging was larger in the
346 vicinity of stumps, with berry production being 22 times higher compared to flat ground areas.
347 This result is in line with expectation given that cowberry thrives in dry, open forests (Kardell
348 1980) and the soil is likely drier near stumps.

349

350 In contrast to cowberry, bilberry was negatively influenced by logging with close to zero berry
351 production in the logged stands, an effect largely driven by reduced cover. Reduced bilberry
352 cover following logging is well known as bilberry is most common in mature mesic spruce
353 (*Picea abies*) forest (Kardell 1980; Johnson et al. 2014), but the magnitude (95%) and the long-
354 lasting effect (>10 yrs) observed in our study is in contrast to studies reporting small and
355 transient effects of clearcutting on bilberry cover (Palviainen et al. 2005; Nielsen et al. 2007).
356 Retention forestry partly mitigated the negative effect, but both cover and berry densities were
357 still much lower than in unlogged stands. The limited effect of patches of trees may not be that
358 surprising, as the size of the retention patches used in our experiment have been shown to be too
359 small to efficiently retain the overall pre-logging composition of the ground vegetation (Johnson
360 et al. 2014). However, the negative effect of logging found inside the retention patches was
361 unexpected, as the more open conditions in these patches should favour bilberry. For example,
362 production of bilberries should be highest when tree canopy cover is in the range of 10 to 50%
363 (Raatikainen et al. 1984), and thus selective logging is suggested as an alternative to clearcutting

364 due to its capacity to preserve high cover of bilberry (Atlegrim & Sjöberg 1996). Possibly, the
365 negative effect on bilberries is due to strong edge effects, resulting in a micro climate that is too
366 dry for bilberry in the entire retention patch.

367

368 *Prescribed burning and retention*

369 Cowberry and bilberry are sensitive to fire, but may be favoured by low severity fires (Schimmel
370 & Granström 1996). In our experiment, prescribed burning increased production of cowberries in
371 unlogged but not in logged stands. The different responses to fire can be ascribed to differences
372 in burn severity, as the effect of prescribed burning on the ground vegetation was more severe in
373 logged (27% of organic layer removed) than unlogged stands (8% of organic layer removed)
374 (Hyvärinen et al. 2006, Johnson et al. 2014). *Vaccinium* species can recover rather quickly
375 following light ground fires through surviving rhizomes (Schimmel & Granström 1996), and
376 therefore, the higher cowberry production in unlogged burned stands is likely a result of rapid
377 recovery following a moderate disturbance, and improved light conditions following burning-
378 related tree mortality. The positive response following prescribed burning is, thus, in accordance
379 with studies suggesting that thinning can be used to promote bilberry yields (Miina et al. 2010;
380 Granath & Strengbom 2017). Evidently, there is need to further explore the underlying
381 mechanisms behind why the response of dwarf-shrubs appears to differ after natural and man-
382 made disturbances.

383

384 **Implications for multi-use forestry**

385 In general, we found no negative effects on NTFPs, here measured as berry production, of tree
386 retention or prescribed burning, although cowberry production was reduced when burning was

387 applied on logged stands. Compared to logging with no retention, retention forestry, with or
388 without burning, had an overall positive impact on the production potential of wild berries.
389 Retention forestry also tended to be most favourable for species richness, with clearly higher
390 values compared to unlogged stands, while richness was higher for only one species group
391 (saproxilic beetles) under retention forestry than on logged stands. Prescribed burning altered
392 which species group was favoured by retention, as pollinator richness increased but bryophyte
393 richness decreased with fire. Previous studies have reported similar positive effects on
394 biodiversity by retention forestry (summarized by Lindenmayer et al. 2012). Although our study
395 indicates that it may also promote the production potential of NTFPs, our results also highlight
396 the complexity of responses. Our results show that not even within the two categories (NFTP and
397 species richness), was retention forestry able to deliver uniform effects.

398

399 A similar inconsistent response pattern was also observed in the unlogged forest. Here,
400 prescribed burning increased cowberry production and species richness of pollinators, beetles
401 and lichens, while richness of vascular plants decreased. Moreover, our results support earlier
402 studies that the conservational value of prescribed burning can be higher if performed in
403 combination with retention forestry, or in unlogged forests (e.g. Hyvärinen et al.2006; Halme et
404 al. 2013, Heikkala et al. 2014, 2016, Rodríguez & Kouki 2017). However, the multi-functional
405 benefits from prescribed burning can, with respect to these aspects, vary highly depending on
406 species groups included, and positive effects that are valid for all measured variables cannot be
407 warranted. The high variation in response among species groups can be related to differences in
408 habitat requirements, but also to differences in life history traits, such as generation time,
409 reproductive strategy and dispersal capacity. Trade-offs in such traits are largely reflected in the

410 variation of responses to the management treatment. For example, it is not surprising that most
411 boreal bryophytes (tolerant to low light and nutrient conditions) are not favoured by the more
412 severe burning in logged and retention treatments (de Grandpre et al. 1993). Additionally,
413 species richness as such, is only one biodiversity target in managed multi-functional forests. In
414 fact, preservation of specific rare or threatened species, may be a more common objective. For
415 example, dead-wood-associated fungi (highly threatened), are favoured by the conservation
416 measures included in our study (Suominen et al. 2015).

417

418 Multi-use management of forests aims to reduce the ecological impact of high-intensive land-
419 use, while still providing resources for humans, and it is gaining increased appreciation (e.g.
420 Bennett et al. 2009; Lindenmayer et al. 2012; Gamfeldt et al. 2013). However, given the
421 multitude of services that forests can provide, it is not unexpected that all targets cannot be
422 reached simultaneously at each site. In fact, altering stand and landscape structure and
423 heterogeneity can have opposing effects on target values as shown here, as well as in agricultural
424 ecosystems (Power 2010). Methods that balance the delivery of different values, to achieve
425 highest delivery of ecosystem goods and services, have been suggested as a way to maximize the
426 simultaneous delivery of a broad set of values (Bradford and D'Amato 2012). Such methods
427 could be used to develop management practices that optimize the delivery of the values included
428 in our study. However, due to the clear trade-offs among values, such optimization will
429 undoubtedly also imply that the values delivered will be far from their full potential, which may
430 be considered a sub-optimization. Instead of aiming at increasing the multi-use delivery of all
431 values by standardized conservational practices (common in Fennoscandia), we suggest a
432 strategy that uses well-defined site and landscape specific management objectives, aiming to

433 optimize the multi-use delivery at the landscape-scale rather than at the site level. This is similar
434 to the suggestions by Raudsepp-Hearne et al. (2010) that correlated services (or values) can be
435 managed together in “bundles”, and different areas of the landscape are then dedicated to
436 specific “bundles” to achieve multifunctionality at a larger scale. Such strategy will require more
437 planning that combines stand- and landscape-scale perspectives – an approach that can be
438 challenging to implement in areas with many small land-owners. However, if this strategy
439 increases the overall positive response of the targeted values at a larger scale, then the total cost
440 per area needed to fulfill the conservational objectives for all values may be relatively small.
441 Also, given the spatial segregation of measures, the costs should be smaller than when applying a
442 uniform or standardized management strategy at all sites.

443

444 **Authors’ contributions:** JK, JS, GG initiated the study. JS, JK, SJ, OH and AR designed
445 data collection and SJ, OH, AR collected the data. GG performed the analyses. GG and JS wrote
446 the first draft and all authors contributed with comments on the manuscript and gave final
447 approval for publication.

448

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458 **Data accessibility**

459 Data are available from the Dryad Digital Repository. DOI: 10.5061/dryad.m7fg0 (Granath et al.
460 2018).

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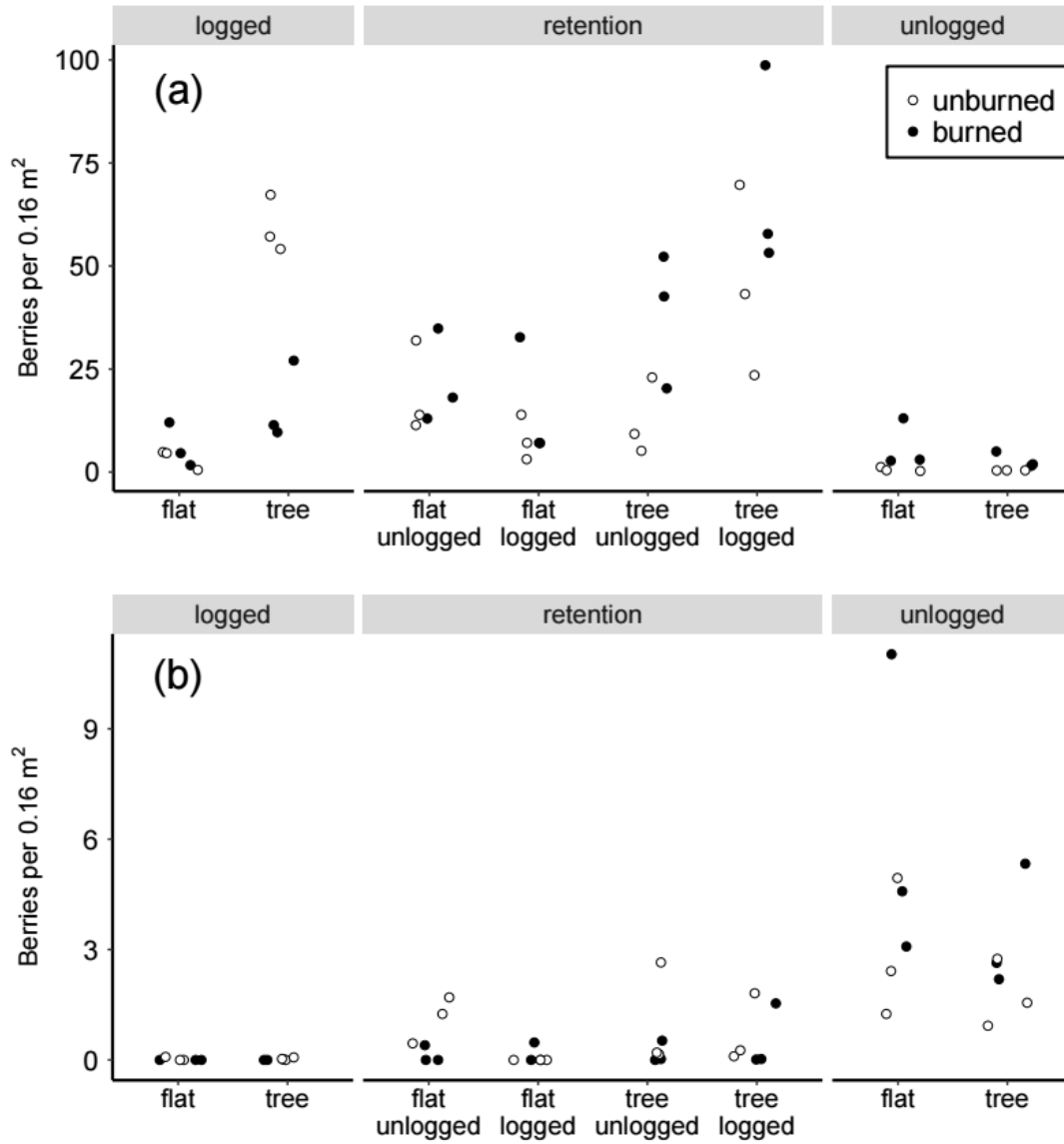
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596 Table 1. Trade-off between the berry production of bilberry and cowberry and the species
597 richness of five species groups in response to tree retention and prescribed burning. Results show
598 contrasts in the response of seven values (cow- and bilberry production, species richness of
599 pollinators (bees and hoverflies), saproxylic beetles, vascular plants, bryophytes (liverworts and
600 mosses) and ground-dwelling macrolichens) expressed as percentage change between unburned
601 logged stands (i.e., set as reference) and logging with groups of trees retained (retention), no
602 logging (unlogged), and prescribed burning on logged stands, retention treated stands and
603 unlogged stands. Bold numbers indicate that the 95% confidence interval (given in parenthesis)
604 does not include zero.

Unburned logged vs.	Values (% change)						
	Berry production		Species richness				
	cowberry	bilberry	pollinators	beetles	vascular plants	bryophytes	lichens
- retention	-32 (-76, 11)	526 (12, 1040)	-24 (-51, 3)	43 (22, 64)	3 (-45, 51)	-6 (-41, 29)	-7 (-45, 32)
- unlogged	-98 (-99,-97)	1751 (231, 3271)	-61 (-75, -48)	38 (18, 59)	-27 (-61, 8)	-37 (-60, -14)	-82 (-90, -75)
Burned							
- logged	-65 (-88, -42)	-21 (-86, 43)	7 (-31, 46)	4 (-11, 19)	3 (-45, 51)	-41 (-63, -19)	-13 (-49, 22)
- retention	16 (-59, 91)	169 (-53, 390)	17 (-25, 59)	34 (14, 53)	11 (-41, 63)	-57 (-73, -41)	0 (-41, 41)
- unlogged	-86 (-95, -76)	3674 (574, 6774)	-36 (-39, -13)	90 (62, 118)	-67 (-82, -52)	-29 (-55, -3)	-18 (-52, 16)

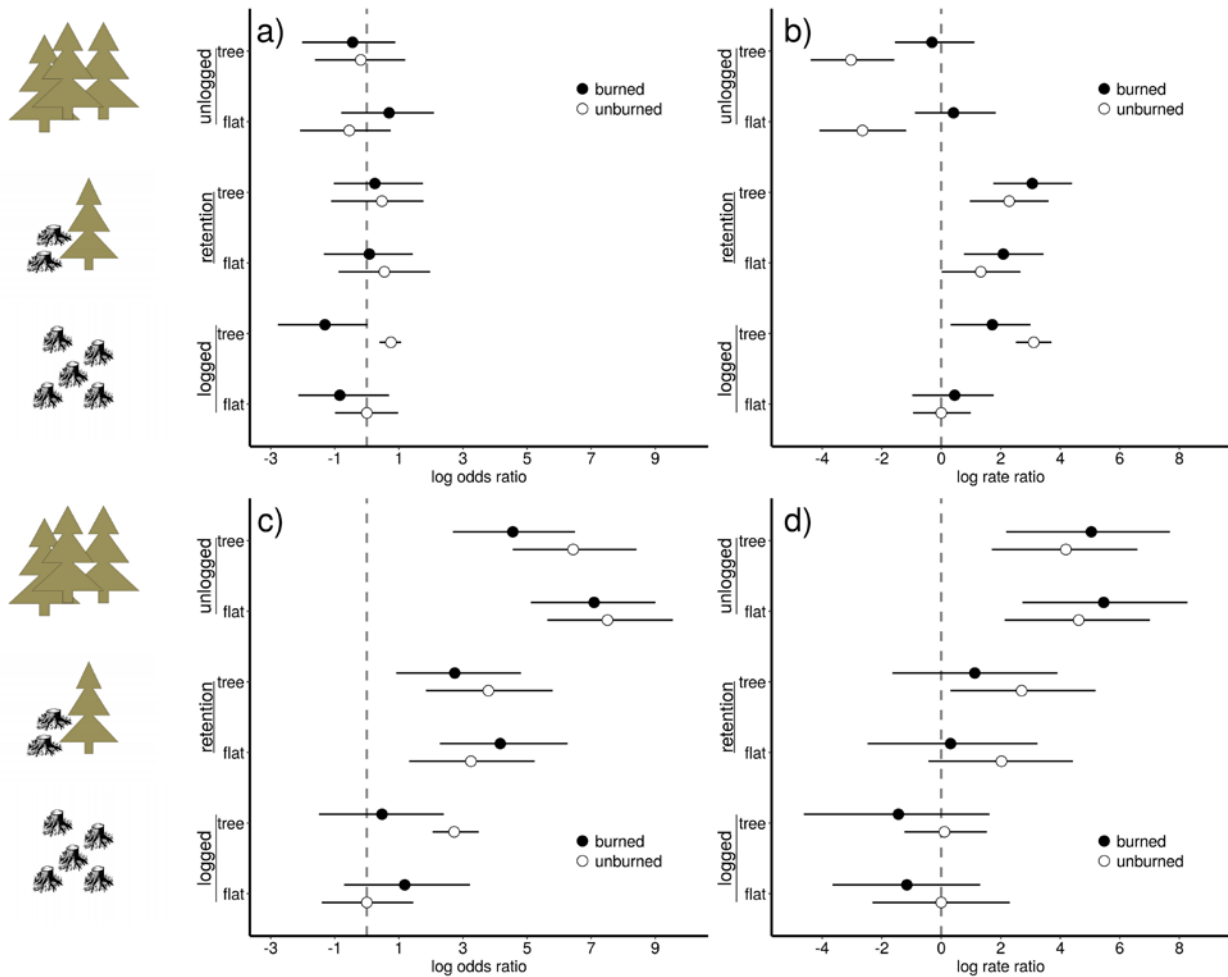
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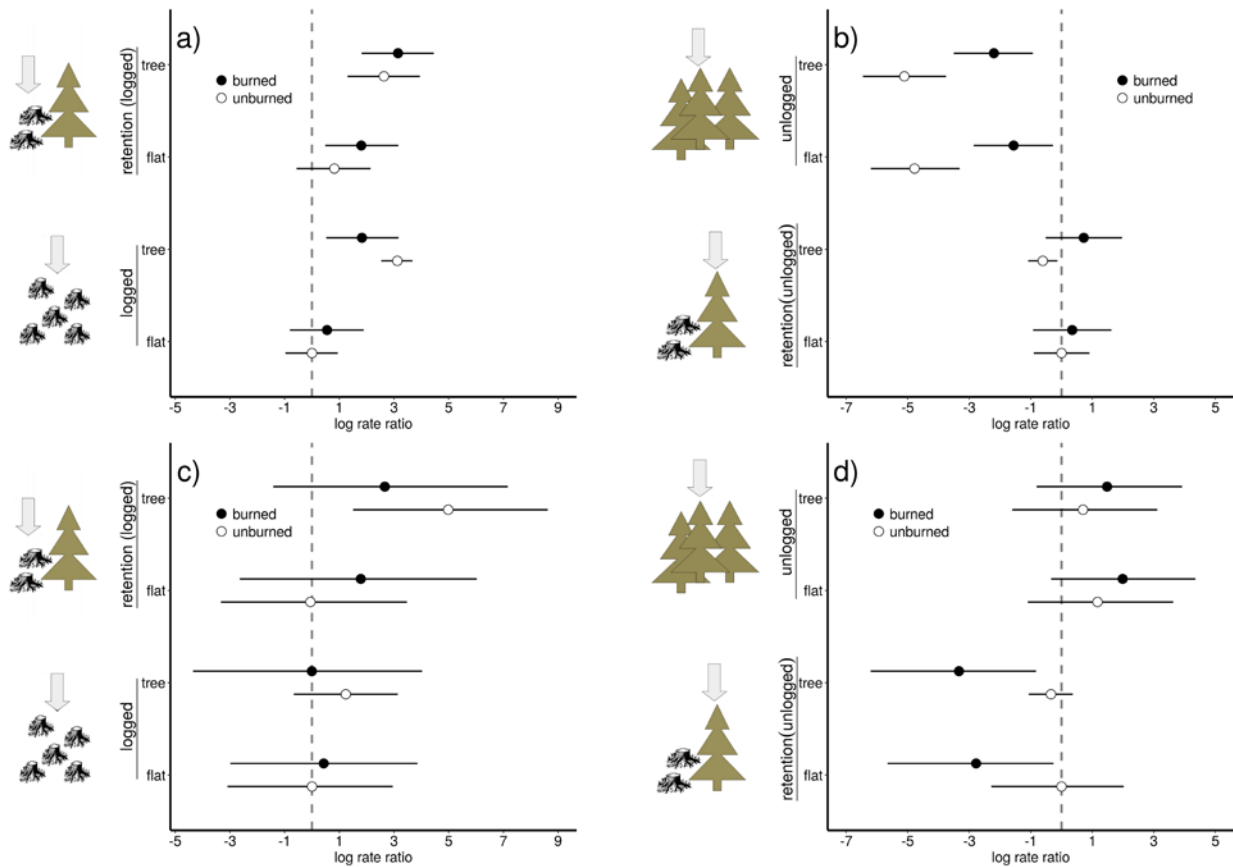
618 Figure 1. Raw means of berries produced for all replicates (i.e. sites) and each treatment
 619 combination. a) Cowberry and b) bilberry. Points are spread out around each treatment for better
 620 visualization. Note the different scales on the y-axes. Logged = all trees removed, Retention =
 621 logged with groups of trees saved (unlogged patches), unlogged = no logging performed.

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626 Figure 2. Effect plots of plant cover (a,c) and berry production (b, d) for, cowberry (a,b), and
 627 bilberry (c, d). Flat ground (flat), unburned, logged is set as reference treatment. Images on the
 628 left illustrate the treatments. Error bars are 95% credible intervals and individual contrasts
 629 between treatments can be viewed as statistically significant if bars do not include the point
 630 estimate. Tree = tree base in forested areas and stumps in cut areas. Logged = all trees removed,
 631 retention = logging with groups of trees saved, unlogged = no logging performed.



635 Figure 3. Effect plots of berry production for, a,b) cowberry, and c,d) bilberry. Panel (a) and (c)
 636 compare the logged treatment (i.e., clearcut) with logged areas in the retention treatment
 637 (retention-L). Panel (b) and (d) compare unlogged patches in the retention treatment (retention-
 638 U) with unlogged stands. Images on the left illustrate the treatments and arrows indicate the
 639 comparisons made in each panel. Flat ground (flat), unburned, clearcut/retention-U is set as
 640 reference treatment. Error whiskers are 95% credible intervals and individual contrasts between
 641 treatments can be viewed as statistically significant if whiskers do not include the point estimate.
 642 Tree = tree base in forested areas and stumps in cut areas. Logged = all trees removed, retention
 643 = logged with groups of trees saved (unlogged patches), unlogged = no logging performed.