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

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19Abstract

- 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.

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

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

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

58Introduction

59Up until the 1990s, forestry was characterized by a single service approach, i.e. maximizing
60production of biomass. However, increased appreciation for the additional values that forests can
61deliver has since then led to the development of new types of forest management systems,
62including retaining groups of trees during clearcut harvest and applying prescribed burning, with
63the aim to support a broader set of ecosystem services and values (Gustafsson et al. 2012;
64Lindenmayer et al. 2012). However, to what extent these conservational measures promote
65services and additional values such as berry production and species richness, are rarely evaluated
66together. Therefore, we set out to explore the impact of the aforementioned conservation
67measures on delivery of multiple values (ecosystem services and biodiversity) in boreal Finland.

68

69Leaving trees and snags during clearcut timber harvest, known as retention forestry, is employed
70to preserve legacies from previous generations of trees, and believed to be fundamental for
71maintaining biodiversity and function of forests (Franklin et al. 1997). Nowadays, practices that
72preserve or restore such legacies are used worldwide to facilitate multifunctional objectives in
73forestry (Gustafsson et al. 2012; Lindenmayer et al. 2012), and considered standard practice in
74Scandinavia (Gustafsson et al. 2010). Prescribed burning, although less widely used as a
75conservation measure, also aims at maintaining or emulating natural legacies lost during harvest
76operations in boreal forests (Heikkala et al. 2016). Efficient fire suppression has led to a lack of
77wildfires in parts of the boreal biome (Niklasson & Granström 2000; Wallenius et al. 2007), and
78prescribed burning is therefore, used to promote biodiversity by restoring the legacies from
79wildfires (Halme et al. 2013). In Fennoscandia, prescribed burning is part of the national forest

80conservational strategies and included in certification schemes such as Forest Steward Council
81(FSC) (Annon 2012, 2014). Although these two conservation measures are intended to promote a
82broad set of ecosystem services, including delivery of non-timber forest products (NTFPs) such
83as production of wild berries and mushrooms (Gustafsson et al. 2012), they have primarily been
84applied to support biodiversity (Gustafsson et al. 2010). This is also reflected in the literature on
85effects of retention forestry and prescribed burning, which is heavily biased towards the
86relationship between timber production and conservation of biodiversity (e.g. Halpern et al.
872012; Johnson et al. 2014; Fedrowitz et al. 2014). Only a few studies have examined effects
88related to ecosystem services (Lazaruk et al. 2005; Rodríguez & Kouki 2015, 2017), and to our
89knowledge, there are no previous studies examining the effects on NTFPs, or studies that have
90explored synergies and trade-offs among the different values that these conservation measures
91are expected to deliver.

92

93Wild berries of boreal forests in Eurasia, mainly produced by the two ericaceous dwarf-shrubs
94bilberry (*Vaccinium myrtillus* L.) and cowberry (*Vaccinium vitis-idaea* L.), are highly valued
95NTFPs (Kangas 2001). In Finland, which has a forest cover of about 23 million ha, the annual
96yields can be as high as 312 million kg for bilberry and 386 million kg for cowberry (Turtiainen
97et al. 2011). Although the proportion of berries picked is rather low, 5-6% for bilberries and 8-
9810% for cowberries (Turtiainen et al. 2011), berry production still represents a large value.
99Estimating the economic value of these berries is complicated, as it will vary greatly depending
100on the proportion of berries picked and on the current market price. However, if forest
101management is adjusted to improve bilberry production, the revenue from bilberry production
102may exceed that of timber production, and the profitability of stand management may potentially

103be doubled (Miina et al. 2010). In addition to this provisioning service, berry picking also
104constitutes a highly-valued cultural ecosystem service (Pouta et al. 2006). Finally, these dwarf
105shrubs are also essential for many herbivores and omnivores (e.g. birds, voles, cervids, and
106invertebrates) and these species often form the basis of complex trophic networks in forests (e.g.
107Lakka & Kouki 2009). Despite the multitude of values that berry production represents, its
108response to forest management has so far received surprisingly little attention (Pohjanmies et al.
1092017).

110

111Developing management schemes that simultaneously deliver multiple values is challenging, as
112the delivery of one type of value often results in lowered revenue from other values (Bennett et
113al. 2009; Strengbom et al. in press). Despite these trade-offs, it is often possible to find
114management options that balance the output between different values, and thus improve multi-
115functionality (Bradford & D'Amato 2012). The possibilities to develop such balanced
116management strategies are, however, often limited by a lack of knowledge on the relationship
117among different services, and how changed revenue from one service influences revenue from
118others (Raudsepp-Hearne et al. 2010). Hence, if the aim is to increase or preserve multi-
119functionality, there is a need for a better understanding of how different management practices,
120such as those primarily applied for preservation of biodiversity, influence the revenue from other
121services such as production of NTFPs.

122

123The aim of our study was two-fold: **firstly**, we wanted to investigate how two common
124conservational practices, prescribed burning and green tree retention, influence production of

125wild berries, and if the effects differ depending on type of microhabitat (near trees or on flat
126ground between trees). **Secondly**, we wanted to explore how these two measures influence multi-
127functionality by examining potential synergies and trade-offs between how these practices
128influence berry production (a NTFP) and biodiversity.

129

130Materials and Methods

131Study area

132The study was conducted in the mid-boreal vegetation zone of Eastern Finland (approx. 63°10'N,
13330°40'E, 165 m asl, see Supplementary information Figure SA1 for map over the experimental
134sites). The area has an annual mean temperature of +2°C (-12°C in January and +15.8°C in July)
135and the annual mean precipitation is in the range of 500-800 mm (about half as snow)
136(Ilmatieteen laitos 1991).

137

138Prior to the experimental manipulations, all sites were covered with about 150 year-old
139coniferous forest of dry *Vaccinium–Empetrum* heath type. Scots pine (*Pinus sylvestris* L.)
140dominated the tree layer, with Norway spruce (*Picea abies* L. H. Karst) and birch species
141(*Betula pendula* R. and *B. pubescens* Ehrh.) as co-dominants. Pre-harvest living volume in the
142stands was on average 288 m³ ha⁻¹. All sites had similar vegetational composition (Johnson et al.
1432014) and overall high cover of bilberry (range among sites=32 to 64%) and cowberry (range
144among sites=18 to 51%). The experimental area has historically only been exposed to very low-
145intensity selective logging during the late 1800s and early 1900s, but no intensive modern

146forestry had been conducted at the experimental sites prior to the experiment (Hyvärinen et al.
1472006).

148

149The experiment consisted of 18 forest stands, each 3-4 ha in size (see Fig. SA1), and subjected to
1506 treatments in a two-factor factorial design (n=3 for each treatment combination). Prescribed
151burning (two levels: unburned or burned) and harvest intensity (management treatment with
152three levels of retention: 1) logged, i.e. no retention and 0% of the pre-harvest tree volume
153retained, 2) retention forestry with 17.4% retained, $\sim 50 \text{ m}^3 \text{ ha}^{-1}$, and 3) unlogged, i.e. 100%
154retained) were the main factors. The stands assigned to be harvested were logged during the
155winter of 2000-2001. In the retention treatment, the retained trees were aggregated into at least
156five evenly sized circular groups. The prescribed burnings were performed during two
157consecutive days at the end of June 2001. Humus layer consumption was higher in logged stands
158(change in average humus depth -27%) than in unlogged stands (-8 %), and average flame
159height, was on average 2.2m and 3.9m in unlogged stands and retention groups, respectively
160(Hyvärinen et al. 2006).

161

162Data collection

163Density of berries and plant cover of the two species were scored in mid-July 2012 (for 2012
164weather data see Table SA1). In 2012, berry yields were above the average in Finland (Kauko
165Salo, Natural Resources Institute Finland, Pers. Comm.). In our inventory, which coincided with
166the peak of berry production, we counted all berries growing on plants rooted within inventory
167frames sized 0.4 by 0.4 m. The frame was divided into 100 four by four cm grid cells, and cover

168was scored as the number of cells with the species present. Cover and berries were counted in
169two types of microhabitat, on flat ground and in the vicinity of a stump or a tree base (north and
170south-facing sides to make sampling consistent). In the treatments with full and no retention, we
171scored cover and berry density at 72 locations in each stand. We used a semi-systematic
172sampling design, with four transects evenly spaced and positioned in the central area of the
173stand, with nine randomly selected locations along each transect (see Fig. SA2 for an illustration
174and details). At each location, the nearest stump/tree base with a diameter greater than 20 cm
175(stumps/trees large enough to potentially create differences in microhabitat) was selected
176together with the corresponding flat ground that fulfilled the criteria of being a potential growth
177location for the species, i.e. wet micro sites and sites with bare rock were excluded. In the
178retention forestry treatment, we used a slightly different sampling design, so that both the
179retention patches and open areas were sampled. Inside the retention patches, we scored cover and
180berry densities at 20 randomly chosen tree bases and 20 locations with flat ground, fulfilling the
181same criteria as described above. In a similar way, we scored cover and berry densities in the
182vicinities of stumps and flat grounds outside the retention patch. We scored 40 stumps and 40
183locations on flat ground in the area starting from the edge of the retention patch to c. 30 m away
184from the group, i.e. approximately the area within one tree-length from the retention patch (Fig.
185SA2).

186

187Data on species richness were retrieved from previous studies conducted by us in the same
188experimental sites. We included data on pollinators (bees and hoverflies collected in 2013, from
189Rodríguez & Kouki 2017), saproxylic beetles (collected 2011, from Heikkala et al. 2016), plants,
190bryophytes (mosses and liverworts) and ground-layer macrolichens (collected 2011, from

191Johnson et al. 2014). These species groups were chosen as they were collected around the same
192time period (2011-2013) and represented a broad range of species groups. These data were
193collected at the stand level and not for each microhabitat as for berries. Pollinators were sampled
194four times during the growing season using twenty-one 500-mL colored pan traps with a surface
195area of 0.47 m². Traps were separated by four meters along two 40 m intersecting transects in
196each stand. In the retention treatment, 12 were placed on the logged part and 9 in the unlogged
197part of the stand. Saproxylic beetles were sampled over the growing season (May-September)
198using flight-interception traps that consisted of two crossed plastic panes (40 cm×60 cm) and a
199funnel (diameter=40 cm) located under the panes. Ten traps separated by 20 meters were placed
200in each stand, and in the retention treatment these ten traps were split between the logged and
201unlogged part. Plant and cryptogram percentage cover at the species level were recorded in each
202stand by evenly placing 15 plots (2×2 m) along three transects, which were ca. 40 m apart from
203each other. These transects intersected with unlogged parts in the retention treatment.

204

205Data analysis

206Effects of the treatments (management: logging, retention, unlogged; fire: unburned, burned;
207microhabitat: tree/stump, flat ground) on plant cover and berry production were statistically
208tested by generalized linear mixed models using the MCMCglmm package (ver. 2.22.1, Hadfield
2092010) in R (ver. 3.3.1, R Development Core Team 2016). Pre-experimental plant cover for each
210shrub species was first included as a covariate, but as this variable had no impact on cover
211models (Bilberry: $P = 0.28$, Cowberry: $P = 0.77$) nor on fruit models (Bilberry: $P = 0.80$,
212Cowberry: $P = 0.60$), it was removed from the final models. Separate models were fitted to (i)

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

226

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

235can be evaluated from effect plots, and can be considered statistically significantly different if
236the 95% credible interval does not include the point estimates of interest.

237

238To compare the response of berry production with species richness (total number of species) to
239our treatments, we estimated treatment effects as percent change relative to the standard
240management practice (i.e., logging without prescribed burning). We did not calculate any
241multifunctionality measures (Byrnes et al. 2014), as we only have one true function – namely
242berry production. We first calculated the mean berry production for each replicate, as the species
243richness studies did not include microhabitat in their sampling design (i.e., $n = 3$ and $N = 18$).
244The investigated variables varied in data range and distribution, with various degrees of
245increasing variance with the mean. To model all variables in the same way and to avoid
246transformations, we employed generalized linear models with a Gamma error distribution and
247log-link. This approach gave robust results and facilitated comparisons between the response
248variables. Approximate confidence intervals were achieved by multiplying the standard errors by
249two.

250

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252

253

254Results

255The unburned, unlogged sites in the study area had a similar cover of cowberry and bilberry (on
256average 28% and 42%, respectively), but berry yield was higher for bilberry than for cowberry (3
257and 14 per per m², respectively). Mean berry production per site and treatment is presented in
258Figure 1 and Table SA2, while modeled effects are described below.

259

260Cowberry

261Logging without subsequent burning increased cover of cowberry in the vicinity of stumps in
262logged areas (Fig. 2a). Burning generally decreased cover, particularly near stumps, but it had a
263positive effect on cover on flat ground in unlogged stands.

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

276production on flat ground, but logged stands had higher production in the vicinity of stumps (Fig.
2772b).

278

279When comparing berry production and cover in the logged area outside retention patches
280(retention-L) with cover and production on logged stands (i.e., clearcuts), we found that the
281response to logging was similar, indicating that the effect of tree retention does not extend
282beyond the retention patch (Fig. 3a, SA3a). In contrast, burning decreased plant cover and berry
283production (-31%) on logged stands, while a positive effect on berries (+100%) was observed in
284the retention treatment (retention-L) (Fig.3a). This contrasting effect of fire on berries was driven
285by different effects near stumps. Unlogged areas (unlogged stands and retention-U) also showed
286a similar pattern to the overall analysis (Fig. 3b; SA3b). Cover and production were higher in
287retention-U, indicating that the effect of logging extended into the retained patches. Moreover,
288our results demonstrate a much stronger effect of prescribed burning in unlogged forests
289compared to retention patches (retention-U).

290

291**Bilberry**

292Logging reduced plant cover, so that on average it was less than 1% on flat ground in clear cuts,
293compared to 49% in unlogged stands. Comparing microhabitats, stumps on logged stands had
294twenty times higher cover than flat ground (absolute cover still low though), while tree bases in
295the unlogged stands had 63% lower cover than the corresponding flat ground (Fig. 2c).
296Prescribed burning, however, reduced plant cover in the vicinity of trees/stumps.

297Differences in berry production between unburned management treatments (logged, retention,
298unlogged) were largely explained by cover (Fig. 2cd). The effect of prescribed burning on
299production differed slightly from the effect on plant cover, with burning reducing berry
300production across microhabitats, in both the logged and retention treatments, but not altering
301production in the unlogged stands.

302

303Comparing bilberry cover and berry production between unburned logged stands and logged
304areas in the retention treatment (i.e. logged vs. retention-L), we observed similar results to the
305overall analyses for cover (Fig. SA3c), but less so for production (Fig. 3c). Thus, retaining trees
306increased cover outside the retention patches (11 times higher cover on flat ground), while berry
307production only increased near stumps. For unlogged and retention-U treatments, the effect of
308burning and microhabitat on cover were almost identical (Fig. SA3d). However, unlogged forest
309had an overall higher cover than retention patches (e.g. in unburned stands: 21 times and 16
310times higher on flat ground and in the vicinity of trees, respectively), suggesting extended effects
311of logging into the patches (i.e., retention-U). Berry production was also higher in unlogged
312stands, but production differed in its response to prescribed burning (Fig. 3d). Inside retention-U
313areas, fire decreased production (-94%), while it had a neutral/positive effect in unlogged stands
314(+226%, but not statistically different from zero).

315

316Non-timber forest products versus species richness

317Trade-offs between effects on berry production and biodiversity were common (Table 1, see
318Supplementary information Table SA2 for species richness treatment means). Only bilberry

319production and beetle richness increased with tree retention or unlogged conditions, compared to
320logged stands (Table 1), and most variables indicated lower values compared to logging
321(cowberry production, pollinator richness, bryophyte richness, lichen richness). Burning
322combined with logging had no positive effects on the investigated variables, but decreased
323cowberry production and bryophyte richness. In contrast, burning combined with retention or
324unlogged treatments increased bilberry production, and richness for pollinators, beetles and
325lichens. The number of red-listed species were few and only found among pollinators and
326beetles: pollinators 1% (1 species), beetles 2.4% (7 species).

327

328

329Discussion

330Our study shows that berry production (a non-timber forest product, NTFP) is not severely
331hampered by retention forestry or by prescribed burning, although the effects vary among
332microhabitats. The conservation measures examined had inconsistent effects on species richness
333of the taxa included, but combining retention forestry and prescribed burning appeared to
334provide the best outcome when all values (NTFPs and richness) were considered, while burning
335of logged stands (i.e., clearcuts) produced the least favourable outcome. Nevertheless, as
336individual values are maximized under different treatments, there were clear trade-offs in the
337delivery of different values that are supposed to be favoured by the conservational measures
338examined.

339

340Berry production

341*Logging and retention*

342Logging increased cowberry production, with berry production being about 80 times higher in
343logged than in unlogged stands 11 years after logging. Thus, our results provide support for the
344idea that cowberry may recover rather quickly from the disturbance induced by logging, and that
345logging can favour cowberry production by creating a more open habitat (Kardell 1980;
346Raatikainen et al. 1984). We also showed that the positive effect of logging was larger in the
347vicinity of stumps, with berry production being 22 times higher compared to flat ground areas.
348This result is in line with expectation given that cowberry thrives in dry, open forests (Kardell
3491980) and the soil is likely drier near stumps.

350

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

362 unexpected, as the more open conditions in these patches should favour bilberry. For example,
363 production of bilberries should be highest when tree canopy cover is in the range of 10 to 50%
364 (Raatikainen et al. 1984), and thus selective logging is suggested as an alternative to clearcutting
365 due to its capacity to preserve high cover of bilberry (Atlegrim & Sjöberg 1996). Possibly, the
366 negative effect on bilberries is due to strong edge effects, resulting in a micro climate that is too
367 dry for bilberry in the entire retention patch.

368

369 *Prescribed burning and retention*

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

384

385 **Implications for multi-use forestry**

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

399

400 A similar inconsistent response pattern was also observed in the unlogged forest. Here,
401 prescribed burning increased cowberry production and species richness of pollinators, beetles
402 and lichens, while richness of vascular plants decreased. Moreover, our results support earlier
403 studies that the conservational value of prescribed burning can be higher if performed in
404 combination with retention forestry, or in unlogged forests (e.g. Hyvärinen et al. 2006; Halme et
405 al. 2013, Heikkala et al. 2014, 2016, Rodríguez & Kouki 2017). However, the multi-functional
406 benefits from prescribed burning can, with respect to these aspects, vary highly depending on
407 species groups included, and positive effects that are valid for all measured variables cannot be

408warranted. The high variation in response among species groups can be related to differences in
409habitat requirements, but also to differences in life history traits, such as generation time,
410reproductive strategy and dispersal capacity. Trade-offs in such traits are largely reflected in the
411variation of responses to the management treatment. For example, it is not surprising that most
412boreal bryophytes (tolerant to low light and nutrient conditions) are not favoured by the more
413severe burning in logged and retention treatments (de Grandpre et al. 1993). Additionally,
414species richness as such, is only one biodiversity target in managed multi-functional forests. In
415fact, preservation of specific rare or threatened species, may be a more common objective. For
416example, dead-wood-associated fungi (highly threatened), are favoured by the conservation
417measures included in our study (Suominen et al. 2015).

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

431be considered a sub-optimization. Instead of aiming at increasing the multi-use delivery of all
432values by standardized conservational practices (common in Fennoscandia), we suggest a
433strategy that uses well-defined site and landscape specific management objectives, aiming to
434optimize the multi-use delivery at the landscape-scale rather than at the site level. This is similar
435to the suggestions by Raudsepp-Hearne et al. (2010) that correlated services (or values) can be
436managed together in “bundles”, and different areas of the landscape are then dedicated to
437specific “bundles” to achieve multifunctionality at a larger scale. Such strategy will require more
438planning that combines stand- and landscape-scale perspectives – an approach that can be
439challenging to implement in areas with many small land-owners. However, if this strategy
440increases the overall positive response of the targeted values at a larger scale, then the total cost
441per area needed to fulfill the conservational objectives for all values may be relatively small.
442Also, given the spatial segregation of measures, the costs should be smaller than when applying a
443uniform or standardized management strategy at all sites.

444

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446data collection and SJ, OH, AR collected the data. GG performed the analyses. GG and JS wrote
447the first draft and all authors contributed with comments on the manuscript and gave final
448approval for publication.

449

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459**Data accessibility**

460Data are available from the Dryad Digital Repository. DOI: 10.5061/dryad.m7fg0 (Granath et al.
4612018).

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464References

- 465Annon. 2012. Finlands FSC-standard. Finlands FSC-organisation. In Swedish.
- 466Annon. 2014. Svensk skogsbruksstandard enligt FSC med SLIMF-indikatorer. FSC-STD-SWE-
467 02-02-2010 SW. Svenska FSC. In Swedish.
- 468
- 469Atleggrim O, Sjöberg K. 1996. Response of bilberry (*Vaccinium myrtillus*) to clear-cutting and
470 single-tree selection harvest in uneven-aged boreal *Picea abies* forests. Forest Ecology and
471 Management 86:39–50.
- 472Bennett EM, Peterson GD, Gordon LJ. 2009. Understanding relationships among multiple
473 ecosystem services. Ecological Letter 12:1394–1404.
- 474
- 475
- 476Bradford JB, D’Amato AWD. 2012. Recognizing trade-offs in multi-objective land management.
477 Frontiers in Ecology and Environment 10:210–216.
- 478Byrnes JEK, Gamfeldt L, Isbell F, Lefcheck JS, Griffin JN, Hector A, Cardinale BJ, Hooper DU,
479 Dee LE, Emmett Duffy J. 2014. Investigating the relationship between biodiversity and
480 ecosystem multifunctionality: challenges and solutions. Methods in Ecology and Evolution 5:
481 111–124.
- 482Fedrowitz K, Koricheva J, Baker SC, et al. 2014. Can retention forestry help conserve
483 biodiversity? A meta-analysis. Journal of Applied Ecology 51:1669–1679
- 484Franklin JF, Berg DR, Thornburgh DA, Tappeiner JC. 1997. Alternative silvicultural approaches
485 to timber harvesting: variable retention harvest systems. Pages 111–139 in Kohm KA,

Franklin JF, editors. Creating a forestry for the 21st century: the science of ecosystem management. Island Press, Washington, D.C., USA.

Gamfeldt L, Snäll T, Bagchi R et al. 2013. Higher levels of multiple ecosystem services are found in forests with more tree species. *Nature communications* 4:1340.

Granath G, Strengbom J. 2017. Nitrogen fertilization reduces wild berry production in boreal forests. *Forest Ecology and Management*. 390: 119–126.

Granath G, Kouki J, Johnson S, Heikkala O, Rodríguez A, Strengbom J (2018) Data from : Trade-offs in berry production and biodiversity under prescribed burning and retention regimes in Boreal forests. Dryad Digital Repository. <http://dx.doi.org/10.5061/dryad.m7fg0>

De Grandpré L, Gagnon D, Bergeron, Y. 1993, Changes in the understory of Canadian southern boreal forest after fire. *Journal of Vegetation Science*, 4: 803–810.

doi:10.2307/3235618 Gustafsson L, Kouki J, Sverdrup-Thygeson A. 2010. Tree retention as a conservation measure in clear-cut forests of northern Europe: a review of ecological consequences. *Scandinavian Journal of Forest Research* 25:295-308.

Gustafsson L, Baker SC, Bauhus J, et al. 2012. Retention forestry to maintain multifunctional forests: A world perspective. *BioScience* 62:633–645

Hadfield JD. 2010. MCMC Methods for Multi-Response Generalized Linear Mixed Models: The MCMCglmm R Package. *Journal of Statistical Software* 33: 1–22.

Halme PK, Allen A, Aunins A, et al. 2013. Challenges of ecological restoration: Lessons from forests in northern Europe. *Biological Conservation* 167:248–256.

Halpern CB, Halaj J, Evans SA, Dovčiak M. 2012. Level and pattern of overstory retention interact to shape long-term responses of understories to timber harvest. *Ecological Applications* 22:2049–2064.

510 Heikkala O, Suominen M, Junninen K, Hämäläinen A, Kouki J. 2014. Effects of retention level
 511 and fire on retention tree dynamics in boreal forests. *Forest Ecology and Management*
 512 328:193–201.

513 Heikkala O, Martikainen P, Kouki J. 2016. Decadal effects of emulating natural disturbances in
 514 forest management on saproxylic beetle assemblages. *Biological Conservation* 194:39-47

515 Hyvärinen E, Kouki J, Martikainen P. 2006. Fire and green-tree retention in conservation of red-
 516 listed and rare deadwood-dependent beetles in Finnish boreal forests. *Conservation Biology*
 517 20:1711–1719.

518 Ilmatieteen laitos. 1991. Tilastoja Suomen ilmastosta 1961–1990—Climatological statistics in
 519 Finland 1961–1990. Ilmatieteen laitos, Helsinki.

520 Johnson S, Strengbom, J, Kouki J. 2014. Low levels of tree retention do not mitigate the effects
 521 of clearcutting on ground vegetation dynamics. *Forest Ecology and Management* 330:67–74,

522 Kangas K. 2001. Commercial wild berry picking as a source of income in northern and eastern
 523 Finland. *Journal of Forest Economics* 7:53–68.

524 Kardell L. 1980. Occurrence and production of bilberry, lingonberry and raspberry in Sweden's
 525 forests. *Forest Ecology and Management* 2:285–298.

526 Lakka J, Kouki J. 2009. Patterns of field layer invertebrates in successional stages of managed
 527 boreal forest: Implications for the declining Capercaillie *Tetrao urogallus* L. population.
 528 *Forest Ecology and Management* 257:600–607.

529 Lazaruk LW, Kernaghan G, Macdonald SE, Khasa D. 2005. Effects of partial cutting on the
 530 ectomycorrhizae of *Picea glauca* forests in northwestern Alberta. *Canadian Journal of Forest*
 531 *Research* 35:1442–1454.

532Lindenmayer DB, Franklin JF, Löhmus A, et al. 2012. A major shift to the retention approach for
 533 forestry can help resolve some global forest sustainability issues. *Conservation Letters*
 534 5:421–431.

535Miina J, Pukkala T, Hotanen J-P, Salo T. 2010. Optimizing the joint production of timber and
 536 bilberries. *Forest Ecology and Management* 259:2065–2071.

537Niklasson M, Granström A. 2000. Numbers and sizes of fires: Long-term spatially explicit fire
 538 history in a Swedish boreal landscape. *Ecology* 81:1484–1499.

539Nielsen A, Totland Ø, Ohlson M. 2007. The effect of forest management operations on
 540 population performance of *Vaccinium myrtillus* on a landscape-scale. *Basic and Applied*
 541 *Ecology* 8:231–241.

542Palviainen M, Finer L, Mannerkoski H, Piirainen S, Starr M. 2005. Responses of ground
 543 vegetation species to clear-cutting in a boreal forest: aboveground biomass and nutrient
 544 contents during the first 7 years. *Ecological Research* 20:652–660.

545Pohjanmies T, Triviño M, Le Tortorec E, Mazziotta, A, Snäll T, Mönkkönen, M. 2017. Impacts
 546 of forestry on boreal forests: An ecosystem services perspective. *Ambio*, In press.
 547 doi:10.1007/s13280-017-0919-5

548Pouta E, Sievänen T, Neuvonen M. 2006. Recreational wild berry picking in Finland–Reflection
 549 of a rural lifestyle. *Society and Natural Resources: An International Journal* 19:285–304.

550Power AG. 2010. Ecosystem services and agriculture: tradeoffs and synergies. *Philosophical*
 551 *transactions of the royal society B: biological sciences* 365: 2959-2971.

552R Development Core Team, 2016. R: a language and environment for statistical computing. R
 553 Foundation for Statistical Computing.

554 Raatikainen M, Rossi E, Huovinen J, Koskela M-L, Niemela M, Raatikainen T. 1984. The yields
 555 of the edible wild berries in Central Finland. *Silva Fennica* 18:199–219 (in Finnish with
 556 English summary).
 557 Raudsepp-Hearne C, Peterson GD, Bennett EM. 2010. Ecosystem service bundles for analyzing
 558 tradeoffs in diverse landscapes. *Proceedings of the National Academy of Sciences*, 107: 5242-
 559 5247.
 560 Rodríguez A, Kouki J. 2015. Emulating natural disturbance in forest management enhances
 561 pollination services for dominant *Vaccinium* shrubs in boreal pine-dominated forests. *Forest*
 562 *Ecology and Management* 350:1–12.
 563 Rodríguez A, Kouki J. 2017. Disturbance-mediated heterogeneity drives pollinator diversity in
 564 boreal managed forest ecosystems. *Ecological Applications*, in press doi: 10.1002/eap.1468
 565
 566 Schimmel J, Granström A. 1996. Fire severity and vegetation response in the boreal Swedish
 567 forest. *Ecology* 77:1436–1450.
 568
 569
 570 Strengbom J, Axelsson EP, Lundmark T, Nordin A. Trade-offs in the multi-use potential of
 571 managed Boreal forests. *Journal of Applied Ecology*. DOI: 10.1111/1365-2664.13019
 572 Suominen M, Junninen K, Heikkala O, Kouki J. 2015. Combined effects of retention forestry
 573 and prescribed burning on polypore fungi. *Journal of Applied Ecology* 52:1001-1008
 574 Turtiainen M, Salo K, Saastamoinen O. 2011. Variation of yield and utilization of bilberries
 575 (*Vaccinium myrtillus* L.) and cowberries (*V. vitis-idaea* L.) in Finland. *Silva Fennica* 45:237–
 576 251.

577 Wallenius TH, Lilja S, Kuuluvainen T. 2007. Fire history and tree species composition in
578 managed *Picea abies* stands in southern Finland: Implications for restoration. Forest Ecology
579 and Management 250:89–95.

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599 Table 1. Trade-off between the berry production of bilberry and cowberry and the species
600 richness of five species groups in response to tree retention and prescribed burning. Results show
601 contrasts in the response of seven values (cow- and bilberry production, species richness of
602 pollinators (bees and hoverflies), saproxylic beetles, vascular plants, bryophytes (liverworts and
603 mosses) and ground-dwelling macrolichens) expressed as percentage change between unburned
604 logged stands (i.e., set as reference) and logging with groups of trees retained (retention), no
605 logging (unlogged), and prescribed burning on logged stands, retention treated stands and
606 unlogged stands. Bold numbers indicate that the 95% confidence interval (given in parenthesis)
607 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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Figure 1. Raw means of berries produced for all replicates (i.e. sites) and each treatment combination. a) Cowberry and b) bilberry. Points are spread out around each treatment for better visualization. Note the different scales on the y-axes. Logged = all trees removed, Retention = logged with groups of trees saved (unlogged patches), unlogged = no logging performed.

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

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