Burning of Logged Sites to Protect Beetles in Managed Boreal Forests

TERO TOIVANEN*‡ AND JANNE S. KOTIAHO*†

*Department of Biological and Environmental Science, P.O. Box 35, 40014 University of Jyväskylä, Finland
†Natural History Museum, P.O. Box 35, 40014 University of Jyväskylä, Finland

Abstract: Natural disturbance-based management and conservation strategies are needed to protect forest biodiversity. Boreal forests of northern Europe are typically clearcut and otherwise intensively managed for timber production. As a result, natural disturbances such as forest fires have become rare and the volume of dead wood has decreased. These changes have had a profound negative effect on species that depend on dead wood (saproxylic). Therefore, it is important to determine whether modifications of forest management methods can enhance the survival of these species. In our study area in southern Finland, we determined whether burning of logged sites and leaving trees (i.e., retention trees) on the sites benefited saproxylic, rare, and red-listed beetle species and how long the burned sites remained suitable habitat for these species. We surveyed the beetle fauna at 40 sites logged 1–16 years previously, 20 of which were burned after logging. The abundance and species richness of saproxylic beetles were positively affected by burning, but the effect depended on the retention of trees in the otherwise clearcut stands. The difference between burned and unburned sites increased with the number of retention trees, and the effect of burning was not significant when there were fewer than approximately 15 retention trees/ha. Most important, the species groups that were unlikely to persist in ordinarily managed forests (rare saproxylic and red-listed beetles), benefited strongly from burning and tree retention. The species richness of saproxylic beetles decreased with time since logging at both burned and at unburned sites. We conclude that burning of logged sites and leaving an adequate number of retention trees may be useful in the conservation of disturbance-adapted species and can be used to improve the environmental quality of the matrix surrounding protected areas. Unfortunately, sites remained high-quality habitat for only a short time; thus, a continuum of burned areas must be ensured.

Keywords: beetle conservation, Coleoptera, disturbance, forest fire, forest management, retention trees, saproxylic species

Quema de Sitios Talados para la Protecció de Escarabajos en Bosques Boreales

Resumen: Se requieren estrategias de manejo y conservación basadas en perturbaciones naturales para proteger la biodiversidad de los bosques. Típicamente, los bosques boreales del norte de Europa son talados y manejados intensivamente para la producción de madera. Como resultado, las perturbaciones naturales, como los incendios forestales, se han vuelto raras y el volumen de madera muerta ha disminuido. Estas modificaciones han tenido un profundo efecto negativo sobre las especies que dependen de la madera muerta (saproxylicas). Por lo tanto, es importante determinar si las modificaciones derivadas de los métodos de manejo forestal pueden incrementar la supervivencia de estas especies. En nuestra área de estudio en el sur de Finlandia, determinamos si la quema o permanencia (i.e., árboles de retención) de árboles en sitios explotados beneficiaba a especies de escarabajos saproxylicos raras y en la lista roja y cuánto tiempo permanecerían como hábitat adecuado para estas especies los sitios quemados. Muestreamos la fauna de escarabajos en 40 sitios talados entre 1 y 16 años antes, 20 de los cuales fueron quemados después de talados. La abundancia y riqueza de especies de escarabajos saproxylicos fueron afectadas positivamente por la quema, pero el efecto dependió de la retención de árboles vivos en las áreas taladas. La diferencia entre sitios quemados y no quemados incremento con

‡email tertoiv@cc.jyu.fi
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el número de árboles de retención, y el efecto de la quema no fue significativa cuando había menos de 15 árboles de retención/ha aproximadamente. En gran medida, los grupos de especies con menor probabilidad de persistir en bosques manejados normalmente (especies de escarabajos saproxilicos, raros y en la lista roja), se beneficiaron fuertemente con las quemas y la retención de árboles. La riqueza de especies de escarabajos saproxilicos disminuyó con el tiempo desde la tala tanto en sitios quemados como no quemados. Concluimos que la quema de sitios talados y la permanencia de un número adecuado de árboles de retención pueden ser útiles para la conservación de especies adaptadas a la perturbación y pueden ser utilizadas para mejorar la calidad ambiental de la matriz que rodea a las áreas protegidas. Desafortunadamente, los sitios permanecieron como hábitat de alta calidad sólo por un corto tiempo; por lo tanto, se debe asegurar un continuo de áreas quemadas.

**Palabras Clave:** árboles de retención, Coleoptera, conservación de escarabajos, especies saproxilicas, incendio forestal, manejo de bosques, perturbación

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**Introduction**

The main problem for ecosystem management and species conservation in forests in general and boreal forests in particular is how to maintain viable populations of specialized species in human-altered landscapes (Kuuluvainen 2002). In boreal forests that are intensively managed for wood production, there is a need for restoring the disturbance regime and accelerating the formation of structural and habitat features typical of natural forests. By implementing natural disturbance-based forest management and restoration strategies (Angelstam 1998; Kuuluvainen et al. 2002), it is possible to increase the conservation contributions of the managed matrix around protected areas (Kouki et al. 2001).

Boreal forests cover about 14 million km², which is about 20% of the forests on Earth. Although boreal forests have not suffered from severe loss of area, intensive forest management for timber production has caused substantial declines of biodiversity and severely deteriorated habitat quality. For example, 90% of the boreal forests of European Russia have been harvested or are otherwise no longer intact (Aksenov et al. 2002). In southern Finland natural forests cover <1% of the forest area, and it has been estimated that the current extinction debt (Tilman et al. 1994) is so high that about half of the species requiring natural forests are likely to go extinct eventually (Hanski 2000).

Biodiversity losses from boreal areas are due to loss of old-growth forests (Esseen et al. 1997), landscape fragmentation (Mladenoff et al. 1993; Komonen et al. 2000), simplified stand structure (Axelsson & Östlund 2001), altered disturbance dynamics (Attiwill 1994; Kuuluvainen 2002), and the decline of essential resources, in particular dead wood (Friedman & Walheim 2000; Uotila et al. 2001). In particular, the negative effect on species that are dependent on dead wood or on the presence of another saproxylic organism (Speight 1989) has been profound. Saproxylic species are a major ecological group in forest ecosystems. For example, in Finland at least 4000 species (20% of all forest-dwelling species) are saproxylic, and the most species-rich taxa are macrofungi, hymenopterans, flies, and beetles (Siitonen 2001). Sixty percent of the threatened or extinct species of forest beetles in Finland are saproxylic (Rassi et al. 2001).

Forest fires of variable size and intensity are a major disturbance in boreal coniferous forests (Wein & McLean 1983; Esseen et al. 1997). In Fennoscandia fire intervals have varied with forest type and latitude, but the average fire interval during the last thousand years has been 50–120 years (e.g., Zackrisson 1977; Wallenius et al. 2004). Fire enhances spatial heterogeneity of forests (Niklasson & Granström 2000), affects species composition and the age distribution of trees (Zackrisson 1977; Axelsson & Östlund 2001), increases the volume of dead wood (Siitonen 2001; Pedlar et al. 2002), and affects soil decomposition and nutrient release (Zackrisson et al. 1996; Dahlberg et al. 2001). In particular, fire creates early stages of forest succession that are important habitats for many saproxylic species (e.g., Kaila et al. 1997; Similä et al. 2002). For example, the species richness of rare and threatened saproxylic beetle species (Hyvärinen et al. 2006b) and polypore fungi (Penttilä 2004) are high in stands after fire.

In contemporary Fennoscandia clearcutting has almost exclusively replaced fires as the major disturbance, and disturbed areas of natural origin are very rare because of efficient fire suppression and harvesting of fallen trees from storm-damaged sites. The average annual area burned by wildfires in Finland has decreased from over 10,000 ha in the late 19th century (Sevola 1999) to about 500 ha over the last 3 decades (Peltola 2004). Clearcut areas lack the structural heterogeneity typical of burned forests and there is a substantial difference in the amount and quality of dead wood (Uotila et al. 2001; Pedlar et al. 2002). Although the number of saproxylic species is often elevated on logged sites (Sipponen et al. 2002; Selonen et al. 2005), the rarest species are usually absent (Similä et al. 2002; Junninen et al. 2006).

Forest management practices that aim to enhance biodiversity may have their greatest potential in young rather
than in old forests because the properties lost from managed forests may be more easily restored to young forests (Kouki et al. 2001) and because many threatened species traditionally associated with old-growth forests may actually prefer disturbed areas (Jonsell et al. 1998; Martikainen 2001). Burning of and leaving some trees (i.e., retention trees) on logged sites are recommended practices (Metsätalous kehittämiskeskus Tapio 2006) that are believed to better mimic natural disturbance dynamics and to create important structures and resources. Nevertheless, the effects of these practices are still inadequately known. In particular, little information is available on the succession of species assemblages beyond the very first years following disturbance. We combined historical, experiment-like setups and a correlative approach to explore the effects of fire and retention trees over 16 years. We sought to determine whether burning made logged sites more suitable for saproxylic, rare, and red-listed beetle species; whether retention trees increased beetle diversity; and how long the burned sites remained suitable habitat for the species concerned.

Methods

Study Sites

Our study area was Evo in southern Finland (61° N, 25° E), which is within the south boreal vegetation zone. In the study area, intensive forest management, such as thinning and clearcutting, has been practiced since the early 20th century. We conducted the study at 40 logged sites on which 2-62 harvestable trees/ha were left standing. Twenty of the sites were burned soon after logging. The study sites were logged from 1 to 16 years previously. Both burned and unburned sites were represented by all of the time periods since burning (except for 4-year-old burned sites and 14-year-old unburned sites). The burned sites were logged during the winter preceding burning, and the burning was conducted in June or July. The sites were located within a 12 × 7 km area and the burned and unburned sites were geographically intermixed. The average area of the burned sites was 5.5 ha (range 2-9 ha), and the average area of the unburned sites was 3.1 ha (range 0.8-9 ha).

There were on average 18.8 (SD 12.4) large retention trees (diameter >20 cm) per hectare at the burned sites and 25.0 (SD 15.0) large retention trees per hectare at the unburned sites. The density of retention trees did not differ between burned and unburned sites (analysis of variance, \( F_{1,38} = 2.011, p = 0.164 \)) and was not correlated with site age in burned\(^1\) (Pearson’s \( r = -0.386, p = 0.092 \)) or unburned sites (\( r = -0.318, p = 0.172 \)). The average age of the retention trees was 124 years (range 85-146 years). The dominant tree species among the retention trees was Scots pine (Pinus sylvestris) (55.4%) and birch (Betula spp.) (32.2%), but there were also some Norway spruce (Picea abies) and aspen (Populus tremula). The majority of the retention trees (81.5%) at the burned sites had died during the fire or after a few years’ delay, whereas the proportion of dead retention trees at the unburned sites was only 22.0%. The proportion of dead retention trees was not correlated with the age of the site among the burned sites (\( r = 0.181, p = 0.444 \)) or among unburned sites (\( r = -0.362, p = 0.117 \)). The youngest study sites were dominated by saplings of birch, whereas the proportion of Scots pine increased with the age of the site.

Sampling and Grouping of Beetles

We sampled beetles from the study sites with window-flight traps. The traps consisted of two crosswise-set transparent 40 × 60 cm plastic panes with a funnel and container below them (for detailed description, see Hyvärinen et al. [2006]). We used fully saturated saline water with detergent in the containers to preserve the beetles. To ensure random sampling, we set the traps hanging on a string between two trees or poles instead of setting them at obvious hotspots such as recently dead trees. We set five traps at random locations within a 1-ha area at each study site, making the total number of traps 200. The trapping period was 20 May through 20 July 2002, which covered at least part of the flying season of most of the beetle species in southern Finland.

We identified the majority of the beetles (99.6%) to species. The exceptions were females of genera Philhygra (Staphylinidae) and Euplectus (Staphylinidae), which were consistently identified to genus level, and a few beetles in the genera Atomaria, Corticaria, Cryptophagus, Gyrophaena, and Leioodes that could not be identified reliably. The nomenclature follows Silfverberg (2004).

In addition to counting the total abundance and species richness of beetles, we classified the species to five nonexclusive groups: saproxylic, nonsaproxylic, rare saproxylic, rare nonsaproxylic, and red-listed species. We classified saproxylic species based on Saalas (1917, 1923), Palm (1951, 1959), Koch (1989-1992), expert opinion, and on our own experience. Species recorded in <25 squares of a 100-km² area in Finland (Rassi 1993) were classified as rare. Species considered critically endangered (category CR of the World Conservation Union), endangered (EN), vulnerable (VU), or near-threatened (NT) in Finland (Rassi et al. 2001) were classified as red-listed species.

Statistical Analyses

We used the pooled data from the five traps of each study site in the analyses. At one of the burned sites, the traps were damaged by strong winds, and the number of beetles caught was therefore reduced. Thus, we excluded this site from the analyses but included the data from this
site in the presented total number of beetle species and individuals.

To analyze the abundance and species richness of the selected species groups, we used analysis of covariance into which burning (burned or unburned site) was entered as a factor and the number of large retention trees and time since logging were entered as covariates. We used the original number of retention trees instead of the current volume of dead wood because the latter is likely to be affected by burning (fire kills some of the retention trees) and by time since logging (the proportion of dead retention trees may increase with time). In addition, the relevant information for any management decision is how many retention trees should be initially left on a logged site to enhance future biodiversity.

We started the analyses with the full model, which included all the main effects and interactions, after which we removed nonsignificant interactions in a stepwise fashion from the model starting from the highest-order interactions (Hendrix et al. 1982). Because the interaction between burning and tree retention was significant in many cases, this interaction was left in all of the models to facilitate the comparison of results among species groups. Because of the interaction, we also standardized the number of retention trees so that we could define the main effect of burning at the mean of the covariate. In addition, we iteratively determined the level of retention trees above which the effect of burning was significant by scaling the number of retention trees such that we were able to repeat the analysis for each level of the covariate. For example, to analyze the effect of burning at 10 retention trees/ha we subtracted 10 from the original number of retention trees (for a detailed description of this method, see Hendrix et al. [1982]). We performed the analyses with SPSS 12.0. for Windows software (SPSS, Chicago, Illinois).

We used detrended correspondence analysis (DCA) with Canoco 4.0 for Windows (ter Braak 1987) to explore how burning, time since logging, and tree retention affected the composition of the assemblages of saproxylic species. The species that only occurred on one study site were excluded and the species abundance data were log10(x+1)-transformed before analyses. Detrending was performed with second-order polynomials. To statistically interpret the clustering in the ordination, analysis of covariance was used to investigate the effects of the factors on the loadings on axes 1 and 2.

Results

Total Species Richness and Abundance of Beetles

We recorded 697 beetle species (23,843 individuals), of which 594 (12,809 individuals) occurred at the burned sites and 485 (11,034 individuals) at the unburned sites. The number of beetle species ($R^2 = 0.72$) decreased with time since logging and was positively affected by burning (Fig. 1a), but the number of retention trees had no effect (Table 1). There was an interaction between burning and tree retention such that the difference between burned and unburned sites increased with the number of retention trees. With the iterative scaling of the covariate, we determined that the effect of burning was significant only if there were 12 or more retained trees per hectare.

The number of beetle individuals ($R^2 = 0.75$) decreased with time and was positively affected by burning (Fig. 1b), but the number of retention trees had no effect (Table 1).

![Figure 1. The number of (a) beetle species and (b) beetle individuals at burned and unburned logged sites in southern Finland relative to time since logging.](image-url)
Table 1. Analysis of covariance results for the effects of the time since logging, burning, the number of retention trees, and the interaction of burning and retention trees on the species richness and abundance of six (partly overlapping) species groups of beetles.

<table>
<thead>
<tr>
<th>Group</th>
<th>Variable</th>
<th>Number of species</th>
<th>p</th>
<th>Number of individuals</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>$F_{1, 34}$</td>
<td>p</td>
<td>$F_{1, 34}$</td>
<td>p</td>
</tr>
<tr>
<td>All species</td>
<td>time since logging</td>
<td>45.877</td>
<td>&lt;0.001</td>
<td>64.184</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>burning</td>
<td>18.919</td>
<td>&lt;0.001</td>
<td>8.930</td>
<td>0.005</td>
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<tr>
<td></td>
<td>retention trees</td>
<td>2.881</td>
<td>0.099</td>
<td>2.093</td>
<td>0.157</td>
</tr>
<tr>
<td></td>
<td>burning $\times$ retention trees</td>
<td>6.711</td>
<td>0.014</td>
<td>8.812</td>
<td>0.005</td>
</tr>
<tr>
<td>Saproxylic species</td>
<td>time since logging</td>
<td>29.329</td>
<td>&lt;0.001</td>
<td>26.842</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>burning</td>
<td>17.325</td>
<td>&lt;0.001</td>
<td>17.234</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>retention trees</td>
<td>4.120</td>
<td>0.050</td>
<td>8.244</td>
<td>0.007</td>
</tr>
<tr>
<td></td>
<td>burning $\times$ retention trees</td>
<td>8.412</td>
<td>0.006</td>
<td>14.491</td>
<td>&lt;0.001</td>
</tr>
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<td>Nonsaproxylic species</td>
<td>time since logging</td>
<td>32.698</td>
<td>&lt;0.001</td>
<td>52.054</td>
<td>&lt;0.001</td>
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<tr>
<td></td>
<td>burning</td>
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<td>0.007</td>
<td>1.085</td>
<td>0.305</td>
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<td>retention trees</td>
<td>0.435</td>
<td>0.514</td>
<td>0.019</td>
<td>0.892</td>
</tr>
<tr>
<td></td>
<td>burning $\times$ retention trees</td>
<td>1.640</td>
<td>0.209</td>
<td>1.614</td>
<td>0.213</td>
</tr>
<tr>
<td>Rare saproxylic species</td>
<td>time since logging</td>
<td>10.126</td>
<td>0.003</td>
<td>11.322</td>
<td>0.002</td>
</tr>
<tr>
<td></td>
<td>burning</td>
<td>34.035</td>
<td>&lt;0.001</td>
<td>44.368</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>retention trees</td>
<td>6.973</td>
<td>0.012</td>
<td>4.968</td>
<td>0.033</td>
</tr>
<tr>
<td></td>
<td>burning $\times$ retention trees</td>
<td>4.453</td>
<td>0.042</td>
<td>4.424</td>
<td>0.043</td>
</tr>
<tr>
<td>Rare nonsaproxylic species</td>
<td>time since logging</td>
<td>3.763</td>
<td>0.061</td>
<td>4.271</td>
<td>0.046</td>
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<tr>
<td></td>
<td>burning</td>
<td>0.726</td>
<td>0.400</td>
<td>0.587</td>
<td>0.449</td>
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<tr>
<td></td>
<td>retention trees</td>
<td>0.055</td>
<td>0.816</td>
<td>0.161</td>
<td>0.691</td>
</tr>
<tr>
<td></td>
<td>burning $\times$ retention trees</td>
<td>0.592</td>
<td>0.447</td>
<td>0.413</td>
<td>0.525</td>
</tr>
<tr>
<td>Red-listed species</td>
<td>time since logging</td>
<td>0.780</td>
<td>0.383</td>
<td>1.285</td>
<td>0.265</td>
</tr>
<tr>
<td></td>
<td>burning</td>
<td>16.597</td>
<td>&lt;0.001</td>
<td>18.856</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>retention trees</td>
<td>5.985</td>
<td>0.020</td>
<td>3.514</td>
<td>0.069</td>
</tr>
<tr>
<td></td>
<td>burning $\times$ retention trees</td>
<td>8.602</td>
<td>0.006</td>
<td>5.844</td>
<td>0.021</td>
</tr>
</tbody>
</table>

There was an interaction between burning and tree retention, and the effect of burning was significant only if there were 18 or more retention trees per hectare.

Saproxylic versus Nonsaproxylic Species

We recorded 291 saproxylic species (10,884 individuals), of which 257 (6,178 individuals) occurred at burned sites and 199 (4,706 individuals) at unburned sites. The number of nonsaproxylic species was 406 (12,959 individuals); 337 (6,631 individuals) were at burned sites and 286 (6,328 individuals) were at unburned sites. The number of saproxylic species ($R^2 = 0.67$) decreased with time, was positively affected by burning, and increased with the number of retention trees (Table 1). There was an interaction between burning and tree retention, and the effect of burning was significant only if there were 14 or more retention trees per hectare.

The number of saproxylic individuals ($R^2 = 0.69$) decreased with time, was positively affected by burning, and increased with the number of retention trees (Table 1). There was an interaction between burning and tree retention.

Rare Saproxylic versus Rare Nonsaproxylic Species

We recorded 33 rare saproxylic species (541 individuals), of which 30 (481 individuals) occurred at burned sites and 15 (60 individuals) at unburned sites. The number of rare nonsaproxylic species was 13 (30 individuals); 10 (17 individuals) at burned sites and 7 (13 individuals) at unburned sites. The number of rare saproxylic species ($R^2 = 0.63$) decreased with time (Fig. 2a), was positively affected by burning (Figs. 2a, b), and increased with the number of retention trees (Fig. 2b) (Table 1). There was an interaction between burning and tree retention, and the effect of burning was significant only if there were five or more retention trees per hectare. None of the factors affected the number of rare nonsaproxylic species ($R^2 = 0.25$) (Table 1).

The number of rare saproxylic individuals ($R^2 = 0.66$) decreased with time, was positively affected by burning, and increased with the number of retention trees. (Table 1). There was an interaction between burning and tree retention, and the effect of burning was significant only if there were two or more retention trees per hectare.
The number of rare nonsaproxylic individuals ($R^2 = 0.17$) only decreased with time, whereas the other factors had no effect (Table 1).

Four of the rare saproxylic species were fire dependent (Wikars 1997). When these species were excluded from the analysis, the number of rare saproxylic species ($R^2 = 0.61$) still decreased with time ($F_{1,34} = 9.319, p = 0.004$), was positively affected by burning ($F_{1,34} = 0.464, p < 0.001$), and increased with the number of retention trees ($F_{1,34} = 6.443, p = 0.016$). There tended to be an interaction between burning and tree retention ($F_{1,34} = 4.062, p = 0.052$).

**Red-Listed Species**

We recorded 12 red-listed species (59 individuals), of which 9 (51 individuals) occurred at the burned sites and 7 (8 individuals) at the unburned sites (Table 2).

**Table 2.** Number of individuals of red-listed beetle species recorded at the burned and unburned logged sites.

<table>
<thead>
<tr>
<th>Species</th>
<th>IUCN category*</th>
<th>Saproxylic</th>
<th>Burned sites</th>
<th>Unburned sites</th>
</tr>
</thead>
<tbody>
<tr>
<td>Platyribinus resinosus (Scopoli) (Anthribidae)</td>
<td>VU</td>
<td>yes</td>
<td>3</td>
<td>0</td>
</tr>
<tr>
<td>Zavallius brunneus (Gyllenhal) (Erotylidae)</td>
<td>VU</td>
<td>yes</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Ampedus suecicus Palm (Elateridae)</td>
<td>NT</td>
<td>yes</td>
<td>4</td>
<td>1</td>
</tr>
<tr>
<td>Eucinetus baemorrhoidalis (Germar) (Eucinetidae)</td>
<td>NT</td>
<td>no</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>Lacon conspersus (Gyllenhal) (Elateridae)</td>
<td>NT</td>
<td>yes</td>
<td>5</td>
<td>1</td>
</tr>
<tr>
<td>Lacon fasciatu (Linnaeus) (Elateridae)</td>
<td>NT</td>
<td>yes</td>
<td>8</td>
<td>2</td>
</tr>
<tr>
<td>Margarinotus purpurascens (Herbst) (Histeridae)</td>
<td>NT</td>
<td>no</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>Peltis grossa (Linnaeus) (Trogossitidae)</td>
<td>NT</td>
<td>yes</td>
<td>5</td>
<td>1</td>
</tr>
<tr>
<td>Rhipidius quadriceps de Perrin (Rhipiphoridae)</td>
<td>NT</td>
<td>no</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>Sphaeriestes stockmanni (Biström) (Salpingidae)</td>
<td>NT</td>
<td>yes</td>
<td>13</td>
<td>0</td>
</tr>
<tr>
<td>Tomoxia bucephala Costa (Mordellidae)</td>
<td>NT</td>
<td>yes</td>
<td>11</td>
<td>0</td>
</tr>
<tr>
<td>Xylotrechus rusticus (Linnaeus) (Cerambycidae)</td>
<td>NT</td>
<td>yes</td>
<td>1</td>
<td>0</td>
</tr>
</tbody>
</table>

*Abbreviations: VU, vulnerable; NT, near threatened.*
Figure 3. The number of red-listed beetle species at burned and unburned logged sites in southern Finland relative to (a) time since logging and (b) the number of retention trees.

The number of red-listed species ($R^2 = 0.46$) was not affected by time (Fig. 3a), but was positively affected by burning (Figs. 3a, b) and increased with the number of retention trees (Fig. 3b) (Table 1). There was an interaction between burning and tree retention, and the effect of burning was significant only if there were 14 or more retention trees per hectare.

The number of individuals of red-listed species ($R^2 = 0.45$) was not affected by time or by the number of retention trees, but was positively affected by burning (Table 1). There was an interaction between burning and tree retention, and the effect of burning was significant only if there were 12 or more retention trees per hectare.

Composition of Assemblages of Saproxylic Species

The DCA ordination (Fig. 4) revealed that the assemblages of saproxylic species were affected by burning (axis 1, $F_{1,54} = 36.167, p < 0.001$), suggesting that the species composition or at least the distribution of species abundances was different between burned and unburned sites. The assemblages changed with time since logging (axis 1, $F_{1,54} = 4.875, p = 0.034$; axis 2, $F_{1,54} = 10.917, p = 0.002$), indicating significant species turnover during the 16 years following logging. The number of retention trees also affected the assemblages (on axis 1, $F_{1,54} = 7.328, p = 0.011$), and the difference between burned and unburned

Figure 4. Results of detrended correspondence analysis (DCA) of the composition of assemblages of saproxylic beetles at burned and unburned logged sites in southern Finland relative to time since logging. Eigenvalues of axes are in parentheses.
sites increased with the number of retention trees (interaction of burning and tree retention: on axis 1, $F_{1.54} = 23.042, p < 0.001$).

**Discussion**

In contemporary Fennoscandia early stages of forest succession are seldom formed by natural disturbances; instead, they are formed by timber harvesting, usually through clearcutting. Given the numerous species adapted to the natural disturbance regime, it is important to determine whether feasible modifications of traditionally implemented forestry methods may enhance the survival of disturbance-associated species. Our main aims were to determine whether burning and leaving retention trees on logged sites improve the quality of these habitats for beetles and how the species richness and species assemblages change with time since logging.

**Effects of Burning and Retention Trees**

Burning and the number of retention trees had a positive effect on the abundance and species richness of saproxylic beetle species, whereas the abundance of nonsaproxylic beetles was not affected. There was also an interaction between burning and tree retention: the effect of burning on saproxylic species was significant only if the number of retention trees exceeded a particular value. Therefore, the usefulness of burning in terms of conservation depended strongly on the number of retention trees. When a logged site is burned, at least some of the retention trees are instantly killed or weakened. Thus, the availability of dead wood resources increases after fire, and this is likely to be the main reason for the observed pattern among saproxylic species. Although saproxylic species associated with warm open habitats may also prefer the burned environment, the successful colonization of burned habitats requires that enough resources be formed during the fire. In some recent studies, tree retention on burned sites has had only minor short-term effects on species richness (e.g., Hyvärinen et al. 2006b), but our results confirm that when the time scale is extended beyond the very first years after burning, the positive effect of retention trees becomes evident.

Species richness alone may be an inadequate indicator of the conservation value of a particular site. For example, the early successional stages of anthropogenic origin are fairly species-rich habitats because of the sun-exposed conditions and the wealth of logging residue that provide suitable, but temporary, habitat and substrate for saproxylic species (Sippola et al. 2002). Thus, to evaluate the effects of natural disturbance–based forest management strategies, species that are unlikely to persist in managed forest landscapes should be the focus.

The groups of rare saproxylic and red-listed species are representative examples of such species. Burning combined with the presence of retention trees had a positive effect on these species groups. Rare saproxylic species benefited especially from burning because their numbers were already elevated at sites with relatively few retention trees. This may be partly because the group included four species (Cryptophagus corticinus Thomson [Cryptophagidae], Denticollis borealis [Paykull] [Elatidae], Platyrhinus resinosus [Scopoli] [Anthribidae] and Sphaeriestes stockmanni [Biström] [Salpingidae]) that are considered fire dependent (Wikars 1997) and that were consistently recorded at the burned sites only. Typically, these species persist at the burned sites only for a few years after fire, and this was evident in this study. Only 1 of 16 individuals occurred at a burned site that was older than 6 years. Nevertheless, the effect of burning and retention trees was not solely due to fire-dependent species because the results remained the same when these species were excluded from the analysis.

The interaction between burning and tree retention suggests also that the effect of retention trees on the species richness of unburned sites was weak. Although retention trees make logged sites more closely resemble natural disturbance areas, the proportion of dead retention trees was low at the unburned sites probably due to the management history of these sites. Nevertheless, leaving retention trees on unburned sites is likely to be beneficial because it increases the future volume of dead wood but it may take several decades for any effects to appear.

**Effect of Time**

Making predictions over the long term is essential for any management or conservation effort. The abundance and species richness of saproxylic species were highest during the first years after burning or logging and decreased with time since logging. Particularly high numbers of rare species were recorded at some of the burned sites that were 3–8 years old. The assemblages of saproxylic species also changed with time, and the assemblages of burned and unburned sites were more similar to each other among oldest study sites (see Fig. 4). Again, a decrease in total species richness, in particular when there is significant species turnover, does not necessarily mean decreased conservation value. Nevertheless, the fact that the group of rare saproxylic species was negatively affected by time since logging suggests that the quality of the burned habitat decreases with time. The lack of effect of time among red-listed species is interesting, but may have been due to the low power of the analysis (because of the relatively low number of species per site, high variation, and zero values among unburned sites).
Species richness is likely to decrease with time because of canopy closure and depletion of dead wood resources, the recruitment of new dead wood being typically very slow during the first decades after logging (Sippola et al. 1998, 2002). At the burned and logged sites, the original volume of retention trees was relatively low, and the proportion of dead trees did not increase with time, which suggests that the majority of retention trees died during the fire and that after the fire the formation of dead wood was negligible. This, together with the fact that the occurrence of the majority of saproxylic beetles is restricted to the first years after tree death (Jonsell et al. 1998) gives good reason to predict that burned, logged sites are unlikely to offer resources for saproxylic species for more than 10 to 15 years. Thus, burned logged sites form a quite different postfire habitat than natural fire areas. After a natural fire, the volume of dead wood is particularly high and this stage may last for several decades (Siitonen 2001; Pedlar et al. 2002).

Methodological Notes

Our finding that species richness decreased with time may be confounded by the fact that the flying activity of beetles is likely to decrease with site closure, which reduces sampling efficiency. Therefore, our results may underestimate the species richness at older study sites. Nevertheless, sampling efficiency is not likely to differ between burned and unburned sites of the same age because they represent structurally similar habitats. Immediately after fire, beetles are attracted to burned sites by heat and volatile compounds; these early colonizers may also include species that are not likely to reproduce at these sites. Nevertheless, the attraction is not likely to last longer than the very first years following fire and thus the assemblages of the older burned sites consist of species that have reproduced successfully. Differences in sampling efficiency or in “false” attractiveness of the sites are also not likely to cause the strong effect that the interaction between burning and the number of retention trees had on the species richness of saproxylic beetles.

Management and Conservation Implications

Today, forest-restoration efforts occur frequently in protected areas in southern Finland. These areas have a long management history and therefore do not meet the criteria of natural forests (Kuuluvainen 2002). Our results for the medium-term responses of saproxylic species to fire and tree retention are likely to be applicable to predicting the effects of these restoration actions, although restored areas may provide resources for saproxylic species for a considerably longer time than the burned logged sites because of higher levels of tree retention.

More important, our results are likely be helpful in evaluating the effects of forest management practices that aim to increase the availability of habitats and resources and thus enable specialized species to persist in currently managed forest landscapes. Our results show that burning of logged sites, provided that an adequate number of retention trees are left on sites, can be used as a tool to improve the quality of the matrix outside protected areas and in particular to create habitats for disturbance-associated species. Nevertheless, the burned logged sites may remain suitable habitats for a limited time only; thus, the continuity of the habitats must be ensured.

The feasibility of burning and tree retention in commercial forests depends on economic costs. The costs can be reduced by selecting weakened trees and tree species of lower economic value for retention. Burning of logged sites is laborious, and it is not profitable to burn areas of <5 ha (Metsätalouskehittämiskeskus Tapio 2006), but burning also can be considered advantageous from the manager’s point of view because it increases nutrient availability and decreases soil acidity (Metsätalouskehittämiskeskus Tapio 2006). Thus, there should not be severe economic constraints on the implementation of burning and tree retention.

Intensive forest management is currently posing a significant threat to forest biodiversity, and there is an increasing interest in the development of natural disturbance-based forest management and conservation strategies in northern Europe (e.g., Angelstam 1998) and in the boreal zone of North America (e.g., Bergeron et al. 2002). Saproxylic species provide a feasible group through which to study the effects of management and restoration, and because the ecological requirements of the species are likely to be the same outside the study region, the results are likely to be applicable over the circumpolar boreal forest zone.

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