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ORIGINAL PAPER

Mimicking natural disturbances of boreal forests: the effects of controlled burning and creating dead wood on beetle diversity

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Abstract The young successional stages of boreal forests are an important habitat for many saproxylic species. These habitats are formed by disturbances such as forest fires and they are characterized by large volumes of dead wood and sun-exposed conditions. Today, young successional stages of natural origin are very rare in Fennoscandia and there is need for restoration. We constructed a large-scale field experiment in which we studied the effects of two restoration practices on beetle diversity: controlled burning and partial harvesting with creating different volumes of dead wood. We sampled beetles with flight-intercept traps recording a total of 56,031 individuals and 755 species. The species richness and abundance of both saproxylic and non-saproxylic beetles were increased by burning and harvesting but the volume of dead wood created on harvested sites had no short-term effect on species richness or abundance. Rare species, especially saproxylic ones, preferred burned sites and a similar trend was observed among red-listed and pyrophilous species. Burning and harvesting also resulted in different species assemblages and there were some additional differences according to the volume of dead wood. We conclude that fire can be successfully used in restoration of managed boreal forests to increase species diversity and to facilitate the recovery of declined species. However, long-term monitoring is needed to clarify the effects of the restoration practices, in particular those of creating dead wood without using fire.

Keywords Coleoptera · Decaying wood · Forest fire · Restoration · Saproxylic species

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Introduction

Human impact, especially the introduction of modern forestry, has greatly altered the boreal forest ecosystem during the last century (Esseen et al. 1997; Östlund et al. 1997). In addition to the loss of old-growth forest and fragmentation at landscape level (Kouki et al. 2001), fundamental changes have taken place in disturbance dynamics (Attiwill 1994; Kuuluvainen 2002). For example, forest fires have been almost totally excluded and the volume of dead wood in managed forests has been reduced to a small fraction of that in unmanaged forests (Siitonen 2001; Rouvinen et al. 2002). In Fennoscandia, of the 19,000 forest-dwelling species at least 4,000 are associated to dead-wood habitats (Siitonen 2001). These saproxylic species are dependent on dead or dying wood, on wood-decaying fungi or on the presence of another saproxylic organism during some part of their life cycle (Speight 1989). Because of the decline in the availability of decaying wood, the populations of saproxylic species have been adversely affected (Grove 2002). In Finland alone, there are 183 threatened or extinct beetle species associated to forests, of which 112 have been primarily affected by the loss of dead wood (Rassi et al. 2001).

In conservation of boreal forests, the focus has traditionally been in preservation of old-growth patches. However, the role of young successional stages as a habitat for many threatened species has recently been emphasized in several studies (Kaila et al. 1997; Jonsell et al. 1998; Martikainen 2001; Sverdrup-Thygeson and Ims 2002; Similä et al. 2002). Today, these habitats of natural origin are virtually absent from Fennoscandia. Human-caused disturbances, such as clear-cutting, create habitats that may be superficially similar to habitats formed by natural disturbances but the ecological effects of these disturbances may be substantially different (Niemelä 1999). In particular, clear-cuts differ from natural disturbance areas in terms of quality and quantity of dead wood (Pedlar et al. 2002; Sippola et al. 2002) thus offering less resources for saproxylic species. Retained snags and logs on harvested areas increase the abundance of habitats for saproxylic organisms (Kaila et al. 1997; Jonsell and Weslien 2003; Jonsell et al. 2004), and leaving small volumes of retention trees on clear-cuts is currently a recommended practice in Finland (Anonym 2001). However, in order to create habitats that more closely resemble natural disturbance areas, restoration practices have been designed to mimic the natural processes.

Forest fires are generally regarded as a major disturbance of unmanaged boreal coniferous forests (Wein and McLean 1983; Esseen et al. 1997). Natural fires enhance spatial heterogeneity of forests (Niklasson and Granström 2000), remould age structure and species composition of trees (Zackrisson 1977; Niklasson and Drakenberg 2001), and provide dead wood for several decades (Siitonen 2001). In Fennoscandia, an average fire interval of 50–120 years during the last thousand years is generally accepted (e.g. Zackrisson 1977; Engelmark 1984; Niklasson and Granström 2000; Wallenius et al. 2004). However, human activities, for example slash-and-burn cultivation, have increased the number of fires during past centuries and the natural fire interval before any significant human impact may actually have been a few hundreds of years (Pitkänen et al. 2003; Wallenius et al. 2004). In addition, there has been much variation in fire frequency depending on latitude and forest type. The density of lightning-ignited fires decreases from south to north (Granström 1993; Larjavaara et al. 2005), implying that fires have occurred less frequently in the northern boreal zone. In spruce-dominated forests, the fire rotation time has been considerably longer than in pine forests (Zackrisson 1977; Engelmark 1987; Wallenius 2002).

During the first years after forest fire, large volumes of decaying wood are available in sun-exposed conditions and this stage is assumed to be particularly important for saproxylic organisms (Kouki et al. 2001; Siitonen 2001). The increase in the abundance of most saproxylic beetle groups after fire has been documented by Muona and Rutanen (1994) and Hyvärinen et al. (2005). Particularly, the burnt areas are preferred by many rare or threatened beetle species (Ahnlund and Lindhe 1992; Similä et al. 2002; Hyvärinen et al. 2005). Some of these species, traditionally assumed to require old-growth forest, may actually be true specialists of open disturbance areas (Siitonen 2001). In addition, approximately 30 species of insects in Fennoscandia are considered to be strictly dependent on forest fires (Wikars 1997). These species are often characterized by strong dispersal abilities and adaptations enabling them to find fires very effectively (e.g. Evans 1966) but they are usually able to survive at the burnt area for a few years only.

The objective of restoration is to rehabilitate natural structures, processes and species composition in ecosystems altered by human actions (Bradshaw 1997). For any successful restoration or conservation effort, it is vital to be able to predict the changes in species richness or in species assemblages. In contemporary restoration of boreal forests, both controlled burning and increasing the volume of dead wood are common practices. Restoration, in particular controlled burning, is not cheap and for example in Finland millions of Euros has been spent on these actions. Despite the fact that several studies have implied that clear benefits can be expected, there is a lack of controlled experiments systematically investigating the effects of restoration. For example, the general effect of fire on species assemblages is still inadequately known and the relative importance of fire compared to other restoration practices, creating dead wood in particular, is poorly understood.

Here, we present the results of a large-scale field experiment in which we included both burning and creating different volumes of decaying wood on harvested sites. The main aims of the study were (1) to determine how burning and increasing the volume of dead wood affect the overall beetle diversity and species assemblages, (2) to study the effects of these restoration practices on the occurrence of saproxylic, rare or red-listed beetle species and (3) to evaluate whether the restoration practices are useful in the conservation of these species.

Material and methods

Study plots

The study was conducted in the vicinity of Evo, Southern Finland (61°11N, 25°05E), within the south boreal vegetation zone. For the study, we selected 24 two-hectare plots located within an area of 25 x 15 km. The lands were owned by Finnish Forest and Park Service (6 plots), Finnish Forest Research Institute (4), forest product company UPM (4), Häme Polytechnic University of Applied Sciences (6), and the town of Hämeenlinna (4). All of the plots were on average 80-years-old managed forests. The initial volume of standing wood on the plots was 251.9 ± 64.8 m^3/ha (mean ± SD) and the volume of dead wood 17.3 ± 13.7 m^3/ha, the volumes of living or dead wood did not differ between the plots (Lilja et al. 2005). The dead wood at the plots consisted almost exclusively of logging waste: small-diameter (< 20 cm) logs and cut stumps (Lilja et al. 2005). The dominant tree species of the plots was Norway spruce (*Picea abies* (L.) Karst) (on average 93% of the volume of standing trees) with some birch (*Betula* spp.) (3%) and Scotch pine (*Pinus sylvestris* L.) (4%).

Experimental design

We constructed a two-factor experimental design in which the factors were fire (two levels: burning versus no burning) and harvesting with creating dead wood (four levels: partially harvested plots with three levels of dead wood and unharvested plots). Each treatment (Fig. 1) was replicated three times. The treatments were randomized among the study plots such that they were geographically intermixed.

During February and March 2002, 18 of the study plots were harvested such that the volume of standing retention trees was set to 50 m^3 per hectare. Six of the study plots were left unharvested. On the harvested plots, cut down trees were left to make the volume of large-diameter dead wood 5, 30 or 60 m^3/ha. Each dead wood level was applied to six harvested plots. The cut down trees were evenly distributed on the study plots.

In summer 2002, half of the study plots (3 plots of each harvesting and dead wood combination and 3 unharvested plots) were burnt. The first five burnings were completed in mid-June, the following five in mid-July and the last two in the beginning of August. The burnings were carried out using the traditional Finnish ‘‘horseshoe’’ technique (for details, see Lilja et al. 2005). At harvested plots, the fires were mainly ground fires with occasional jumps to the canopy, the intensity of fire increased with the amount of cut down wood on the ground. The volume of standing dead trees after the fire was 24.1 ± 17.2 m^3/ha (mean ± SD) at the plots with 5 m^3/ha of cut down wood, 14.8 ± 21.6 m^3/ha at the plots with 30 m^3/ha of cut down wood, and 43.8 ± 31.0 m^3/ha at the plots with 60 m^3/ha of cut down wood (Lilja et al. 2005). At unharvested plots, the fires were less intense and large patches inside the plots did not burn at all. The volume of standing dead trees after the fire was 1.4 ± 2.3 m^3/ha at the unharvested plots (Lilja et al. 2005).

Sampling and grouping of beetles

We sampled beetles from the study plots with flight-intercept traps. The traps consisted of two crosswise-set transparent plastic panes with a funnel and container below them (for more details, see Hyvärinen et al. 2006). We used saline water with detergent in the

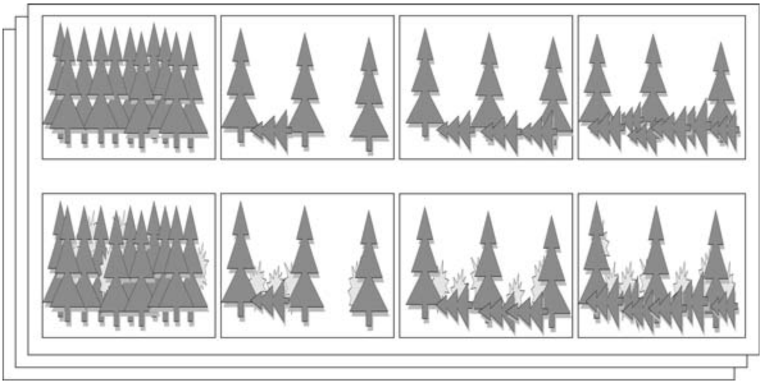

Fig. 1 The experimental design (n = 3 in each treatment). Above: unburnt, below: burnt. From the left: unharvested; harvested with 5 m^3/ha of dead wood; harvested with 30 m^3/ha of dead wood; harvested with 60 m^3/ha of dead wood

containers to preserve the beetles. To collect random samples, we set the traps hanging on a string between two trees or poles. We set five traps at random locations at each study plot, thus the total number of traps was 120. The trapping period was 10 May–10 September 2003, during which we emptied the traps six times.

We identified the majority of the beetles caught (99.9%) to species level. The identification of females of genera *Philhygra* and *Euplectus* was left to genus level as a rule. In addition, a few beetles of the genera *Acrotrichis*, *Atheta*, *Atomaria*, *Epuraea* and *Leiodes* could not be reliably identified. The nomenclature follows Silfverberg (2004).

We classified the beetles to saproxylic and non-saproxylic species following grouping originally based on literature (e.g. Saalas 1917, 1923; Palm 1951, 1959; Koch 1989–1992) and also on unpublished database of Jogeir Stokland. Only obligatorily saproxylic species were classified as saproxylic. Furthermore, we classified the species as common or rare according to the frequency score list of Finnish beetles (Rassi 1993), which gives the species' actual or estimated number of occurrences in Finland (the number of 10 x 10 km squares in which the species has been recorded) between years 1960 and 1990. The total number of these squares in Finland is 3900 and the species recorded in up to 25 squares were classified as rare. The beetle species considered threatened (IUCN categories CR, EN and VU) or near threatened (NT) in Finland (Rassi et al. 2001) were classified as ''red-listed'' species. Pyrophilous (fire-dependent) species were classified according to Wikars (1997).

Statistical analyses

We used the pooled data of the five traps of each study plot in the analyses. We analyzed the main effects of burning and harvesting with creating dead wood with two-way ANOVA followed by Tukey's pairwise comparisons. If there was interaction between the factors, simple effects test was used to analyse the effect of one factor within the other factor. The simple effect tests were followed by pairwise comparisons. Before analyses, the numbers of beetle individuals were $\log_{10}(x + 1)$-transformed. We performed the analyses with SPSS 11.0 for Windows software (SPSS Incorporated).

We used detrended correspondence analysis (DCA) with Canoco 4.0 (ter Braak 1987) to explore the compositional variation in beetle assemblages. We performed the analyses separately for saproxylic and non-saproxylic species. The species which occurred on one study plot only were excluded and the species abundance data were $\log_{10}(x + 1)$-transformed before analyses. Detrending was performed using second order polynomials. To statistically interpret the clustering in the ordination, we analyzed the loadings on axes 1 and 2 with two-way ANOVA followed by simple effects tests (if necessary) and pairwise comparisons.

Results

Species richness and abundance of beetles

A total of 755 beetle species consisting of 56,031 individuals were recorded. At burnt plots, we recorded 655 species and 40,576 individuals. At unburnt plots, the number of species was 532 and the number of individuals 15,455. There were 223 species that occurred at burnt plots only and 100 species that occurred at unburnt plots only.

Both burning and harvesting with creating dead wood had a positive effect on the number of beetle species (Table 1, Fig. 2a). Harvested plots had more species than unharvested ones (Tukey's pairwise comparisons, $P < 0.01$ in all comparisons) but the volume of dead wood on the harvested plots had no effect on the number of species.

The number of beetle individuals (Table 1, Fig. 2b) was increased by burning. Harvesting with creating dead wood had a positive effect in general, but there was an interaction between the factors: harvesting with creating dead wood increased the number of individuals among unburnt plots (simple effects test, $F_{3,16} = 11.676$, $P < 0.001$) but it had no effect among burnt plots ($F_{3,16} = 1.462$, $P = 0.262$) . Among unburnt plots, there were more individuals at harvested plots than at unharvested plots (pairwise comparisons, $P < 0.001$ in all comparisons) but the volume of dead wood on the harvested plots had no effect on the abundance of beetles.

Table 1 ANOVA statistics for the number of species and individuals in the different (partly overlapping) species groups

Group	Treatment	d*f**	Number of species		Number of individuals	
			F	*P*	*F*	*P*
All	Burning	1	105.661	<0.001	124.497	<0.001
	HDW	3	12.553	<0.001	8.587	0.001
	Burning* HDW	3	0.965	0.434	4.551	0.017
Saproxylic	Burning	1	82.335	<0.001	80.802	<0.001
	HDW	3	7.764	0.002	5.194	0.011
	Burning* HDW	3	0.880	0.472	4.138	0.024
Non-saproxylic	Burning	1	110.666	<0.001	180.467	<0.001
	HDW	3	15.418	<0.001	13.120	<0.001
	Burning* HDW	3	1.626	0.223	6.734	0.004
Rare	Burning	1	11.893	0.003	29.972	<0.001
	HDW	3	3.997	0.027	0.947	0.441
	Burning* HDW	3	0.346	0.792	2.639	0.085
Rare saproxylic	Burning	1	9.152	0.008	49.953	<0.001
	HDW	3	2.625	0.086	0.324	0.808
	Burning* HDW	3	0.416	0.744	1.922	0.167
Rare non-saproxylic	Burning	1	0.800	0.384	0.005	0.947
	HDW	3	1.267	0.319	1.099	0.378
	Burning* HDW	3	0.267	0.848	5.696	0.008
Red-listed	Burning	1	4.050	0.061	21.363	<0.001
	HDW	3	2.450	0.101	6.906	0.003
	Burning* HDW	3	0.050	0.985	3.526	0.039
Pyrophilous	Burning	1	75.000	<0.001	153.363	<0.001
	HDW	3	0.444	0.725	0.956	0.437
	Burning* HDW	3	1.222	0.334	1.997	0.155

* $df_{error} = 16$ in all cases

HDW = harvesting with creating dead wood

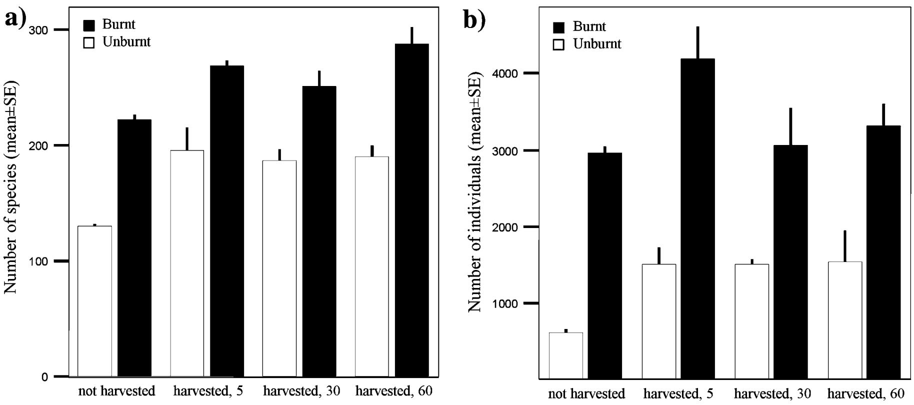

Fig. 2 The number of (**a**) beetle species and (**b**) individuals at burnt (black bars) and unburnt plots (white bars). The *X*-axis represents unharvested plots and harvested plots with different volumes of dead wood (m^3/ha). The data presented are means (n = 3 in each treatment) and standard errors

Saproxylic species

Of the 755 recorded species, 314 were classified as saproxylic. At burnt plots, we recorded 273 saproxylic species (28,069 individuals) and at unburnt plots 251 species (11,169 individuals). Both burning and harvesting with creating dead wood increased the number of saproxylic species (Table 1, Fig. 3a). Harvested plots had more species than unharvested ones (Tukey's pairwise comparisons, $P < 0.05$ in all comparisons) but the volume of dead wood on the harvested plots had no effect on the number of species.

The number of saproxylic individuals (Table 1, Fig. 3c) was increased by burning. Harvesting with creating dead wood had a positive effect in general, but there was an interaction between the factors: harvesting with creating dead wood increased the number of saproxylic individuals among unburnt plots (simple effects test, $F_{3.16} = 7.959$, $P = 0.002$) but it had no effect among burnt plots ($F_{3.16} = 1.374$, $P = 0.287$). Among unburnt plots, there were more individuals at harvested plots than at unharvested plots (pairwise comparisons, $P < 0.01$ in all comparisons) but the volume of dead wood on the harvested plots had no effect on the number of individuals.

Non-saproxylic species

Of the 441 non-saproxylic species, 382 (12,507 individuals) occurred at burnt plots and 281 (4,286 individuals) at unburnt plots. The number of non-saproxylic species was positively affected by both burning and harvesting with creating dead wood (Table 1, Fig. 3b). Harvested plots had more species than unharvested ones (Tukey's pairwise comparisons, $P < 0.01$ in all comparisons) but the volume of dead wood on the harvested plots had no effect on the number of species.

The number of non-saproxylic individuals was also increased by burning and harvesting with creating dead wood and there was an interaction between the factors (Table 1, Fig. 3d). Among burnt plots (simple effects test for the effect of harvesting, $F_{3.16} = 3.484$, $P = 0.041$), harvested plots with 60 m^3/ha of dead wood had more individuals than unharvested plots (pairwise comparison, $P = 0.013$). Among unburnt plots (simple effects

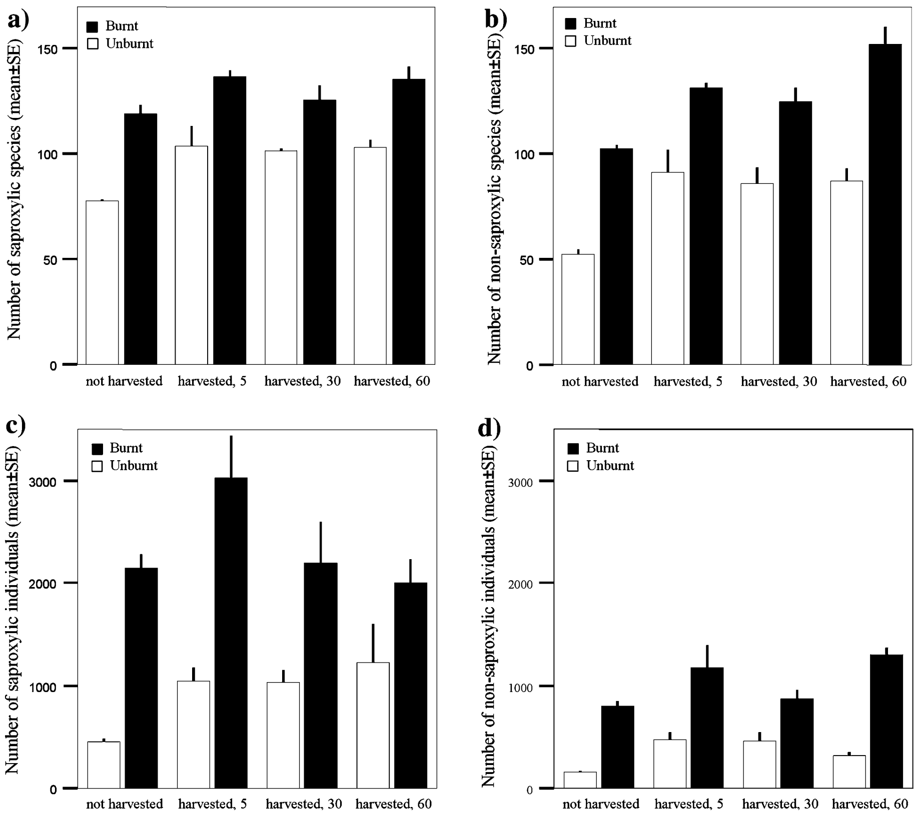

Fig. 3 The number of (**a**) saproxylic and (**b**) non-saproxylic species and the number of (**c**) saproxylic and (**d**) non-saproxylic individuals at burnt (black bars) and unburnt plots (white bars). The *X*-axis represents unharvested plots and harvested plots with different volumes of dead wood (m^3/ha). The data presented are means ($n = 3$ in each treatment) and standard errors

test for the effect of harvesting, $F_{3,16} = 16.370$, $P < 0.001$), all harvested plots had more individuals than unharvested plots ($P < 0.01$ in all comparisons) and the plots with 60 m^3/ha of dead wood had less individuals than other harvested plots ($P < 0.05$ in both comparisons).

Rare species

A total of 46 rare species (1,458 individuals) was recorded, 34 species (1,192 individuals) at burnt plots and 27 species (266 individuals) at unburnt plots. Of these species, 33 were classified as saproxylic (of which 27 occurred at burnt plots and 18 at unburnt plots). Burning increased the number of rare species and also harvesting with creating dead wood had a positive effect (Table 1). Harvested plots with 60 m^3/ha of dead wood had more species than unharvested plots (Tukey's pairwise comparison, $P = 0.019$), the other differences between harvested and unharvested plots or among harvested plots were not significant. The number of individuals of rare species was elevated by burning but harvesting with creating dead wood had no effect (Table 1).

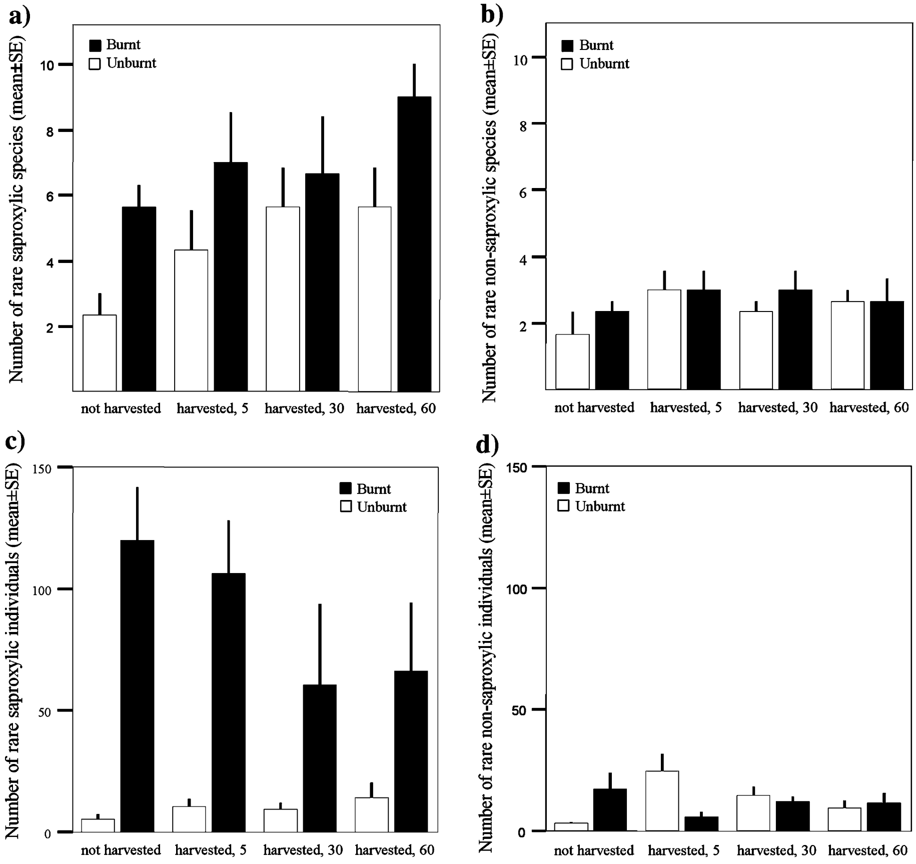

Fig. 4 The number of (**a**) rare saproxylic and (**b**) non-saproxylic species and the number of (**c**) rare saproxylic and (**d**) rare non-saproxylic individuals at burnt (black bars) and unburnt plots (white bars). The *X*-axis represents unharvested plots and harvested plots with different volumes of dead wood (m^3/ha). The data presented are means ($n = 3$ in each treatment) and standard errors

The number of rare saproxylic species was increased by burning and harvesting with creating dead wood only tended to increase it (as the criteria of statistical significance was not met but P was < 0.10) (Table 1, Fig. 4a). The number of rare saproxylic individuals was increased by burning but harvesting with creating dead wood had no effect (Table 1, Fig. 4c). In contrast, the numbers of rare non-saproxylic species or individuals did not differ between any treatments (Table 1, Fig. 4b,d).

Red-listed species

A total of 12 red-listed species (72 individuals) belonging to categories VU and NT was recorded, 8 species (64 individuals) occurred at burnt plots and 6 species (8 individuals) at unburnt plots. Burning tended to increase the number of red-listed species (as the criteria of statistical significance was not met but P was < 0.10) and harvesting with creating dead wood had no effect (Table 1, Fig. 5a). The number of individuals of red-listed species was

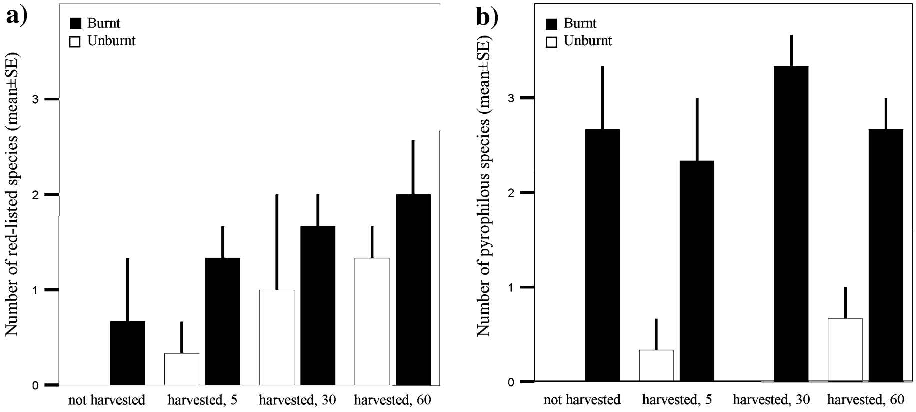

Fig. 5 The number of (**a**) red-listed and (**b**) pyrophilous species at burnt (black bars) and unburnt plots (white bars). The *X*-axis represents unharvested plots and harvested plots with different volumes of dead wood (m^3/ha). The data presented are means ($n = 3$ in each treatment) and standard errors

positively affected by both burning and harvesting with creating dead wood (Table 1). However, the effect of harvesting with creating dead wood was largely due to the high abundance of *Sphaeriestes stockmanni* (Biström) (Salpingidae) at the burnt plots with 30 m^3/ha of dead wood; the differences between other categories were not significant.

Pyrophilous species

A total of 6 pyrophilous species were recorded. All of the species (186 individuals) occurred at burnt plots and two species (3 individuals) were also recorded at unburnt plots. Burning increased the number of pyrophilous species and individuals but harvesting with creating dead wood had no effect (Table 1, Fig. 5b).

The composition of beetle assemblages

In the DCA ordination of saproxylic species (Fig. 6), there was distinct grouping according to burning and harvesting with creating dead wood (on axis 1, for burning $F_{1,16} = 399.513$, $P < 0.001$, for harvesting $F_{3,16} = 58{,}979$, $P < 0.001$ and for their interaction $F_{3,16} = 6.221$, $P = 0.005$; on axis 2, for burning $F_{1,16} = 16.408$, $P = 0.001$, for harvesting $F_{3,16} = 13.394$, $P < 0.001$ and for their interaction $F_{3,16} = 7.103$, $P = 0.003$). Among burnt plots, unharvested plots were separated from harvested ones (pairwise comparisons: on axis 1, $P < 0.001$ in all comparisons; on axis 2, $P < 0.05$ in all comparisons) but there was no grouping according to the volume of dead wood on the harvested plots. Among unburnt plots, unharvested plots were separated from harvested plots on axis 1 ($P < 0.001$ in all comparisons) and harvested plots with 60 m^3/ha of dead wood were separated from other harvested plots ($P < 0.05$ in both comparisons). On axis 2, unharvested plots and harvested plots with 60 m^3/ha of dead wood did not differ but both of them were separated from other harvested plots ($P < 0.01$ in all comparisons).

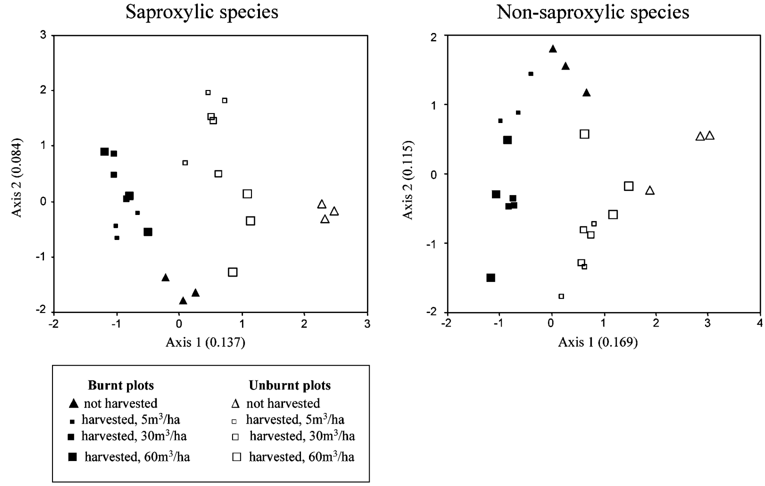

Fig. 6 DCA ordinations for saproxylic and non-saproxylic species. The eigenvalues of axes are presented in parentheses

Non-saproxylic species showed quite a similar pattern in the DCA as saproxylic ones (Fig. 6). Although there was more heterogeneity in the ordination, grouping according to burning and harvesting with creating dead wood was distinct (on axis 1, for burning $F_{1,16} = 164.428$, $P < 0.001$, for harvesting $F_{3,16} = 29.588$, $P < 0.001$ and for their interaction $F_{3,16} = 3.566$, $P = 0.038$; on axis 2, for burning $F_{1,16} = 19.453$, $P < 0.001$, for harvesting $F_{3,16} = 10.152$, $P = 0.001$ and for their interaction $F_{3,16} = 7.098$, $P = 0.003$). Among burnt plots, unharvested plots were separated from all harvested ones on axis 1 (pairwise comparisons, $P < 0.01$ in all comparisons). On axis 2, unharvested plots and harvested plots with 5 m^3/ha of dead wood did not differ but both were separated from other harvested plots ($P < 0.01$ in all comparisons). Among unburnt plots, unharvested plots were separated from harvested plots on axis 1 ($P < 0.001$ in all comparisons). On axis 2, unharvested plots and harvested plots with 60 m^3/ha of dead wood did not differ but both of them were separated from other harvested plots ($P < 0.05$ in all comparisons).

Species responses

Of the 20 most abundant species (Table 2), 11 were obligatorily saproxylic species and 2 species (*Corticaria ferruginea* Marsham and *Corticaria rubripes* Mannerheim (Latridiidae)) were defined as facultatively saproxylic. The abundance of 17 of the 20 species was increased by burning, 2 species were indifferent to burning, and one species, *Enicmus rugosus* (Herbst) (Latridiidae) was less abundant at the burnt plots. Harvesting with creating dead wood increased the abundance of 10 of the 20 species. However, 4 of these species showed an interaction between the treatments: harvesting increased their abundance at unburnt plots but not at burnt plots. In addition, 6 species that were not affected by harvesting in general showed similar interaction: they were more abundant at harvested unburnt plots than at unharvested unburnt plots but there were no differences among the burnt plots.

Table 2 The total abundance of the 20 most common beetle species at burnt ($n = 12$) and unburnt plots ($n = 12$) and ANOVA statistics for the species-level effects of burning and harvesting with creating dead wood (HDW)

Species	Classification	Burnt plots	Unburnt plots	Burning	HDW	Burning* HDW
Pityogenes chalcographus Linnaeus	S	6,686	2,792	$F_{1,16} = 44.251$	$F_{3,16} = 20.392$	$F_{3,16} = 14.177$
(Curculionidae)				$P < 0.001$	$P < 0.001$	$P \leq 0.001$
Hylastes cunicularius Erichson	S	2,897	1,120	$F_{1,16} = 18.792$	$F_{3,16} = 1.813$	$F_{3,16} = 3.489$
(Curculionidae)				$P = 0.001$	$P = 0.185$	$P = 0.040$
Dryocoetes autographus (Ratzeburg)	S	2,785	583	$F_{1,16} = 85.180$	$F_{3,16} = 7.707$	$F_{3,16} = 7.652$
(Curculionidae)				$P < 0.001$	$P = 0.002$	$P = 0.002$
Enicmus rugosus (Herbst)	S	612	1,179	$F_{1,16} = 16.812$	$F_{3,16} = 16.195$	$F_{3,16} = 14.177$
(Latridiidae)				$P = 0.001$	$P = 0.244$	$P < 0.001$
Rhizophagus ferrugineus (Paykull)	S	1,688	44	$F_{1,16} = 156.380$	$F_{3,16} = 1.314$	$F_{3,16} = 4.194$
(Monotomidae)				$P < 0.001$	$P = 0.304$	$P = 0.023$
Orthoperus rogeri Kraatz	S	1,439	241	$F_{1,16} = 39.611$	$F_{3,16} = 0.881$	$F_{3,16} = 8.243$
(Corylophidae)				$P < 0.001$	$P = 0.472$	$P = 0.002$
Athous subfuscus (Müller)	N	1,099	512	$F_{1,16} = 6.317$	$F_{3,16} = 7.796$	$F_{3,16} = 3.194$
(Elateridae)				$P = 0.023$	$P = 0.002$	$P = 0.052$
Trypodendron lineatum (Olivier)	S	1,092	458	$F_{1,16} = 20.364$	$F_{3,16} = 9.202$	$F_{3,16} = 1.163$
(Curculionidae)				$P < 0.001$	$P = 0.001$	$P = 0.355$
Cyphon coarctatus Paykull	N	943	181	$F_{1,16} = 14.708$	$F_{3,16} = 5.143$	$F_{3,16} = 2.807$
(Scirtidae)				$P = 0.001$	$P = 0.011$	$P = 0.073$
Corticaria ferruginea Marsham	F	1,040	17	$F_{1,16} = 248.402$	$F_{3,16} = 0.336$	$F_{3,16} = 1.132$
(Latridiidae)				$P < 0.001$	$P = 0.799$	$P = 0.366$
Cortinicara gibbosa (Herbst)	N	761	144	$F_{1,16} = 43.975$	$F_{3,16} = 15.857$	$F_{3,16} = 1.790$
(Latridiidae)				$P < 0.001$	$P < 0.001$	$P = 0.190$
Amischa nigrofusca (Stephens)	N	755	140	$F_{1,16} = 65.468$	$F_{3,16} = 15.089$	$F_{3,16} = 2.111$
(Staphylinidae)				$P < 0.001$	$P < 0.001$	$P = 0.139$

Table 2 continued

Species	Classification	Burnt plots	Unburnt plots	Burning	HDW	Burning* HDW
Epuraea pygmaea (Gyllenhal) (Nitidulidae)	S	723	141	$F_{1,16} = 50.509$ $P < 0.001$	$F_{3,16} = 2.144$ $P = 0.135$	$F_{3,16} = 2.353$ $P = 0.111$
Epuraea muehli Reitter (Nitidulidae)	S	826	24	$F_{1,16} = 33.758$ $P < 0.001$	$F_{3,16} = 0.652$ $P = 0.593$	$F_{3,16} = 1.164$ $P = 0.354$
Atheta myrmecobia (Kraatz) (Staphylinidae)	N	522	287	$F_{1,16} = 22.690$ $P < 0.001$	$F_{3,16} = 8.369$ $P = 0.001$	$F_{3,16} = 17.947$ $P < 0.001$
Melanotus castanipes (Paykull) (Elateridae)	S	448	344	$F_{1,16} = 2.886$ $P = 0.109$	$F_{3,16} = 2.122$ $P = 0.138$	$F_{3,16} = 1.205$ $P = 0.340$
Dasytes niger (Linnaeus) (Melyridae)	S	628	163	$F_{1,16} = 74.962$ $P < 0.001$	$F_{3,16} = 37.870$ $P < 0.001$	$F_{3,16} = 6.500$ $P = 0.004$
Corticaria rubripes Mannerheim (Latridiidae)	F	667	72	$F_{1,16} = 93.386$ $P < 0.001$	$F_{3,16} = 1.974$ $P = 0.159$	$F_{3,16} = 4.100$ $P = 0.025$
Dalopius marginatus (Linnaeus) (Elateridae)	N	264	387	$F_{1,16} = 3.056$ $P = 0.100$	$F_{3,16} = 3.426$ $P = 0.043$	$F_{3,16} = 0.392$ $P = 0.760$
Acrotrichis intermedia (Gillmeister) (Ptiliidae)	N	388	219	$F_{1,16} = 8.371$ $P = 0.011$	$F_{3,16} = 0.280$ $P = 0.839$	$F_{3,16} = 7.306$ $P = 0.003$

The species have been classified as obligatorily saproxylic (S), facultatively saproxylic (F) or non-saproxylic (N)

The species that increased the most due to burning were typically species living under the bark of recently died or dying trees (for example *Pityogenes chalcographus* Linnaeus (Curculionidae), *Rhizophagus ferrugineus* (Paykull) (Monotomidae) and *Epuraea* spp. (Nitidulidae)) or species utilizing corticoid fungi that rapidly colonize burnt trees (for example *Corticaria* spp.). In contrast, many species living in fruiting bodies of polypores or mushrooms declined after burning (for example *Agathidium seminulum* (Linnaeus) (Leiodidae): for burning $F_{1,16} = 47.915$, $P < 0.001$, for harvesting with creating dead wood $F_{3,16} = 1.161$, $P = 0.355$, and for interaction $F_{3,16} = 1.024$, $P = 0.408$). Some forest-dwelling species preferring shady conditions had a negative response to both burning and harvesting (for example *Quedius xanthopus* Erichson (Staphylinidae): for burning $F_{1,16} = 21.534$, $P < 0.001$, for harvesting with creating dead wood $F_{3,16} = 3.870$, $P = 0.030$, and for interaction $F_{3,16} = 1.426$, $P = 0.272$).

Discussion

The effect of burning

The importance of burnt forests for many specialized beetle species (Ahnlund and Lindhe 1992; Wikars 1997), for rare and threatened species (Similä et al. 2002; Hyvärinen et al. 2005), and for species richness in general (Muona and Rutanen 1994; Hyvärinen et al. 2005) has been documented in several studies. However, the importance of burning as a restoration tool, in particular compared to other restorative treatments, has not been systematically explored. In this study, where both burning and the volume of dead wood were manipulated, we still found a strong positive effect of fire on species richness and abundance of beetles. The species richness was highest at the plots which were both burnt and harvested, where also the fire was most intense. At these plots, also rare and red-listed species were most abundant. The beetle assemblages were also affected by burning, and in particular saproxylic beetle species showed a distinct grouping in the DCA ordinations.

Burning increases the abundance of resources for saproxylic beetles by killing and weakening trees and also the sun-exposed burnt environment per se may be favoured by beetles. Immediately after fire, beetles are attracted to the burnt areas by smoke and heat and some of these early colonizers may not actually be able to reproduce at these areas. However, the attraction to smoke is likely to be restricted to the first weeks following burning. Our data, which was collected during the first post-fire summer, is likely to include both species that have already reproduced at the burnt plots and species that are still actively colonizing the habitats.

The effect of harvesting with creating dead wood

The volume and quality of dead wood is considered a major factor affecting the species richness of saproxylic beetles in boreal forests (Martikainen et al. 2000; Siitonen 2001; Grove 2002). In this study, harvesting with creating dead wood increased the number of beetle species and individuals but the effect was mainly due to harvested plots differing from unharvested ones. Among unburnt plots, the volume of decaying wood was elevated on the harvested plots not only by the dead wood created but also by cut stumps, branches and other logging waste which is known to host diverse species assemblages during the first years after logging (Sippola et al. 2002; Junninen et al. 2005; Selonen et al. 2005). The species richness of the harvested plots may also be partly explained by the attraction of beetles to the warmth of these plots and the odours of fresh dead wood and logging waste. Among burnt plots, the fire was less intense at the unharvested plots and thus the volume of trees that died immediately after the fire was low. Therefore, these plots may have initially offered fewer resources for saproxylic beetles than the plots that were both harvested and burnt. However, the unharvested burnt plots are likely to provide a more continuous supply of dead wood in the future.

The volume of large-diameter dead wood created on harvested plots had no clear short-term effect on species richness, although some trends were evident among rare species. At harvested burnt plots, the cut down trees burnt intensively and their value as a resource for saproxylic beetles may have been small compared to the standing trees damaged by fire. For example, bark beetles avoid fire-scorched logs (Wikars 2002). Among harvested unburnt plots, the lack of effect is more difficult to explain but can be due to several factors. First, the abundance of logging waste (equal at all harvested sites) made the proportional differences in the amount of resources smaller between the treatments. Second, during the first post-harvesting year, the large logs may have hosted the first primary colonizers only. As the decay process takes several decades (see Kruys et al. 2002; Storaunet and Rolstad 2002), the importance of the dead wood created is likely to increase in the future when species favouring later decay stages appear at the study plots. Third, the effect of the amount of resource may have been ‘‘masked’’ by the beetle activity caused by the odours and warmth of freshly logged plots.

Species responses

Burning and increasing the volume of dead wood create resources for saproxylic species while non-saproxylic species are not likely to benefit from these actions, although for example the species richness of ground beetles has been documented to increase after clear-cutting (Niemelä et al. 1993). In our experiment, however, also non-saproxylic species responded positively to burning and harvesting. This result is in concordance with Hyvärinen et al. (2005) and it seems probable that non-saproxylic species are attracted to these plots due to features characteristic of freshly logged areas, such as sun-exposed conditions and increased amount of needle litter. Many non-saproxylic species may also use dead wood for habitat or shelter. In addition, some species classified as non-saproxylic are actually facultative utilizers of dead wood or associated fungi. Of these species, for example *Atomaria pulchra* Erichson (Cryptophagidae) and *C. ferruginea* Marsham (Latridiidae) were very abundant in our samples.

Even though saproxylic and non-saproxylic species responded similarly to our restoration treatments in general, a closer look to the rare species reveals a different pattern. The number of rare saproxylic species was elevated by both burning and harvesting with creating dead wood. The number of rare saproxylic individuals showed a dramatic increase after burning, while harvesting had no effect. In contrast, the numbers of rare non-saproxylic species and individuals did not differ between any treatments. It is also worth noting that the abundances of non-saproxylic species were generally relatively low (see Fig. 3) and that the majority of the species showing the strongest responses to the treatments were saproxylic ones (or facultative saproxylics described above). This implies that fire is truly effective in creating habitats for saproxylic species, and that the preference for burnt areas is particularly evident among rare saproxylic species.

The beetle assemblages were strongly modified by both burning and harvesting and there were also some differences according to the volume of dead wood. In the DCA ordinations, burnt plots with 5 m^3/ha of cut down wood were separated from other harvested burnt plots and the assemblages of non-saproxylic species were more similar to those of unharvested plots. Because the intensity of fire increased with the volume of cut down wood, the effect on the ground and field layers was most profound at the plots with plenty of burning material. Fire has severe effects on soil-dwelling arthropods (Wikars and Schimmel 2001) and the turnover of the assemblages of these species may have been greatest at the most intensively burnt plots. Among unburnt plots, the plots with 60 m^3/ha of dead wood had distinct assemblages of both saproxylic and non-saproxylic species that were more similar to those of unharvested plots. Therefore, these plots may have retained some features of the original forest. It seems likely that the plots with plenty of large trees lying on the ground form a less open and sun-exposed habitat than the plots with smaller volumes of cut down wood.

The impact of surrounding landscape

One of the high-priority aims of restoration is to improve habitats for red-listed species. Today, the distribution of many red-listed forest beetles in Finland is restricted to the eastern part of the country and they are practically extinct from southern and western Finland. As the beetle communities of restored plots strongly reflect the quality of surrounding habitats, it was not surprising that the number of red-listed species was generally low in our data, although the positive effect of burning was evident. However, disturbance-associated species are likely to be capable of long-distance dispersal (Southwood 1962) and thus more red-listed species may colonize the restored habitats in the long run. It remains to be seen whether restoration efforts directed to areas with impoverished fauna will result in the recovery of species that are still present or in the recolonization of species that have already gone extinct.

Sampling effort versus sampling efficiency

A common criticism to sampling studies focusing on habitats of varying structure is that the sampling efficiency may differ even if the sampling effort has been controlled by the experimental design. For example, the high abundance of beetles at burnt and harvested plots could also be due to beetles flying more actively at warm open areas being therefore more numerous in the traps. This might partly explain the large differences between harvested and unharvested plots. However, the flying activity of beetles is likely to be equal between structurally similar areas, for example between burnt and unburnt plots with equal volume of standing and cut down trees. Therefore, the observed differences between these plots in the number of beetles trapped are likely to reflect the real abundance of beetles at the plots. Moreover, the DCA ordinations revealed clear differences in the community composition between the treatments and it is difficult to see how sampling efficiency could cause this effect. Thus, we conclude that any minor variance in sampling efficiency is not likely to generate such strong and clear results that we observed.

Conclusions

It has been stated that just preserving the remaining fragments valuable for threatened species may not be sufficient to stop the wave of extinctions in boreal forests, but restoration of human altered habitats is required (Hanski 2000). In this study, which deals with restoration actions directed to managed forests, the positive effects of restoration on species diversity appear straightforward. Using fire as restoration tool benefits not only pyrophilous species, but leads to an increase in the overall abundance and species richness of beetles. Of special interest is the positive response among rare saproxylic species, which implies that fire can be successfully used to create habitats for highly specialized beetle species and to facilitate the recovery of declined species. When burning is not included, harvesting with creating dead wood still increases beetle diversity. Due to the adequate volume of standing retention trees, also the continuous supply of dead wood is likely to be guaranteed at these plots. Although the species richness is not immediately affected by the actual volume of dead wood left on harvested plots, the plots with large volumes of dead wood may host a more diverse fauna in the future. Beetle assemblages are also affected by burning and harvesting, different types of restored plots hosting distinct communities. Therefore, varying the methods of restoration within landscape level may be the best option to guarantee the survival of disturbance-associated species.

Although promising results of restoration can be seen in a short time, we stress that the processes of wood decay and species recolonization proceed slowly and long-term monitoring of restored sites is needed to clarify the effects of the restoration actions. Because young successional stages are today not formed by natural disturbances, it is important to determine how long the restored sites remain a suitable habitat for species adapted to open disturbance areas. A continuum of these habitats, both in time and within the dispersal abilities of these species, must be ensured to make the restoration efforts successful.

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