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

Gustaf Granath[*a], Jari Kouki[b], Samuel Johnson[a], Osmo Heikkala[b], Antonio Rodríguez[b], Joachim Strengbom[a]

[a] Department of Ecology, Swedish University of agricultural Sciences, box 7044, SE-750 07 Uppsala, Sweden.

[b] School of Forest Sciences, University of Eastern Finland, PO Box 111, FI-80101 Joensuu, Finland.

*Corresponding author: gustaf.granath@gmail.com, +46732032176

Abstract

1. Green tree retention and prescribed burning are practices used to mitigate negative effects of boreal forestry. Beside their effects on biodiversity, these practices should also promote non-timber forest products (NTFPs). We assessed: **(1)** how prescribed burning and tree retention influence NTFPs by examining production of bilberry *Vaccinium myrtillus* and cowberry; *Vaccinium vitis-idaea* **(2)** if there are synergies or trade-offs in the delivery of these NTFPs in relation to delivery of species richness, focusing on five groups of forest dwelling species.

1. We used a long-term experiment located in eastern Finland with three different harvesting treatments: clearcut-logging, logging with retention patches and unlogged, which were combined with or without prescribed burning. Eleven years after the treatment application, we scored plant cover and berry production in different microhabitats within these treatments, while species richness data for five species groups (ground-layer lichens and bryophytes, vascular plants, saproxylic beetles, pollinators – here bees and hoverflies) were collected at the stand level.

2. Logging favoured cowberry production, particularly for plants growing in the vicinity of stumps. Logging was detrimental for cover and berry production of bilberry. Retention mitigated these negative effects slightly, but cover and berry production were still substantially lower compared to unlogged forests. Prescribed burning increased cowberry production in retention patches and in unlogged forest. Bilberry production decreased 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

Introduction

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

Leaving trees and snags during clearcut timber harvest, known as retention forestry, is employed to preserve legacies from previous generations of trees, and believed to be fundamental for maintaining biodiversity and function of forests (Franklin et al. 1997). Nowadays, practices that preserve or restore such legacies are used worldwide to facilitate multifunctional objectives in forestry (Gustafsson et al. 2012; Lindenmayer et al. 2012), and considered standard practice in Scandinavia (Gustafsson et al. 2010). Prescribed burning, although less widely used as a conservation measure, also aims at maintaining or emulating natural legacies lost during harvest operations in boreal forests (Heikkala et al. 2016). Efficient fire suppression has led to a lack of wildfires in parts of the boreal biome (Niklasson & Granström 2000; Wallenius et al. 2007), and prescribed burning is therefore, used to promote biodiversity by restoring the legacies from wildfires (Halme et al. 2013). In Fennoscandia, prescribed burning is part of the national forest conservational strategies and included in certification schemes such as Forest Steward Council (FSC) (Annon 2012, 2014). Although these two conservation measures are intended to promote a broad set of ecosystem services, including delivery of non-timber forest products (NTFPs) such as production of wild berries and mushrooms (Gustafsson et al. 2012), they have primarily been applied to support biodiversity (Gustafsson et al. 2010). This is also reflected in the literature on effects of retention forestry and prescribed burning, which is heavily biased towards the relationship between timber production and conservation of biodiversity (e.g. Halpern et al. 2012; Johnson et al. 2014; Fedrowitz et al. 2014). Only a few studies have examined effects related to ecosystem services (Lazaruk et al. 2005; Rodríguez & Kouki 2015, 2017), and to our knowledge, there are no previous studies examining the effects on NTFPs, or studies that have explored synergies and trade-offs among the different values that these conservation measures are expected to deliver.

Wild berries of boreal forests in Eurasia, mainly produced by the two ericaceous dwarf-shrubs bilberry (*Vaccinium myrtillus* L.) and cowberry (*Vaccinium vitis-idaea* L.), are highly valued NTFPs (Kangas 2001). In Finland, which has a forest cover of about 23 million ha, the annual yields can be as high as 312 million kg for bilberry and 386 million kg for cowberry (Turtiainen et al. 2011). Although the proportion of berries picked is rather low, 5-6% for bilberries and 8-10% for cowberries (Turtiainen et al. 2011), berry production still represents a large value. Estimating the economic value of these berries is complicated, as it will vary greatly depending on the proportion of berries picked and on the current market price. However, if forest management is adjusted to improve bilberry production, the revenue from bilberry production may exceed that of timber production, and the profitability of stand management may potentially be doubled (Miina et al. 2010). In addition to this provisioning service, berry picking also constitutes a highly-valued cultural ecosystem service (Pouta et al. 2006). Finally, these dwarf shrubs are also essential for many herbivores and omnivores (e.g. birds, voles, cervids, and invertebrates) and these species often form the basis of complex trophic networks in forests (e.g. Lakka & Kouki 2009). Despite the multitude of values that berry production represents, its response to forest management has so far received surprisingly little attention (Pohjanmies et al. 2017).

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

The aim of our study was two-fold: **firstly**, we wanted to investigate how two common conservational practices, prescribed burning and green tree retention, influence production of wild berries, and if the effects differ depending on type of microhabitat (near trees or on flat ground between trees). **Secondly**, we wanted to explore how these two measures influence multi-functionality by examining potential synergies and trade-offs between how these practices influence berry production (a NTFP) and biodiversity.

Materials and Methods

Study area

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

Prior to the experimental manipulations, all sites were covered with about 150 year-old coniferous forest of dry *Vaccinium–Empetrum* heath type. Scots pine (*Pinus sylvestris* L.) dominated the tree layer, with Norway spruce (*Picea abies* L. H. Karst) and birch species (*Betula pendula* R. and *B. pubescens* Ehrh.) as co-dominants. Pre-harvest living volume in the stands was on average 288 m^3 ha^{-1}. All sites had similar vegetational composition (Johnson et al. 2014) and overall high cover of bilberry (range among sites=32 to 64%) and cowberry (range among sites=18 to 51%). The experimental area has historically only been exposed to very low-intensity selective logging during the late 1800s and early 1900s, but no intensive modern forestry had been conducted at the experimental sites prior to the experiment (Hyvärinen et al. 2006).

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

Data collection

Density of berries and plant cover of the two species were scored in mid-July 2012 (for 2012 weather data see Table SA1). In 2012, berry yields were above the average in Finland (Kauko Salo, Natural Resources Institute Finland, Pers. Comm.). In our inventory, which coincided with the peak of berry production, we counted all berries growing on plants rooted within inventory frames sized 0.4 by 0.4 m. The frame was divided into 100 four by four cm grid cells, and cover was scored as the number of cells with the species present. Cover and berries were counted in two types of microhabitat, on flat ground and in the vicinity of a stump or a tree base (north and south-facing sides to make sampling consistent). In the treatments with full and no retention, we scored cover and berry density at 72 locations in each stand. We used a semi-systematic sampling design, with four transects evenly spaced and positioned in the central area of the stand, with nine randomly selected locations along each transect (see Fig. SA2 for an illustration and details). At each location, the nearest stump/tree base with a diameter greater than 20 cm (stumps/trees large enough to potentially create differences in microhabitat) was selected together with the corresponding flat ground that fulfilled the criteria of being a potential growth location for the species, i.e. wet micro sites and sites with bare rock were excluded. In the retention forestry treatment, we used a slightly different sampling design, so that both the retention patches and open areas were sampled. Inside the retention patches, we scored cover and berry densities at 20 randomly chosen tree bases and 20 locations with flat ground, fulfilling the same criteria as described above. In a similar way, we scored cover and berry densities in the vicinities of stumps and flat grounds outside the retention patch. We scored 40 stumps and 40 locations on flat ground in the area starting from the edge of the retention patch to c. 30 m away from the group, i.e. approximately the area within one tree-length from the retention patch (Fig. SA2).

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

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

Data analysis

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

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

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

Results

The unburned, unlogged sites in the study area had a similar cover of cowberry and bilberry (on average 28% and 42%, respectively), but berry yield was higher for bilberry than for cowberry (3 and 14 per per m^2, respectively). Mean berry production per site and treatment is presented in Figure 1 and Table SA2, while modeled effects are described below.

Cowberry

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

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

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

Bilberry

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

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

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

Non-timber forest products versus species richness

Trade-offs between effects on berry production and biodiversity were common (Table 1, see Supplementary information Table SA2 for species richness treatment means). Only bilberry production and beetle richness increased with tree retention or unlogged conditions, compared to logged stands (Table 1), and most variables indicated lower values compared to logging (cowberry production, pollinator richness, bryophyte richness, lichen richness). Burning combined with logging had no positive effects on the investigated variables, but decreased cowberry production and bryophyte richness. In contrast, burning combined with retention or unlogged treatments increased bilberry production, and richness for pollinators, beetles and lichens. The number of red-listed species were few and only found among pollinators and beetles: pollinators 1% (1 species), beetles 2.4% (7 species).

Discussion

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

Berry production

Logging and retention

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

In contrast to cowberry, bilberry was negatively influenced by logging with close to zero berry production in the logged stands, an effect largely driven by reduced cover. Reduced bilberry cover following logging is well known as bilberry is most common in mature mesic spruce (*Picea abies*) forest (Kardell 1980; Johnson et al. 2014), but the magnitude (95%) and the long-lasting effect (>10 yrs) observed in our study is in contrast to studies reporting small and transient effects of clearcutting on bilberry cover (Palviainen et al. 2005; Nielsen et al. 2007). Retention forestry partly mitigated the negative effect, but both cover and berry densities were still much lower than in unlogged stands. The limited effect of patches of trees may not be that surprising, as the size of the retention patches used in our experiment have been shown to be too small to efficiently retain the overall pre-logging composition of the ground vegetation (Johnson et al. 2014). However, the negative effect of logging found inside the retention patches was unexpected, as the more open conditions in these patches should favour bilberry. For example, production of bilberries should be highest when tree canopy cover is in the range of 10 to 50% (Raatikainen et al. 1984), and thus selective logging is suggested as an alternative to clearcutting due to its capacity to preserve high cover of bilberry (Atlegrim & Sjöberg 1996). Possibly, the negative effect on bilberries is due to strong edge effects, resulting in a micro climate that is too dry for bilberry in the entire retention patch.

Prescribed burning and retention

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

Implications for multi-use forestry

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

A similar inconsistent response pattern was also observed in the unlogged forest. Here, prescribed burning increased cowberry production and species richness of pollinators, beetles and lichens, while richness of vascular plants decreased. Moreover, our results support earlier studies that the conservational value of prescribed burning can be higher if performed in combination with retention forestry, or in unlogged forests (e.g. Hyvärinen et al.2006; Halme et al. 2013, Heikkala et al. 2014, 2016, Rodríguez & Kouki 2017). However, the multi-functional benefits from prescribed burning can, with respect to these aspects, vary highly depending on species groups included, and positive effects that are valid for all measured variables cannot be warranted. The high variation in response among species groups can be related to differences in habitat requirements, but also to differences in life history traits, such as generation time, reproductive strategy and dispersal capacity. Trade-offs in such traits are largely reflected in the variation of responses to the management treatment. For example, it is not surprising that most boreal bryophytes (tolerant to low light and nutrient conditions) are not favoured by the more severe burning in logged and retention treatments (de Grandpre et al. 1993). Additionally, species richness as such, is only one biodiversity target in managed multi-functional forests. In fact, preservation of specific rare or threatened species, may be a more common objective. For example, dead-wood-associated fungi (highly threatened), are favoured by the conservation measures included in our study (Suominen et al. 2015).

Multi-use management of forests aims to reduce the ecological impact of high-intensive land-use, while still providing resources for humans, and it is gaining increased appreciation (e.g. Bennett et al. 2009: Lindenmayer et al. 2012; Gamfeldt et al. 2013). However, given the multitude of services that forests can provide, it is not unexpected that all targets cannot be reached simultaneously at each site. In fact, altering stand and landscape structure and heterogeneity can have opposing effects on target values as shown here, as well as in agricultural ecosystems (Power 2010). Methods that balance the delivery of different values, to achieve highest delivery of ecosystem goods and services, have been suggested as a way to maximize the simultaneous delivery of a broad set of values (Bradford and D'Amato 2012). Such methods could be used to develop management practices that optimize the delivery of the values included in our study. However, due to the clear trade-offs among values, such optimization will undoubtedly also imply that the values delivered will be far from their full potential, which may be considered a sub-optimization. Instead of aiming at increasing the multi-use delivery of all values by standardized conservational practices (common in Fennoscandia), we suggest a strategy that uses well-defined site and landscape specific management objectives, aiming to optimize the multi-use delivery at the landscape-scale rather than at the site level. This is similar to the suggestions by Raudsepp-Hearne et al. (2010) that correlated services (or values) can be managed together in “bundles”, and different areas of the landscape are then dedicated to specific “bundles” to achieve multifunctionality at a larger scale. Such strategy will require more planning that combines stand- and landscape-scale perspectives – an approach that can be challenging to implement in areas with many small land-owners. However, if this strategy increases the overall positive response of the targeted values at a larger scale, then the total cost per area needed to fulfill the conservational objectives for all values may be relatively small. Also, given the spatial segregation of measures, the costs should be smaller than when applying a uniform or standardized management strategy at all sites.

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

Acknowledgments

We thank Finnish Forest and Park Service (Metsähallitus) for providing the study forests and for their considerable efforts and collaboration in creating the harvest and burning treatments during

2000-01. We also thank Mikko Heikura, Emelie Lager, Evelina Lindgren, Martin Kellner and Mar Ramos Sanz for their involvement in the field work. The initiation phase (1999-2003) of the study was funded by University of Eastern Finland and the Academy of Finland (through their Centre of Excellence Programme), Finnish Forest and Park Service (Metsähallitus), Finnish Forest Research Institute, Ministry of Environment and Ministry of Agriculture and Forestry (all grants to JK). Economic support was also given by the Swedish Research Council FORMAS.

Data accessibility

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

References

Annon. 2012. Finlands FSC-standard. Finlands FSC-organisation. In Swedish.

Annon. 2014. Svensk skogsbruksstandard enligt FSC med SLIMF-indikatorer. FSC-STD-SWE-02-02-2010 SW. Svenska FSC. In Swedish.

Atlegrim O, Sjöberg K. 1996. Response of bilberry (*Vaccinium myrtillus*) to clear-cutting and single-tree selection harvest in uneven-aged boreal *Picea abies* forests. Forest Ecology and Management 86:39–50.

Bennett EM, Peterson GD, Gordon LJ. 2009. Understanding relationships among multiple ecosystem services. Ecological Letter 12:1394–1404.

Bradford JB, D'Amato AWD. 2012. Recognizing trade-offs in multi-objective land management. Frontiers in Ecology and Environment 10:210–216.

Byrnes JEK, Gamfeldt L, Isbell F, Lefcheck JS, Griffin JN, Hector A, Cardinale BJ, Hooper DU, Dee LE, Emmett Duffy J. 2014. Investigating the relationship between biodiversity and ecosystem multifunctionality: challenges and solutions. Methods in Ecology and Evolution 5: 111–124.

Fedrowitz K, Koricheva J, Baker SC, et al. 2014. Can retention forestry help conserve biodiversity? A meta-analysis. Journal of Applied Ecology 51:1669–1679

Franklin JF, Berg DR, Thornburgh DA, Tappeiner JC. 1997. Alternative silvicultural approaches 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:10.2307/3235618Gustafsson 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.

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

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

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

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

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

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

Kardell L. 1980. Ocurrence and production of bilberry, lingonberry and raspberry in Swedens's forests. Forest Ecology and Management 2:285–298.

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

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

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

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

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

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

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

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

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

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

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

Raatikainen M, Rossi E, Huovinen J, Koskela M-L, Niemela M, Raatikainen T. 1984. The yields of the edible wild berries in Central Finland. Silva Fennica 18:199–219 (in Finnish with English summary).

Raudsepp-Hearne C, Peterson GD, Bennett EM. 2010. Ecosystem service bundles for analyzing tradeoffs in diverse landscapes. Proceedings of the National Academy of Sciences, 107: 5242-5247.

Rodríguez A, Kouki J. 2015. Emulating natural disturbance in forest management enhances pollination services for dominant Vaccinium shrubs in boreal pine-dominated forests. Forest Ecology and Management 350:1–12.

Rodríguez A, Kouki J. 2017. Disturbance-mediated heterogeneity drives pollinator diversity in boreal managed forest ecosystems. Ecological Applications, in press doi: 10.1002/eap.1468

Schimmel J, Granström A. 1996. Fire severity and vegetation response in the boreal Swedish forest. Ecology 77:1436–1450.

Strengbom J, Axelsson EP, Lundmark T, Nordin A. Trade-offs in the multi-use potential of managed Boreal forests. Journal of Applied Ecology. DOI: 10.1111/1365-2664.13019

Suominen M, Junninen K, Heikkala O, Kouki J. 2015. Combined effects of retention forestry and prescribed burning on polypore fungi. Journal of Applied Ecology 52:1001-1008

Turtiainen M, Salo K, Saastamoinen O. 2011. Variation of yield and utilization of bilberries (*Vaccinium mytrillus* L.) and cowberries (*V. vitis-idaea* L.) in Finland. Silva Fennica 45:237–251.

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

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

Unburned logged	**Values (% change)**						
	Berry production		Species richness				
vs.	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)

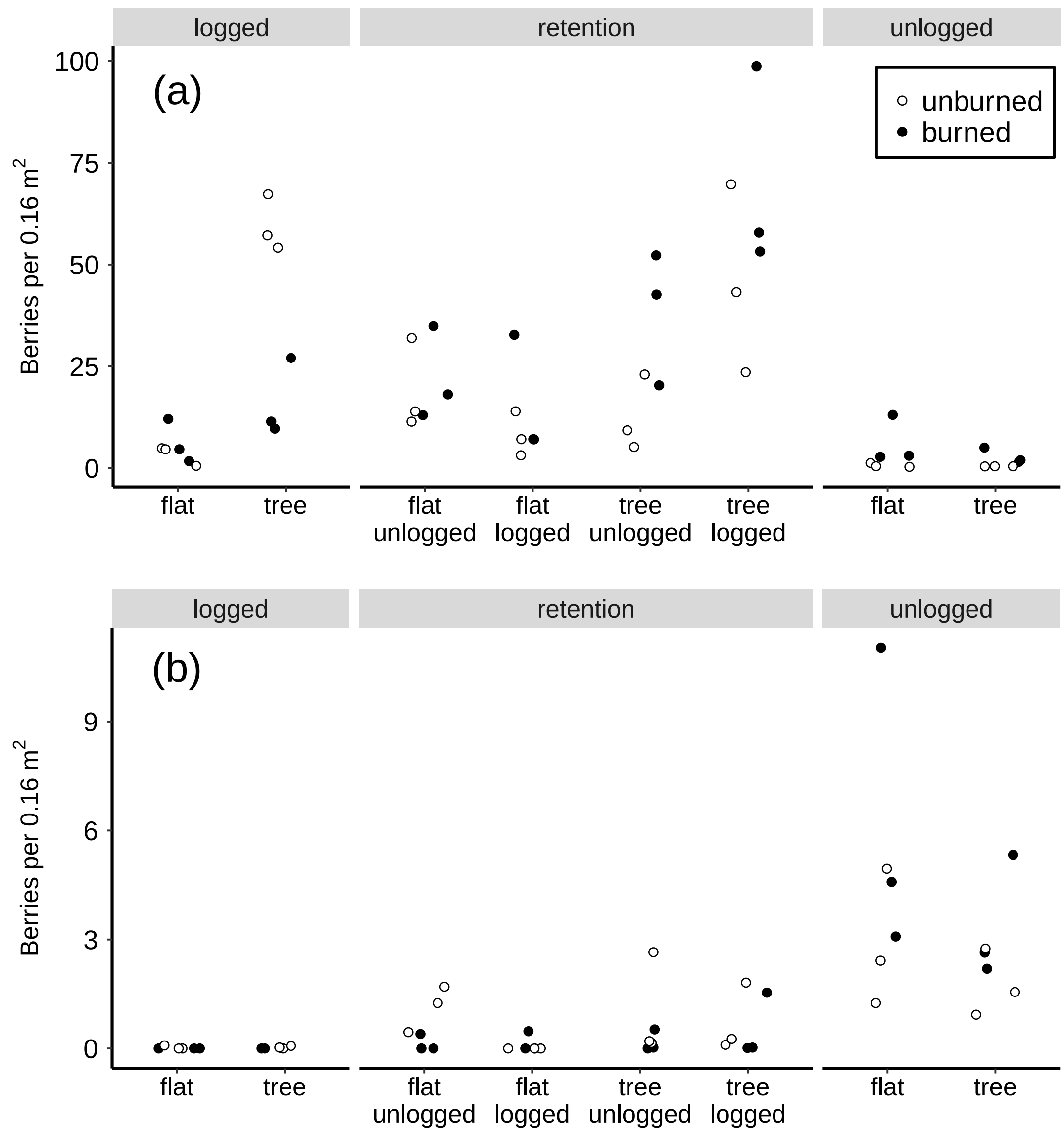

Figure 1. Raw means of berries produced for all replicates (i.e. sites) and each treatment combination. a) Cowberry and b) bilberry. Points are spread out around each treatment for better visualization. Note the different scales on the y-axes. Logged = all trees removed, Retention = logged with groups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

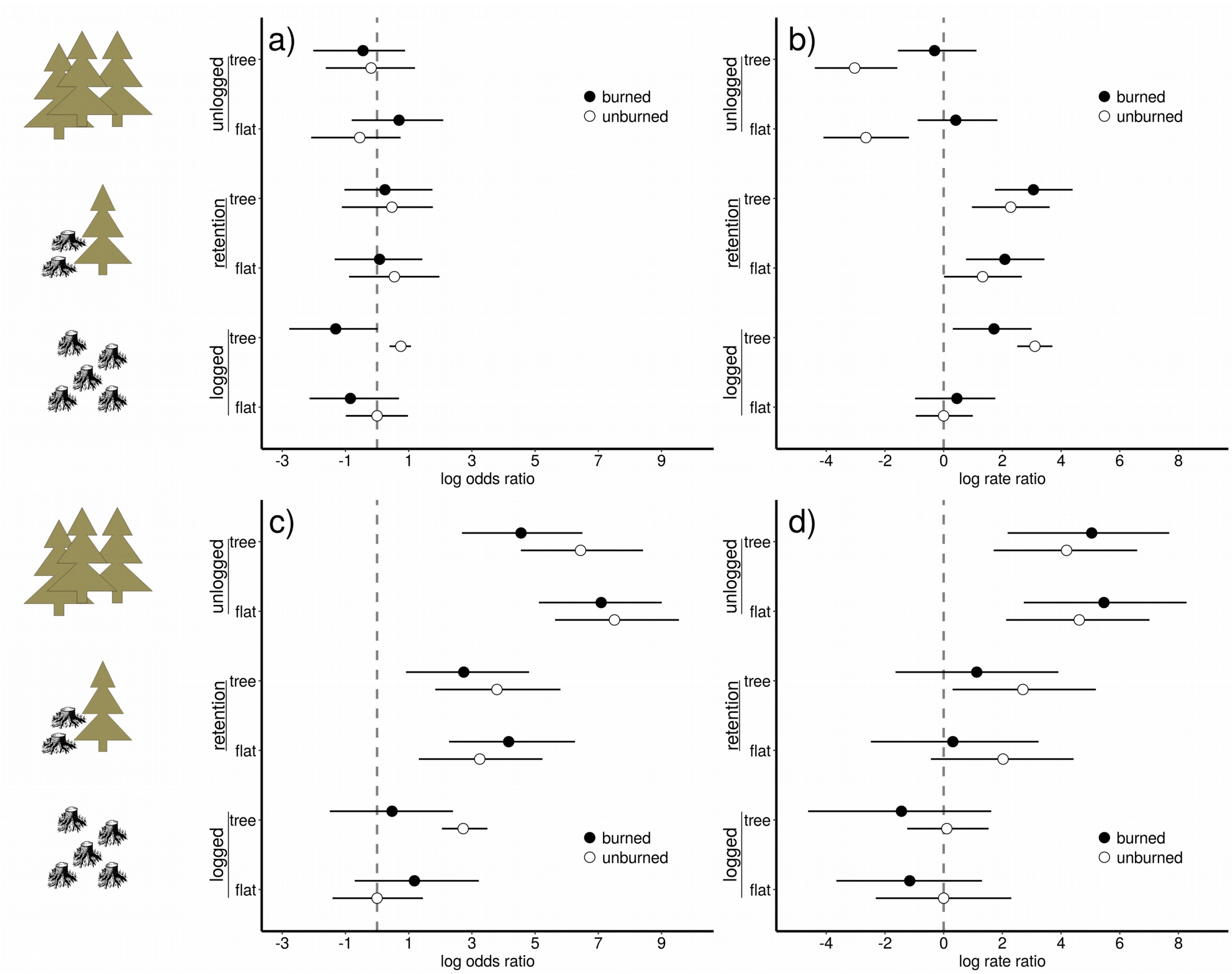

Figure 2. Effect plots of plant cover (a,c) and berry production (b, d) for, cowberry (a,b), and bilberry (c, d). Flat ground (flat), unburned, logged is set as reference treatment. Images on the left illustrate the treatments. Error bars are 95% credible intervals and individual contrasts between treatments 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.

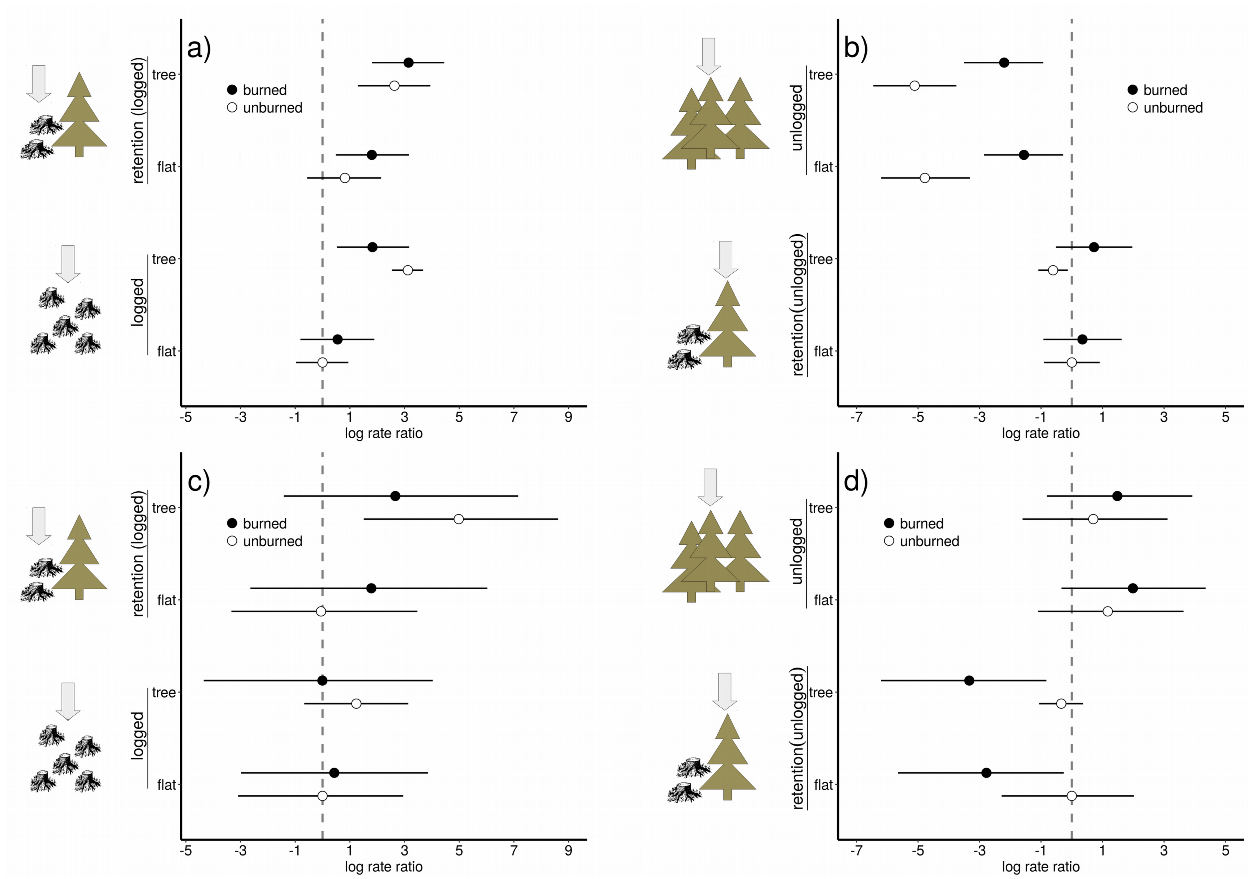

Figure 3. Effect plots of berry production for, a,b) cowberry, and c,d) bilberry. Panel (a) and (c) compare the logged treatment (i.e., clearcut) with logged areas in the retention treatment (retention-L). Panel (b) and (d) compare unlogged patches in the retention treatment (retention-U) with unlogged 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.