Retention forestry and prescribed burning result in functionally different saproxylic beetle assemblages than clear-cutting

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Abstract
In fire-susceptible boreal forests, clear-cutting has been justified as being a harvesting regime that mimics natural stand-replacing dynamics, despite obvious differences in its biological legacies. Prescribed burning and retention forestry are commonly applied to better maintain naturally occurring legacies, but the community-level effects of different disturbances on the functional characteristics of biota remains still largely unknown. In this study, we investigated the effects of prescribed fire, clear-cutting and retention forestry on the functional properties of saproxylic beetle assemblages in Eastern Finland, using stand-level data from a before-after field experiment with four levels of tree retention (0, 10 and 50 m³ ha⁻¹ and control) and prescribed burning. We analyzed the functional-phylogenetic diversity and a set of species traits that link species to resources. The data include 377 beetle species and 38549 individuals. Functional-phylogenetic diversity decreased from a random to a clustered pattern after burning and logging with retention trees, indicating environmental filtering of both processes. These effects became more pronounced with increasing logging intensity. Species-level traits that were favored by burning and tree retention were connected to open-habitat conditions and fresh dead wood, whereas clear-cutting revealed a random pattern without reference to specific resources. Our functional approach thus shows that clear-cutting does not mimic the dynamics of wildfire, but leads to different functional composition of species assemblages. Therefore, prescribed burning or wildfire should be incorporated and sufficient amount of trees retained in forest management to conserve functional processes and natural composition of saproxylic species assemblages in boreal forests.

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1. Introduction
Since the early-1900s, prevention of natural disturbances in forests has been efficient in many regions, and clear-cut harvesting has become the dominant stand-replacing forest disturbance. Although some authors have proposed clear-cutting as a harvesting system that closely mimics natural dynamics, particularly in boreal forests with fire-dominated, stand-replacing dynamics (Parviainen and Seppänen, 1994; Mielikäinen and Hynynen, 2003), several studies have documented major differences in biological legacies, e.g. dead trees, between natural stand-replacing disturbances and clear-cutting (e.g. Franklin et al., 2000; Kouki et al., 2001; Swanson et al., 2011). The loss and fragmentation of such biological legacies due to large-scale application of clear-cutting with accompanied planting or seeding, pre-commercial thinning and removal of damaged and dead trees in managed forests (Kouki et al., 2001; Swanson et al., 2011) have been identified as serious threats to biodiversity (Tikkanen et al., 2006; Rassi et al., 2010; Stokland et al., 2012; Anonymous, 2015). Moreover, biodiversity loss may seriously alter ecosystem functioning, in turn having profound consequences on critical ecosystem processes, such as decomposition rates of woody biomass or carbon and nutrient cycling (Hooper et al., 2012; Tilman et al., 2014).

To counter these negative impacts, forest management has begun to adopt new techniques that are believed to complement rare habitat types and support threatened species, such as prescribed burning and green-tree retention. Burning supports species associated with charred or dead wood and early-successional habitats (e.g. Hyvärinen et al., 2009; Johnson et al., 2014), while green-tree retention – commonly known as retention forestry – has been
developed as a universal concept of mitigation and has been proposed as a means to sustain continuities of ecosystem structures, functioning, and species composition in post-harvest forests (Franklin et al., 1997; Gustafsson et al., 2012; Lindenmayer et al., 2012; Fedrowitz et al., 2014). Prescribed burning and retention forestry target particularly the conservation of saproxylic species, i.e., species directly or indirectly dependent on dead or dying wood, as both methods directly (fire) or indirectly (retention forestry) contribute to the amount and continuity of large-sized dying and dead wood (Heikala et al., 2014). Positive effects of prescribed burning have been shown for pyrophilous and saproxylic species if the amount of burned wood is sufficiently high (e.g. Wikars, 1997). The potential positive effects of retention trees for saproxylic species include, e.g., maintaining the quality of coarse woody debris through a sheltering effect against extreme wind, sunlight, temperature and moisture variation (e.g. Barnes et al., 1997); increasing dead wood by wind-caused falls and deaths of retention trees (Hautala and Vanha-Majamaa, 2006; Heikala et al., 2014); and by allowing retention trees to become old and senescent (Hautala et al., 2004; Widerberg et al., 2012). Moreover, both fire and harvesting modify habitat conditions and the quality of dead wood regarding, e.g., sun-exposure or decay stage, and thus affect the available niche space for saproxylic species (Azeria et al., 2012; Mouillot et al., 2013).

Among saproxylic taxa, beetles comprise a large portion of biodiversity and contribute significantly to ecosystem functioning through the decomposition of wood (Schowalter, 1992; Angers et al., 2012; Jacobs and Work, 2012; Ulyshen, 2014) and thus by promoting post-disturbance recovery of vegetation (Cobb et al., 2010). However, due to the shortage of dead wood in Fennoscandian managed, clear-cut originated forests, hundreds of beetle species are threatened today (Rassi et al., 2010; Anonymous, 2015). Earlier research on saproxylic organisms and beetles in particular have demonstrated strong impacts of prescribed burning, clear-cutting and retention forestry on their richness and species-specific abundances (e.g. Hyvärinen et al., 2005; Saint-Germain et al., 2005; Boucher et al., 2012). These analyses have revealed higher abundance of threatened and pyrophilous species at stands subject to prescribed burning or retention forestry than at clear-cut stands (Hyvärinen et al., 2006b). Furthermore, community analyses, based on species occurrences, have indicated that these differences may be accompanied by changes in the assemblage composition (Saint-Germain et al., 2004; Hyvärinen et al., 2005; Cobb et al., 2011). While these sorts of evaluations coarsely reveal treatment-caused assemblage shifts, they do not directly provide information on the driving mechanisms behind these changes. Such information can be obtained, however, through an approach that links species traits to forestry-caused structural changes in forests. These sorts of approaches are rapidly gaining appreciation in conservation where the paradigm is shifting from focusing on single rare species to complete communities (Devictor et al., 2010; Cadotte et al., 2011). To meet this claim for forest conservation, it is crucial to understand how forest management strategies affect the functional structure of species assemblages (Gossner et al., 2013; Bässler et al., 2014; Seibold et al., 2015).

In the present paper we apply a functional-phylogenetic approach (Cadotte et al., 2013) based on two biological traits and four traits that describe required resources to evaluate effects of fire and logging on the functional composition of saproxylic beetle assemblages. While we acknowledge that not all traits studied here are functional, they nevertheless link species to the impacts of forestry on habitat conditions, particularly related to dead wood and microclimate (Gossner et al., 2013; Thorn et al., 2014; Seibold et al., 2015). Our data originate from a large-scale, replicated field experiment conducted in the boreal zone of Eastern Finland. The experiment represents a stand-level, before-after-control-impact design with prescribed fire and four levels of harvesting intensity, including clear-cutting, two levels of tree retention and an unlogged control.

We expected that prescribed fire and logging would cause environmental filtering by selecting specific traits that allow to cope with habitat conditions resulting from treatments and thus lead to a reduction in the total trait diversity of the local community (Azeria et al., 2012; Mouillot et al., 2013). Specifically, we put forward the following hypotheses regarding single traits. Prescribed burning should favor species that (1) require large pieces of dead wood objects and (2) are large bodied, as fire produces vast quantities of large snags and logs (Siitonen, 2001) and large species cannot occupy very small pieces of wood. With increasing harvesting intensity, we predicted a decrease in species that (3) require large dead-wood objects and (4) are large, as their required resources are removed and small-sized logging residues are produced in harvesting operations (Hautala et al., 2004). Moreover, increasing logging intensity should favor species that benefit from (5) well-illuminated conditions and (6) the logging-caused increase in the diversity of flowering plants (Jalonen and Vanha-Majama, 2001; Pykälä, 2004; Johnson et al., 2014). Finally, (7) specialists that reproduce on fresh dead wood and other substrates that are formed in fires and logging operations should increase with prescribed burning and increasing logging intensity (e.g. Moretti et al., 2010).

2. Methods

2.1. Study area and experimental design

The study area was located in the municipalities of Lieksa and Ilomantsi in Eastern Finland (63°10’N, 30°40’E), in the southern part of the middle-boreal vegetation zone (Ahti et al., 1968). A total of 24 stands, each 3–5 ha, were randomly assigned to an area of 20 km × 30 km (Appendix A, Fig. A1). These stands were Scots pine (Pinus sylvestris L.) dominated forests with dominant canopy trees being approximately 150 years old, and had not been subject to intensive forestry previously. Pre-treatment conditions of the stands are described in Hyvärinen et al. (2005).

The experiment was set up as a two-factorial design, combining prescribed burning and four levels of harvesting; clear-cutting, 10 and 50 m² ha⁻¹ retention, and unharvested control, and followed the before-after-control-impact (BACI) principle (Green, 1979). Each harvesting treatment was replicated six times and half of them were subsequently burned. The stands were harvested during the winter of 2000/2001 and burning was conducted during two consecutive days in late June 2001: for details, see Hyvärinen et al. (2005). Retained trees were mostly left in circular groups of 15–30 m in diameter. The retention level of 10 m² ha⁻¹ was chosen so as to be comparable (albeit slightly higher) with current guidelines and industry-certification regulations in Fennoscandia. The higher retention level, 50 m² ha⁻¹, was chosen so as to roughly correspond with the dead-wood volume that can maintain the diversity of saproxylic beetles in mature forests (Martikainen et al., 2000).

2.2. Beetle sampling

We sampled beetle communities in the years 2000 and 2002, i.e., one year before and one year after the treatments. As we were interested in beetle assemblages at the stand level, we used flight-interception traps that efficiently reflect beetle diversity at the stand level (Wikars et al., 2005; Hyvärinen et al., 2006a; Sverdrup-Thygeson and Birkemoe, 2008). We used a total of 240 traps (ten per stand) in each study year from mid-May to early
September. We pooled the samples over each stand and year, which resulted in a total of 48 community samples. A photo of a trap used in this study can be found in Hyvärinen et al. (2006a).

2.3. Trait characterization and phylogeny

We collected a total of 377 species (38,549 individuals), for which we used the phylogeny and six traits described in Seibold et al. (2015): (1) body size; (2) association with particular trunk diameter (snag or log size, hereafter referred to as wood diameter niche); (3) association with particular decay stage (decay niche); (4) association with particular level of canopy cover (canopy niche); (5) adult habit for visiting flowers (flower visiting); and (6) larval foraging strategy (foraging strategy). First four traits were numerical, but last two (5–6) categorical variables. For each species, mean niche positions for traits 2–4 were calculated with weighting scores according to their frequency in occurrence in ordered classes of the traits: wood-diameter classes ranging from 1 to 4 (<15 cm, 15–35 cm, 35–70 cm, >70 cm), decay stage from 0 to 4 (alive, freshly dead, initiated, extremely decomposed) and canopy cover from 1 to 3 (open, semi-open, closed) (For details, see Gossner et al., 2013; Seibold et al., 2015). Flower visiting of species was defined as being either yes (=1) or no (=0). The larval foraging strategy comprised the following categories: (1) early-stage xylophagous, (ii) late-stage xylophagous, (iii) mycetophagous, (iv) detrivorous and (v) predatory. Seibold et al. (2015) did not differentiate between early-stage xylophagous (colonization starts typically within the first year after tree die-off) and late-stage xylophagous species, hence we followed Schmidl and Bussler (2004) for this characteristic. The sub-category detrivorous was excluded from analysis due to low number of specimens. We categorized a low number of species (9) not classified by Seibold et al. (2015) using our own field observations and other experience on these species. See supplementary material (Appendix B) for the classification of each species.

2.4. Data analysis

We conducted all analyses in R version 2.15.0 (R Development Core Team, 2011). Phylogeny may provide additional or even complementary information to functional traits and thus, we applied a recently proposed approach to combine functional and phylogenetic information (Cadotte et al., 2013). We calculated functional (F) and phylogenetic (P) distance matrices as mean pairwise distances between co-occurring species for each sample, based on either the branch lengths of a phylogenetic tree or a Gower distance of functional traits. These distance matrices were combined to 41 matrices of mean functional-phylogenetic distance (MFPD) with varying contribution of F and P using the function FPDist in the R add-on package funphylocom. The contribution of F and P to MFPD is determined by the weighting parameter (a). When a = 0, MFPD only includes functional distances and when a = 1, MFPD only includes phylogenetic distances. At intermediate values of a, both functional and phylogenetic distances contribute to MFPD. We calculated MFPD for 41 levels of a from 0 to 1 by increasing a in steps of 0.025.

To gain independence from the number of species per sample, we calculated standardized effect sizes for each MFPD matrix (Laliberte and Legendre, 2010; Mouillot et al., 2013) by comparing the observed MFPD value of each community with the MFPD value of an equal number of randomly selected species from the regional species pool (all species recorded in this study). This was achieved by using null models with 999 randomizations by tip shuffling (Webb et al., 2002) using the R function ses.mpd in the add-on package picante (Kembel and Hubbell, 2006). Obtained effect-size values >0 indicate over-dispersion resulting from competition or facilitation, whereas values <0 indicate clustering, which in turn is a sign of environmental filtering (Pausas and Verdú, 2010). Finally, we calculated the abundance-weighted mean and the standardized effect size of diversity of each of the four numerical traits (i.e. excluding the two categorically measured traits) for each assemblage.

To evaluate the effects of prescribed fire and logging treatments on the effect size of MFPD as well as on the community mean and diversity of the numerical traits, we calculated linear models using the function lm. We tested the effect of the treatments on the abundance of species specific for each category of the trait foraging strategy in a Poisson generalized linear mixed model with stand as a random variable using the function glm.r in the R add-on package lm4. In both approaches, we set the data of the pretreatment year 2000 as a baseline to compare treatment effects and to account for initial differences between study stands. In the models, we tested the effect of fire as a binomial variable (burned/unburned), the effect of the three harvesting levels (0, 10 or 50 m³ ha⁻¹) compared to the unharvested stands and the interaction of both variables.

3. Results

3.1. Functional-phylogenetic diversity of the assemblages

Our successive consideration of phylogenetic distance in the combined measure of phylogenetic and functional diversity, based on 41 models that tested the effect of fire and tree retention, revealed a unimodal curve in which the adjusted $R^2$ reached its maximum ($\bar{R}_{max}^2 = 0.64$; Fig. 1; Appendix A, Table A1) with values of 0.35 and 0.40. The $\bar{R}_{min}^2$ was lowest when only functional distances were considered ($\bar{R}_{min}^2 = 0.35$) and intermediate for phylogeny only ($\bar{R}_{min}^2 = 0.59$), indicating important species dissimilarity information in both distance matrices with respect to the assembly process. Our linear model of the standardized effect sizes of MFPD with highest $\bar{R}_{max}^2$ revealed independent effects of prescribed fire and logging (Fig. 2; Appendix A, Table A2). Fire decreased the standardized effect sizes of MFPD from a random to a clustered community pattern, indicating environmental filtering. Clear-cutting did not change the standardized effect size, thus suggesting a random pattern in these stands. The standardized effect size decreased with decreasing retention level, which also indicated environmental filtering. In addition, there was a positive interaction between fire and the 10 m³ ha⁻¹ retention, which indicates that burning alleviated the clustering effect of logging at this retention level.

3.2. Single functional traits

The mean body size of species was not affected by fire but it increased with decreasing retention level and after clear-cutting (Fig. 3; Appendix A, Table A2). To explore whether this was caused by a decline in small species and/or an increase in large species, we classified all species as “small”, “medium-sized” or “large” and compared their abundances and proportions (Appendix A, Fig. A2). To evaluate differences between treatments we modeled the share of small species in a binomial generalized model with amount of retention trees and fire as predictors including their interaction. This interaction was positive, thus we tested the effect of logging specifically for burned and unburned stands. The model revealed a stronger effect of logging at burned stands indicated by a higher z-value (Appendix A, Table A4). This suggests that logging
reduced the share of small species more strongly in burned than in unburned stands.

Mean niche positions in regard to decay stage and canopy cover decreased after fire and logging with tree retention but not after clear-cutting (Fig. 3). This finding suggests that species associated with well-illuminated conditions (i.e. open canopies) and those associated with fresh dead wood increased in burned stands and in harvested stands with retention trees but not in clear-cut stands. This effect was weaker for both traits when fire occurred in stands with 10 m$^3$ ha$^{-1}$ retention, as indicated by a significant and positive interaction term (Appendix A, Table A2).

Overall, the response to treatments was strongest for species foraging on fresh dead wood, followed by late-stage xylophagous, predatory and mycetophagous species. After fire, fresh-wood feeders increased strongly whereas predators and late-stage xylophagous species increased only slightly (Appendix A, Table A3). Clear-cutting increased both fresh-wood feeders and late-stage xylophagous species, although the effect of cutting was weaker than that of fire in the former. Harvesting with 50 m$^3$ ha$^{-1}$ retention favored both fresh-wood feeders and late-stage xylophagous species, while harvest decreased mycetophagous species. Burning of harvested stands decreased these effects. Mean wood-diameter niche and flower visiting were not affected by treatments, and neither were the diversities of single traits (Appendix A, Table A2).

4. Discussion

The present study provides a considerably deeper insight into the effects of logging and prescribed burning than previous papers that have focused on patterns of community variation and species richness (Hyvärinen et al., 2005, 2006b; Gustafsson et al., 2010; Azeria et al., 2012; Toivanen and Kotiaho, 2007). The novelty in the present study lies in analyzing functional characteristics of species assemblages, an approach that allows a considerably deeper understanding on mechanisms that drive assemblage changes caused by forestry. Our results support the hypothesis that fire – or prescribed burning – acts as an environmental filter for saproxylic beetle communities, in particular by favoring species associated with well-illuminated conditions and early decay stages. In contrast, clear-cutting resulted in random communities without clear resource specialization. This finding suggests that clear-cutting is accompanied not only by a loss of species, but by a general alteration of species assemblages with differing functional properties. Harvesting with tree retention caused clustering – more pronounced at lower retention levels, independent from fire – and favored large-bodied, light-associated and fresh-wood specialist species. Thus, beetle assemblages in stands with retention trees differed strongly from those of clear-cuts that offer only stumps and logging residuals. An interaction between fire and tree retention indicated that, at low retention levels, these effects were weaker when both measures had been applied.

4.1. Ecological effects of fire on the assembly of saproxylic beetles

Fire affects biotic assembly processes by killing most of the original insect populations (McCullough et al., 1998; Schowalter, 2012), hence enabling colonization by species that have evolved to rapidly colonize and utilize the new competition-free space found in the post-fire environment (Evans, 1966; Wikars, 1997; Schütz et al., 1999; Boulanger and Sirois, 2007). Several colonizing species, such as bark beetles, may occur with very high abundances. Some wood-consuming species, however, also survive fire, mostly inside large-diameter logs that protect them from extreme temperature (Ulyshen et al., 2010; Schowalter, 2012). Furthermore, fire releases new resources such as damaged and dead wood, changes the microclimate toward open and less shady conditions, and increases the range of food sources and reproduction substrates (Moretti et al., 2010). In our study stands, these effects likely resulted in species-rich but functionally and phylogenetically clumped communities that can cope with post-fire
conditions. As expected, the post-fire communities included many species that favor well-illuminated conditions and are able to reproduce under the new climatic conditions. Furthermore, the high immediate mortality rate of trees after fire – almost half of the trees died during burning (Heikkala et al., 2014) – caused a dominance in feeders of fresh dead wood and in specialists of early decay stages in the post-fire communities. The increased availability of prey, as a result of rapid colonization, was apparently followed by an increase in the population of predatory beetles. Fire also led to an increase in late-stage xylophagous species, possibly because in areas where fire is most intense, it damages phloem and cambium. Hence, fire opened niches for late-stage xylophagous species depending on xylem. Furthermore, fire might reveal old dead wood by burning humus and vegetation covering those trees.

4.2. Effects of logging and tree retention on the assembly of saproxylic beetles

Clear-cuts hosted strikingly different beetle assemblages in comparison to burned stands and harvested stands with retention trees. Although our measure of functional diversity did not differ between clear-cut and unharvested stands, their species compositions were different (see also Hyvärinen et al., 2005; Stenbacka et al., 2010). Species foraging on fresh dead wood increased only slightly on clear-cut stands, but increased more strongly on stands with retention trees, in comparison to unharvested stands. The data had been collected approximately one and half years after logging, when stumps and logging residues are often unsuitable for reproduction for most bark beetle species (Raffa et al., 1993). In clear-cuts, dead wood consists mostly of logs, stumps and logging...
residues resulting from regeneration harvesting, and new dead wood is no longer produced, whereas in retention stands, fire and wind-throws may prolong the accumulation of dead wood for several years after disturbance. Similarly, the light-association of species (mean canopy niche) was less affected in clear-cut stands than in stands with retention trees. This pattern resembles salvage-logged wind-throws with branches left on the forest floor. Such areas host fewer light-associated species than unsalvaged wind-throw plots where the branches remain attached to the trunks of dead trees (Thorn et al., 2014).

Many retention trees in our study stands had been wind-blown or had died standing soon after logging (Heikkala et al., 2014). Species that are associated with an open canopy and fresh wood, such as bark beetles, apparently took advantage of the newly emerged resources. Their response is a good example of environmental filtering. This effect was stronger when fewer trees were retained, which indicates that at higher retention levels, there is a broader spectrum of resources and, potentially, a structurally more complex stand, in comparison to the pre-harvest stands. For example, late-stage xylophagous species continued to increase after cutting at the 50 m² ha⁻¹ retention but not at the 10 m² ha⁻¹ level. Similarly, mycetophagous species decreased only in stands with 10 m² ha⁻¹ retention.

Interaction between fire and logging in models of functional-phylogenetic diversity and several single traits suggests that the effects of these two were weaker when both treatments were applied simultaneously. Indeed, the fewer trees are retained, the fewer trees can be killed by fire. In these treatments, the dead wood mostly consisted of logging residues and stumps, which are more likely to be exposed to high temperatures and thus more readily consumed by fire: in our study, prescribed burning was conducted mostly as ground fire and did not reach the canopies (Hyvärinen et al., 2005).

In contrast to our expectation, the mean body size of beetles increased with harvesting intensity, apparently mostly due to a decline in the share of small species as the abundance of medium-sized species increased more than that of small species after harvesting (Fig. A2). Small species increased in abundance after all logging treatments but this effect decreased with increasing logging intensity. This finding may have resulted from post-harvest resources being less abundant for small than for large species and that fire further reduced the amount of substrates, particularly for small species. Although the diameter niche and body size are generally not correlated, most large species require large dead-wood objects for larval development (Bussler et al., 2011). Such species could, therefore, at least partly develop in stumps which, in comparison to branches and other residues, were less severely affected by the fire due to their larger size. Furthermore, as the total cut-face area of stumps was greater than that of residues, they could have emitted more olfactory cues and consequently attracted more species (Tilles et al., 1986). Small species in contrast include specialists for both trunks and branches. More branches are probably transferred to the ground when the intensity of harvesting is increased. This can result in changes in microclimatic conditions (e.g. altered shading and humidity for ground-lying branches) and may have decreased the suitability of this substrate (Thorn et al., 2014). Moreover, exposure to fire was more severe when more residues were present, reducing probably further the amount of substrates typically consumed by small-sized species.

The early-successional species assemblages can have long-term founder effects that determine future assembly processes (Weslien et al., 2011). However, initial differences may also converge over time (Hobson and Schieck, 1999). Therefore, long-term studies that evaluate the longevity of the effects of fire and harvesting on saproxylic beetle communities are crucial and should follow the assembly over the full decay process, particularly during the early successional phases. An analysis of the turnover rate of retention trees has shown that when few trees are retained, the number of live trees quickly reach zero while at higher retention levels trees die at a slower rate and therefore provide continuous rather than ephemeral supply of dead-wood substrates (Heikkala et al., 2014). When stands with low retention levels are additionally burned, the die-off process of trees is accelerated and the benefits for saproxylics can be very short-term.

5. Conclusions and applications

Several earlier studies have demonstrated that saproxylic beetle communities in forest stands subject to fire, retention forestry or clear cutting differ in terms of species richness, particularly red-listed and pyrophilous ones (Saint-Germain et al., 2004; Hyvärinen et al., 2006b, 2009; Toivanen and Kotiaho, 2007). This study revealed that these differences are accompanied by strong shifts in the functional composition, with possible consequences to ecosystem functioning. The functional analyses provided new insights into the mechanisms driving these assembly processes. Fire and retention forestry independently cause environmental filtering and result in non-random communities of saproxylic beetles, and this effect increases with decreasing retention level. Sunlit conditions and drying and freshly dead trees after prescribed fire and tree retention promote species associated with light and early decay stages. Large species benefit more from the dead wood created by a combination of logging and burning than small species. Dead wood substrates produced by clear-cutting, basically logging residues and stumps, host functionally randomized communities of saproxylic beetles which differ from those after prescribed fire or retention forestry. This indicates that clear-cutting does not mimic the dynamics of fire. Instead, prescribed burning should be applied in selected stands to support the landscape-level continuity of early-successional habitats and specific saproxylic communities, particularly in regions where wildfires are scarce. In addition, retention forestry appears to be contributing efficiently to conserving a high functional diversity of saproxylic beetle species at the landscape scale.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2015.09.043.

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