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Tero Toivanen

Short-term Effects of Forest Restoration on Beetle Diversity

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ABSTRACT

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The need for forest restoration to create structural elements and resources important for biodiversity is widely recognized. In boreal forests, restoration activities are frequently based on mimicking the disturbance dynamics of natural forests, reintroducing fire to forest ecosystem and increasing the volume of dead wood being the most common practices. The aim of this thesis was to explore the effects of forest restoration on beetle diversity, and in particular on a group that is most likely to benefit from the restoration activities, dead wood dependent (saproxylic) beetles. The results are based on a large-scale restoration experiment conducted in southern Finland, in which controlled burning and partial harvesting of managed forest combined with down wood retention were applied as restoration tools. In addition, I studied the importance of two currently recommended forest management practices, burning of and leaving retention trees on logged sites. I found that fire can be successfully used to increase beetle diversity in managed forests and in particular rare saproxylic species benefit from fire. Also partial harvesting increased beetle diversity, but the volume of down wood retention had no clear short-term effect. In general, fire had a positive effect on resource quality, but the effect was different between tree species such that while birch-living species consistently benefited from fire, the effect was much weaker among spruce-living species. As forest management practice, the usefulness of burning was strongly dependent on the level of tree retention: fire had a positive effect on beetle diversity only if an adequate number of retention trees was left on the logged site. Finally, I found that forest restoration is unlikely to cause any risk of bark beetle –induced forest damage in nearby commercial forests. The results are likely to be helpful in planning future restoration activities but further monitoring is needed to clarify the long-term effects of restoration.

Key words: Biodiversity; dead wood; disturbance; forest fire; forest management; restoration; saproxylic species

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CONTENTS

LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following original studies, which are referred to in the text by their Roman numerals (I-IV). I am the corresponding author in all the articles, and have done a substantial part of the field and identification work in each study.

I Toivanen, T., & Kotiaho, J.S. 2007. Mimicking natural disturbances of boreal forests: the effects of controlled burning and creating dead wood on beetle diversity. Biodiversity and Conservation, in press.

II Toivanen, T. & Kotiaho, J.S. 2007. Does forest restoration alter the suitability of dead wood resources for saproxylic beetle species? Manuscript (submitted).

III Toivanen, T., Liikanen, V. & Kotiaho, J.S. 2007. The effect of forest restoration on bark beetle populations: does restoration cause a risk of pest-induced damage in commercial forests? Manuscript (submitted).

IV Toivanen, T. & Kotiaho, J.S. 2007. Burning of logged sites as tool to protect beetles in managed boreal forests. Manuscript (submitted).

1 INTRODUCTION

1.1 The history of boreal forest landscape

Boreal forests cover an area of about 14 million km^2 that comprises about 20% of the forest cover worldwide. In Fennoscandia, boreal forests are the dominant biome (Esseen et al. 1997) that has a long utilization and management history dating back to ship construction and tar production in the 18th century and slash-and-burn cultivation in the 19th century. However, the most dramatic changes in the boreal forest ecosystem have occurred during the last 50 years due to modern forest management for timber production. Although the total area covered by forests has not decreased and the volume of timber in the forests has even increased (Peltola 2005), important alterations have occurred in the structure and dynamics of the forests. The factors that have lead to the decline of biodiversity in the boreal forests include e.g. the loss of old-growth forests (Esseen et al. 1997), fragmentation at landscape level (Mladenoff et al. 1993, Komonen et al. 2000, Kouki et al. 2001), the structural simplification within stands (Axelsson & Östlund 2001), the alteration of disturbance dynamics (Esseen et al. 1997), and the decline of the quality and quantity of resources, in particular the attributes of dead wood (Friedman & Walheim 2000, Siitonen 2001, Rouvinen et al. 2002). For example, in southern Finland natural forests cover today less than 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 specialized to live in natural forests are likely to eventually go extinct (Hanski 2000). Consequently, the main problem of ecosystem management and species conservation is how to maintain viable populations of specialized species in managed forest landscapes (Kuuluvainen 2002).

1.2 Disturbances in boreal forests

The contemporary paradigm in ecology views ecosystems as dynamic and non-equilibrial in contrast to the former "balance of nature" –view (Wu & Loucks 1995). In conjunction with the prevailing view, disturbances of variable scale and intensity can be seen as main driving forces in ecosystems (Attiwill 1994). In boreal forests, disturbances range from large stand-replacing events such as forest fires and windstorms that shift a particular habitat to a new successional trajectory to small-scale gap-dynamics represented by deaths of individual trees operating in e.g. old-growth forests (Niemelä 1999, Kuuluvainen & Angelstam 2004). Disturbances create multiscale heterogeneity to the ecosystems (Lilja 2006) by modifying canopy structure and enhancing the formation of multilayered, uneven-aged forest (Östlund et al. 1997, Axelsson & Östlund 2001), increasing the diversity of forest floor microhabitats (Kuuluvainen & Laiho 2004) and increasing the volume and diversity of dead wood (Siitonen 2001,).

Today, natural large-scale disturbances in boreal forests have been almost exclusively replaced by methods of commercial forest management, in particular clear-cutting. Although dynamics driven by forestry may seem superficially similar to natural disturbance –driven dynamics, there are several fundamental differences (see Niemelä 1999). Clear-cut areas lack the structural heterogeneity typical of e.g. burnt forests and there is a substantial difference in the volume and quality of dead wood. In addition, the short and fixed rotation times of managed forests do not allow forest characteristics typical of biologically old forests to develop.

1.3 Forest fire in northern boreal ecosystems

Forest fires are generally regarded as a major disturbance of unmanaged boreal coniferous forests (Wein & McLean 1983, Esseen et al. 1997). In Fennoscandia, an average fire interval of 50-120 years during the last thousand years has been generally accepted (e.g. Zackrisson 1977, Engelmark 1984, Niklasson & Granström 2000, Wallenius et al. 2004) but the role of human impact on the fire regime has recently caused some debate. 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 ignition and spread probability according to e.g., latitude, forest type, and topography and fire regimes are also known to vary through time according to climatic fluctuations (Johnson et al. 1998). 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. Pine-dominated forests are likely to be characterized by shorter fire rotation time than spruce forests (Zackrisson 1977, Engelmark 1987, Wallenius 2002). However, fires in pine forests are typically of lower intensity allowing at least the largest trees with thick bark to survive, while in spruce forests large-scale stand-replacing fires can occur especially during dry climatic periods (Axelsson & Östlund 2001).

In any case, the efficient fire fighting and the removal of burning fuel (dead wood in particular) from the forests have dramatically reduced the number and sizes of forest fires during the last century. The average annual area burnt by wildfires in Finland has decreased from over 10,000 ha (ranging up to 70,000 ha in some years) in the late 19th century (Saari 1923, Sevola 1999) to about 500 ha during the last three decades (Peltola 2004). As forest regeneration method, controlled burning of logged sites was introduced in Finland in the 1920s and the peak was reached in the 1950s when over 30,000 hectares were burnt annually. Since the decline of the method in late 1960s, the total area burnt has remained at 500-1000 hectares a year (Sevola 1999). Today, burning of logged sites is again a recommended forest management practice but the consequences of this recommendation are yet to be seen. As a restoration practice, controlled burning of standing or partly harvested forest has also been recently adopted in Finland with about 100 hectares burnt annually mainly on state-owned lands (Hokkanen et al. 2005).

1.4 The importance of dead wood and fire for species diversity

The volume of dead wood in natural boreal forests varies between 20 and 120 m^3/ha decreasing with the decrease of forest productivity from south to north (Siitonen 2001). In contrast, in managed forests within most parts of Fennoscandia the volume of dead wood is only 4 to 10 m^3/ha (Jonsson et al. 2005). Dead wood is widely seen as one of the most essential elements in forest ecosystems and for example in Finland there are about 5000 species that are dependent on dead wood or on another dead wood dependent organism (see Speight (1989) for the definition of saproxylic species). This number comprises 20-25% of all forest-dwelling species (Siitonen 2001). The abundance and species richness of saproxylic species have been shown to increase with the total volume and diversity of dead wood and with the diameter of individual dead trees and to be dependent on the decay stage of the dead wood (e.g. Jonsell et al. 1998, Kruys et al. 1999, Martikainen et al. 2000, Penttilä et al. 2004). Not surprisingly, saproxylic species have been adversely affected by modern forest management (see Grove 2002), and the decline of saproxylic species in Finland is well illustrated by the fact that 60 % of the threatened or extinct beetle species that are associated to forest habitats are saproxylic (Rassi et al. 2001).

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 (Pedlar et al. 2002, Siitonen 2001). In particular, the young successional stages created by fire or other disturbances are important habitats for saproxylic species (Kaila et al. 1997, Jonsell et al. 1998, Martikainen 2001, Similä et al. 2002, Sverdrup-Thygeson & Ims 2002). In addition to the pyrophilous species that are conspicuously favoured by fires (Wikars 1997), many other species benefit from fire or are attracted to burnt habitats (Muona & Rutanen 1994, Hyvärinen et al. 2005, 2006). For example, the species richness of rare and threatened saproxylic beetle species (Similä et al. 2002, Hyvärinen et al. 2006) and polypore fungi (Penttilä 2004) have been observed to be particularly high at post-fire stands.

1.5 Restoration

The need of developing restoration-oriented forest management strategies has been widely recognized in Fennoscandia during the last decade (Angelstam 1998, Kouki et al. 2001, Kuuluvainen et al. 2002). Restoration has been defined to aim at the rehabilitation of natural structures, processes and species composition in ecosystems altered by human actions (Bradshaw 1997). Although the protection of pristine ecosystems must still be regarded as the primary option in nature conservation, restoration may well be used to complement the conservation efforts by improving the quality of matrix outside reserves (Kouki et al. 2001). Even within conservation areas, which may have a long history of forest utilization and of which only a small proportion can be classified as natural or nearly natural in Southern Finland, restoration is likely to be needed to accelerate the formation of structural and habitat features typical of natural forests (Kuuluvainen 2002). In managed forests, restoration may help to increase the connectivity between protected areas and it is suggested to be most efficient when the restoration efforts are directed to areas close to existing source areas, e.g. old-growth forests (Hanski 2000, Kouki et al. 2001).

In Fennoscandian boreal forests, the guideline of restoration has been to mimic the disturbance dynamics of natural forests (Kuuluvainen et al. 2002). This approach is based on the assumption that species are adapted to the disturbance regime of the forest type they occupy (Niemelä 1999). The restoration practices that aim at creating structural elements and resources important for biodiversity are suggested to have their greatest potential on young rather than on old successional stages, because the properties lost from managed forests may be more easily restored to young forests (Kouki et al. 2001). Thus, while the short-term goal of restoration is to improve the quality of habitats such that they can maintain populations of rare and threatened species, the long-term goal is to bring a particular stand to a more natural successional trajectory and, at larger scale, to create a natural mosaic of habitats representing different successional phases such that habitats for species populations occurring in a given area are provided (Kuuluvainen 2002).

1.6 Aims of the thesis

For any management or restoration action to be successful, we should be able to predict the changes in species richness and species assemblages. So far, there has been a lack of experiments dealing with different aspects of restoration (Kuuluvainen et al. 2002). The aim of this thesis was to yield information for planning and conducting future restoration actions. I focused on the effects of forest restoration on a species group that is likely to benefit from restoration actions, saproxylic beetles (Coleoptera). The specific questions were:

(1) To determine the short-term effect of forest restoration (fire, partial harvesting and down wood retention) on the abundance, species richness, and species assemblages of beetles in spruce-dominated forests (I)
(2) To determine whether rare and red-listed beetle species benefit from the restoration actions (I, II)
(3) To determine whether restoration alters the suitability of dead wood resources for saproxylic beetle species (II)
(4) To study the effect of restoration on bark beetle populations and to evaluate whether there is a risk of forest damage in surrounding commercial forests (III)
(5) To determine the effects of restoration-like forest management practices (burning and leaving retention trees on logged sites) on beetle diversity (IV)
(6) To predict the long-term effects of fire and retention trees (IV)

2 MATERIAL AND METHODS

2.1 Study area

The study area was located at the municipalities of Lammi and Padasjoki in Southern Finland (61°11N, 25°05E), within the south boreal vegetation zone (Ahti et al. 1968). The area has a long forest management history but there still exist some patches of old-growth forest (e.g. Vesijako strict natural reserve at Padasjoki and Kotinen and Sudenpesänkangas at Lammi). There is also an exceptional fire continuum in the region of Evo due to prescribed burning activities that were started during the 1950s. Consequently, source populations of specialized saproxylic species as well as those of fire-dependent species are still likely to survive within the area making the area rather suitable for studying the effects of restoration.

2.2 The experimental setups

2.2.1 The restoration experiment (I, II, III)

In year 2002, a large-scale restoration experiment consisting of 24 study plots of about two hectare area was established. The study plots were managed mesic forests of *Vaccinium-Myrtillus* site type (Cajander 1949) of about 80 years of age. 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 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 study plots was Norway spruce (*Picea abies*) (over 90% of the volume of standing trees) with some birch (*Betula spp.*) and Scots pine (*Pinus sylvestris*).

In the experimental design (Figure 1), the treatments were partial harvesting (50 m^3/ha of standing trees were left on the harvested plots) with down wood retention (six unharvested plots; six harvested plots with 5 m^3/ha of down wood; six harvested plots with 30 m^3/ha of down wood; and six harvested plots with 60 m^3/ha of down wood) and controlled burning (12 of the plots were burnt and 12 were left unburnt). Each treatment combination was replicated three times and the treatments were randomized among the study plots.

The harvesting treatments were conducted in February and March 2002 and the burnings were conducted in June-August 2002 (for detailed description of the experiment, see Lilja et al. 2005). The fires were mainly ground fires with occasional jumps to the canopy, At the unharvested plots, the fires were of low intensity and the direct mortality of standing trees was thus low. At the harvested plots, the intensity of fire increased with the amount of cut down wood (Lilja et al. 2005).

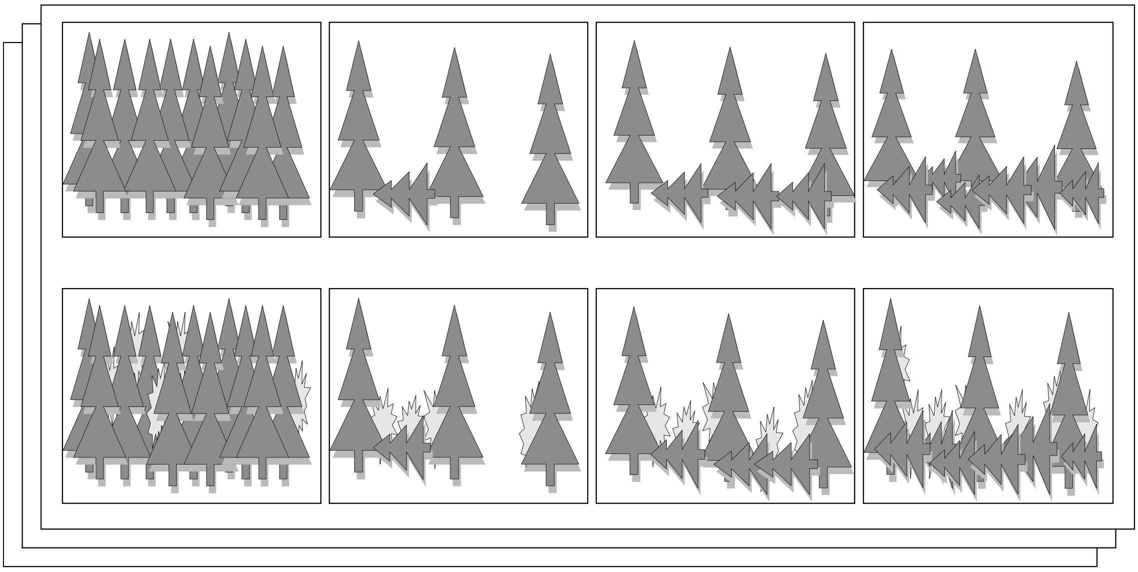

FIGURE 1 The experimental design in the restoration experiment.

2.2.2 The correlative study (IV)

The correlative study was conducted at 40 logged sites on which some retention trees had been left; 20 of the study sites had been burnt after logging. The study sites had been logged from 1 to 16 years ago. The sites were located within 12 x 7 km area and the burnt and unburnt sites were geographically intermixed within that area. The average area of the burnt sites was 5.5 ha (range 2—9 ha) and the average area of the unburnt sites 3.1 ha (range 0.8—9 ha). There were 18.8±12.4 large retention trees (DBH > 20 cm) per hectare at the burnt sites and 25.0±15.0 large retention trees per hectare at the unburnt sites. The dominant tree species among the retention trees were Scots pine and birch but there were also some Norway spruce and aspen (*Populus tremula*). The majority of the retention trees (81.5%) at the burnt sites had died during the fire or after a few years delay while the proportion of dead retention trees at the unburnt sites was only 22.0%. The youngest study sites were dominated by saplings of birch while the proportion of Scots pine increased with the age of the site.

2.3 Sampling and data processing

2.3.1 Study species

Beetles (Coleoptera) represent an important part of biodiversity since they are the most species rich order worldwide with over 350 000 species described so far. In Finland, 3670 beetle species have been recorded (Silfverberg 2004), of which about 2000 are associated to forest habitats (Siitonen 2001). Due to the high number of species and the variable ecological requirements of the species, beetles are an exceptionally suitable group for studying the effects of conservation, management and restoration. However, this requires large samples and time-consuming identification work including many difficulties in identifying the specimens. Worldwide, the use of beetles in ecological studies is further complicated by the wealth of undescribed species. In Fennoscandia, there is a long entomological tradition and hence the researchers have the privilege of being able to exploit the extensive knowledge of the beetle fauna of the region. In addition, the ecological requirements of the species, in particular those of saproxylic species are also reasonably well known (e.g. Saalas 1917, 1923, Palm 1951, 1959, Koch 1989-1992, Ehnström & Axelsson 2002).

2.3.2 Sampling of beetles

We sampled beetles with window traps. The traps consisted of two crosswise-set 40x60 cm transparent plastic panes with a funnel and container below them. Saline water with detergent was used in the containers to preserve the beetles. The traps were emptied at every three or four weeks.

In studies I and IV, the sampling design consisted of five free-hanging window traps that were randomly placed at the plots. The traps were set hanging from a string between two trees or poles. In study II, we used window traps that were attached to standing dead trees. The upper edge of the funnel was formed heart-shaped such that the length it touched the tree trunk was about 25 cm. In study III, we used the same traps as in studies I and II. In addition, we constructed a line consisting of six freely hanging window traps. The line was perpendicular to the edge of the study plot and it extended 100 m outside the plots.

The sampling periods were: (I) 10 May – 10 September 2003; (II) 10 May – 10 July 2003 and 10 May – 10 July 2004; (III) 10 May – 10 July 2003; and (IV) 20 May – 20 July 2002.

2.3.3 Identification and classification of beetles

The majority of the trapped beetles (99.6 to 99.9% in the different studies) were identified to species. The identification of females of genera *Philhygra* and *Euplectus* (Staphylinidae) was left to genus level as a rule. In addition, odd beetles of e.g. genera *Acrotrichis*, *Atheta*, *Atomaria*, *Corticaria*, *Cryptophagus*, *Leiodes* and *Oxypoda* could not be reliably identified. The nomenclature follows Silfverberg (2004). In total, the data of the four studies consists of 249045 beetle individuals representing 1005 species.

In studies I, II and IV the beetles were classified to saproxylic and non-saproxylic species according to relevant literature (Saalas 1917, 1923, Palm 1951, 1959, Koch 1989-1992), expert opinions and our own experience. Only obligatorily saproxylic species were classified as saproxylic. In study II, only obligatorily saproxylic species were included in the analyses. In addition, beetles were classified to rare species (the species recorded in up to 25 squares of 100km^2 in Finland) according to Rassi (1993), red-listed species (species classified as threatened or near threatened in Finland) according to Rassi et al. (2001) and pyrophilous (fire-dependent) species according to Wikars (1997)

2.3.4 Analyzing the data

In studies I, II, and III, factorial ANOVA was used to analyze the effects of fire, harvesting with down wood retention and tree species (II) on the abundance and species richness of beetle groups and on the abundance of individual species. If there were interactions between the factors, simple effects tests followed by pairwise comparisons were used to investigate the interactions in detail. In study IV, analysis of covariance was used to explore the effects of fire, retention trees and time since logging on the species richness and abundance. These analyses were performed with SPSS 13.0 for Windows (SPSS Incorporated). Detrended correspondence analysis with Canoco 4.0 for Windows (ter Braak 1987) was used to interpret the compositional variation in beetle assemblages (I, II, IV). Species accumulation patterns (II) were investigated with EstimateS computer program (Colwell 2005).

3 RESULTS AND DISCUSSION

3.1 The short-term effect of fire

Fire increased the abundance and species richness of beetles at the study plots and modified strongly the beetle assemblages (I). The effect was quite similar among saproxylic and non-saproxylic species, but when rare species were considered, only the species richness and abundance of rare saproxylic species were increased by the fire while the number of rare non-saproxylic species was not affected by the fire. Fire had also a positive effect on the abundance and species richness of red-listed beetle species.

Large-scale disturbances such as forest fire lead to a dramatic habitat alteration and the species turnover is likely to be high as species of old forests disappear and species favouring open habitats increase. Thus, the general increase of species richness after fire, in particular that of non-saproxylic species, may be due to the increase among species favouring open habitats. Beetles are also likely to prefer the warm and sun-exposed burnt environment and the heat and odors of freshly burnt sites may attract more colonizing beetles. However, the increase among saproxylic species is most likely to be due to the increased availability of resources since a large proportion of retention trees were killed or weakened in the fire. The number of rare saproxylic species increased after fire, which suggests that fire can be successfully used to create habitats and resources for specialized saproxylic species. In contrast, the non-saproxylic species colonizing burnt areas are more likely to be common generalist species of open habitats, since there was no change in the number of rare non-saproxylic species. However, also non-saproxylic species may benefit from the increase in the amount of dead wood since they may use dead wood as habitat or shelter. In addition, many of the non-saproxylic species that showed most dramatic increase after fire can be classified as facultative saproxylics that are able to utilize e.g. some species of corticoid fungi (Penttilä & Kotiranta 1996) and in particular the ascomycete fungi (Petersen 1970, Wikars 2002) that rapidly colonize burnt trees.

In general, fire had also a positive effect on the abundance and species richness of saproxylic beetles in individual trees (II). However, the effect of fire was dependent on tree species such that the abundance of beetles was lower in burnt spruces than in unburnt dead spruces while birch-living species consistently benefited from fire. This was mostly due to the fact that many primary colonizers such as bark beetles (III) were far less abundant in burnt spruces. These species have been reported to avoid fire-scorched trees that desiccate very rapidly (e.g. Wikars 2002) and that thus may not provide as good resource for the phloem-feeding primary colonizers as the unburnt dead trees do. The species richness of saproxylic beetles was increased by fire both among spruces and among birches, but the increase was much smaller among spruces. The positive effect of fire on species richness in individual trees may be due to e.g. reduced competition, increased variability of resources or microhabitats, beetles preferring the burnt environment to unburnt environment, or beetles normally utilizing only a particular tree species or genus being able to use different species of burnt wood. The last explanation is supported by the fact that the beetle assemblages of burnt spruces and birches were more similar to each other than those of unburnt spruces and birches, but this may also be due to that the beetle assemblages of burnt wood are to a large extent dominated by generalist species.

3.2 The effect of partial harvesting

Partial harvesting, combined with leaving variable volumes of down wood, had a positive short-term effect on beetle diversity at the study plots (I). The effect of harvesting was dependent on fire: among unburnt plots harvesting had a consistent positive effect on species richness and abundance of beetles, but among burnt plots the abundance of beetles did not differ between unharvested and harvested plots. However, the species richness of beetles was higher at harvested plots than at unharvested plots also among burnt plots.

Partial harvesting increased the species richness of both saproxylic and non-saproxylic species. When rare and red-listed species were considered, harvesting tended to increase the number of rare saproxylic species but it did not have significant effect on the number of red-listed species. The beetle assemblages were strongly affected by harvesting both at burnt and at unburnt sites.

Partial harvesting is likely to lead to a similar, albeit smaller, change in species assemblages as burning such that species requiring closed forests decrease and species favouring open habitats increase. In addition to the down wood created on the plots, harvesting also increases the availability of resources for saproxylic species via increased amount of logging residue such as cut stumps, branches and tops of trees (Sippola et al. 2002). The odours of freshly logged areas may also attract colonizing beetles to harvested sites. The interaction between burning and harvesting is easily explained by the fact that harvesting with down wood retention had a much larger effect on the amount of resources among unburnt plots. Among the burnt plots, fire reduced the difference between harvested and unharvested plots because a substantial part of standing retention trees were killed or weakened in the fire both at harvested and at unharvested plots and because the down retention trees may have lost their value as a resource because they burnt very heavily (see below). Thus, the equal amount of resources is likely to explain why the abundance of saproxylic beetles did not differ between harvested and unharvested burnt plots. The increase of species favouring open habitats may explain that there were more species at the burnt harvested than at the burnt unharvested plots.

Partial harvesting affected also the number of beetle individuals and species colonizing dead standing trees (II). However, while the positive effect of harvesting was evident during the first post-fire-year during the second year harvesting had only minor effects. In addition, in the second year there was a three-way interaction between burning, harvesting and tree species that arose from harvesting having a negative effect among unburnt spruces. The primary colonizers that dominated the beetle assemblages in the first year are known to favour disturbance areas and consequently, the sun-exposed harvested sites (Jonsell et al. 1998). Trees at harvested (sun-exposed) sites may desiccate more rapidly than trees at unharvested (shaded) sites. Trees at harvested sites may also be more rapidly colonized and thus the resource depletion is likely to be faster. Although sun-exposition is often regarded as major factor that increases the species richness of saproxylic species, our results, in particular those concerning spruces, suggest that the positive effect of sun-exposition on the species assemblages of individual trees might be restricted to the very first years following disturbance.

3.3 The effect of down wood retention

The volume of dead wood has been indicated to be a major factor influencing the species richness of saproxylic beetles in several studies. Since the positive effect of burning on species richness in this study was also likely to be due to increased availability of dead wood resource, it was surprising that the volume of down wood left on harvested sites had no clear short-term effect (I). At burnt plots, it seems likely that the standing retention trees (the volume of which was equal at the harvested sites) that typically die during the fire or after a few years delay form the major resource for saproxylic beetles. In addition, the value of the down retention trees is likely to be dependent on fire intensity such that the retention trees that burn most intensively attract less beetles (Saint-Germain et al. 2002). Because the fires were most intense at the sites with the highest volume of down wood retention, the higher volume of dead wood may have been counteracted by the decline in the quality of resource.

At unburnt plots, the lack of effect of the volume of down retention trees is more difficult to explain. However, one plausible explanation is the abundance of logging residue at the harvested plots that is known to be utilized by several saproxylic species during the first post-logging years. Because the amount of logging residue was equal among all the harvested plots, the proportional differences in the amount of resource were smaller between the treatments. In addition, the number of beetles colonizing the harvested plots may also have been restricted by the size of source populations. This explanation is supported by the result that the abundance of *Pityogenes chalcographus* in the unburnt standing trees was negatively affected by the volume of down retention trees on the plots (III). In a concurrent study that was conducted at the harvested plots (Eriksson et al. 2006), the number of down retention trees colonized by bark beetles was also negatively correlated with the volume of retention trees.

3.4 The importance of early successional stages for species diversity

The results confirm that a substantial part of saproxylic species have the ability to quickly locate new resources and disperse to the restored forests. The most striking example of dispersal ability comes from pyrophilous species that are able to detect the resources from tens of kilometres distance (e.g. Evans 1966). However, also other species that are adapted to ephemeral habitats such as disturbance areas are likely to have great dispersal potential (Southwood 1962, Jonsson et al. 2005). In contrast, species that are adapted to old-growth forest and that require forest continuity are likely to have weak dispersal abilities (Jonsson et al. 2005). Thus, forest restoration is likely to have its greatest potential in creating habitats for species that require large quantities of dead wood located at habitats representing early successional stages.

The majority of the threatened saproxylic species have been traditionally associated to old-growth forests. However, this may be partly due to that the old-growth forests are currently the only habitat where enough dead wood is provided, since the impact of forest management has been particularly high on the volume of dead wood at forests of early successional phases (Kouki et al. 2001, Uotila et al. 2001, Siitonen 2001). It is likely that a substantial part of the threatened species are more dependent on the availability of resources than e.g. on the microclimate of old-growth forest, and there is some evidence that many threatened species that are traditionally associated to old-growth forests may even prefer disturbance areas with wealth of dead wood (see Jonsell et al. 1998, Martikainen 2001, Similä et al. 2002).

The success of restoration by the means of imitating natural disturbances requires that two assumptions are true. First, the species must be adapted to the disturbance regime of the particular forest type (Niemelä 1999), and second, the disturbance that is imitated must be typical of the forest type. In spruce-dominated forests, forest fires are likely to be naturally scarce and unpredictable (but they can be large and stand-replacing when they occur) (Kuuluvainen 2002) and hence a substantial part of the species inhabiting dead spruces may not be adapted to burnt sites. Although burning seemed to have a positive short-term effect on the species richness and abundance of beetles, the effect on resource quality differed between tree species such that while the birch-living species consistently benefit from burning, there was no clear effect among spruce-living species. Therefore, the usefulness of reintroducing fire into spruce-dominated landscapes, or that of creating habitats that imitate the structure of post-fire areas, should be critically considered. However, assessing the success of restoration must not be based on how it affects on one particular resource. In addition to being a natural and efficient way to create large quantities of dead wood that is essential for the persistence of many saproxylic species of boreal forests, burning promotes the formation of deciduous successional stages in spruce forests and creates structures and resources that are likely to be important during the later stages of forest succession.

3.5 The risk of forest damage

Restoration actions that include creating substantial volumes of dead wood can be seen to form a contradiction with the traditional view of “forest hygiene” and thus the possible negative effects of restoration must also be considered. One negative effect could arise from forest damage in surrounding areas caused by bark beetles that are likely to increase due to restoration. The abundance of bark beetles was increased by burning and harvesting with down wood retention, being highest at the sites that were both burnt and harvested (III). This was likely due to burnt sites offering most resources for bark beetles, while the quality of resources was in fact decreased by burning (see also Eriksson et al. 2006). The volume of down wood on the harvested plots had only minor effects on the abundance of bark beetles, which may be due to that the number of colonizing individuals was restricted by the size of source populations and that at the burnt plots the quality of the down wood resource decreased with the intensity of fire (Eriksson et al. 2006). The abundance of bark beetles was slightly increased also outside the restored plots but the abundance was still very low compared to that inside the plots. In addition, the most likely pest species, *Ips typographus*, did not show any dispersal into the surrounding forests. Thus, restoration seems very unlikely to cause any damage in commercial forests. Although burning leads to the highest availability of resources for bark beetles, this is counteracted by decreased resource quality. However, restoration actions conducted at consecutive years within a small area might enable the populations to grow to outbreak levels. It must also be noted that the results of this particular study may not be applicable to other geographic regions that may provide more favourable conditions for the reproduction of bark beetles, in particular to regions where bark beetles are able to produce several generations per year.

3.6 Fire and retention trees as forest management practices

Some of the currently recommended forest management practices (Anonym 2006) such as the retention of living or dead trees, burning of logged sites, and favouring deciduous admixture (Fries et al. 1997, Vanha-Majamaa & Jalonen 2001, Bergeron 2002, Franklin et al. 2002) can be regarded as restoration in its widest sense. The correlative study (IV) was designed to compare the effects of two recommended forest management practices, burning and leaving retention trees on clearcut areas, over 16 years time period. Studying the effects of management or restoration typically requires decades of monitoring, but by combining correlative approach to historical experiment-like setups it is possible get some insight to the long-term effects.

The species richness and abundance of beetles were highest immediately after fire or logging and decreased steeply with time. There were more species at the burnt sites than at the unburnt sites, and in particular saproxylic, rare, and red-listed species were more common at the burnt sites. There was no interaction between burning and the age of the site suggesting that also the older burnt sites were more species-rich than unburnt sites. The decrease in the species richness is likely to be due to the depletion of resources, since the initial volume of dead wood was relatively low and new dead wood was not formed after the death of the retention trees at the burnt sites. Habitat alteration, such as the closure of the sites and the decrease of sun-exposure, is also likely to have decreased the species richness.

The results also revealed that the effect of burning was strongly dependent on the level of tree retention. At the burnt logged sites, the number of retention trees (of which the majority were killed during or after the fire) had a strong positive effect on the abundance and species richness of saproxylic species, and also on rare and red-listed species. It was also noteworthy that the burnt sites that had only a small number of retention trees did not differ from the corresponding unburnt sites. At the unburnt sites, the effect of retention trees on species richness was much weaker which suggests that tree retention on logged sites is not likely to have strong diversity effects within the first 16 years after logging. However, the retention trees at unburnt logged sites are likely to contribute to the future volume of dead wood.

The results show that feasible alterations in current forest management, in particular burning of logged sites combined with leaving retention trees, can increase the diversity of saproxylic species in managed forests. Burnt sites seem to be able to retain their species richness compared to unburnt sites despite the general decrease of species richness with time. The results can also be used to predict the long-term effects of restoration actions, but it should be noted that the restored forests (such as those in paper I) hold much larger volumes of dead wood, and new dead wood is likely to be formed continuously as the weakened trees fall down at the burnt sites and windfalls occur at the unburnt sites. Therefore, the decrease of species richness with time at restored sites may not be as steep as suggested in paper IV.

4 IMPLICATIONS FOR RESTORATION AND MANAGEMENT

The main aim of restoration is to create structures and resources typical of natural forests. While the short-term goal is to enable specialized species to persist in the landscape, the long-term goal is to bring the particular stand to a more natural successional trajectory. Determining the success of restoration actions requires long-term monitoring, and only some insight can be given in a study covering the first two years after restoration. However, the results of this thesis show that fire has a strong positive short-term effect on beetle diversity in managed boreal forests. Combining partial harvesting to burning creates habitats that host highest species diversity with specific beetle assemblages. This is likely to be due to these habitats providing large quantities of dead wood in sun-exposed conditions that attract large numbers of colonizing beetles.

Fire can not be expected to benefit the whole saproxylic species pool of boreal forest, and the results clearly show that fire modifies strongly the beetle assemblages, species requiring the microclimate of closed forests decreasing and the species favouring disturbance areas and sun-exposition increasing. The species that are most likely to benefit from fire are those that are adapted to the disturbance regime of the particular forest type. These species are typically good dispersers, fire-dependent species with their specific adaptations being the best example. In contrast, species depending on the continuity of old-growth forest habitat are unlikely to benefit from fire and it remains to be seen whether these species are able to colonize the restored sites during the later stages of succession.

So far, fire has mainly been applied in the restoration of pine-dominated forests, and the short-term effects on species diversity have been promising (see Hyvärinen et al. 2005, 2006). The disturbance regimes of pine- and spruce-dominated forests differ from each other. Pine forests are characterized by recurrent low-intensity fires, while in spruce forests fire intervals are longer but fire can be of high intensity when they occur (see Brown et al. 2004, Kuuluvanen 2002). Therefore, it is questionable how many species really are adapted to burnt spruce forests. Our results show that fire had much weaker effect on spruce-living species than on birch-living species, and the effect was negative on the most abundant primary colonizers that should prefer disturbance areas. However, the fact that fire had a consistent positive effect on rare and red-listed species suggests that fire can be successfully used to create habitats for specialized species also in spruce-dominated forests. In addition, fire can be seen as the most natural and effective way to create large quantities of dead wood and this is likely to compensate the possible decrease in the quality of resource. Nevertheless, it is clear that restoration actions should not be conducted at the expense of protecting pristine forest, because these actions are likely to benefit totally different species.

Partial harvesting combined with down wood retention can also be seen as a method that creates structures that mimic disturbance areas. Our results show that beetle diversity is also increased by this restoration method, but since the volume of down wood had no clear short-term effect, the increase is likely to be due to beetles preferring the sun-exposed environment and possibly utilizing the logging waste. Since the results strongly reflect the colonization of beetles to the study plots, it is possible that the number of colonizing beetles has been restricted by the size of source populations. If this is the case, the volume of down wood should have clear long-term effects because the plots with more dead wood provide more breeding material for saproxylic beetles. In the long run, the death of standing retention trees is likely to ensure the continuity of dead wood resource at the harvested plots. However, long-term monitoring is needed before any recommendations on harvesting and down wood retention can be given.

The current forest management recommendations include some practices that can be seen as restoration in its widest sense. In particular, controlled burning and leaving retention trees on logged sites are believed to create and maintain structures and resources important for biodiversity. Our results show that the usefulness of “silvicultural” burning in terms of species conservation is strongly dependent on the number of retention trees such that burning increases species diversity only if an adequate number of retention trees are left on the site. It is important to note that the numbers of retention trees above which the effect of burning was significant should not be interpreted as threshold values. While threshold values are species-specific minimum amounts needed for the persistence of populations, the significant effect of burning on e.g. species richness tells only that there are more species surviving at burnt sites, not that the survival of all target species is guaranteed. Without burning, retention trees had only a small effect on species diversity. This is likely to reflect the fact that the number of dead retention trees was very low (but typical of managed forests!) at the study sites and thus the sites have not provided resources for saproxylic species. However, the retention trees at unburnt sites are likely to contribute the future volume of dead wood and thus the lack of effect within the first 16 years after logging does not mean that retention trees are useless without burning.

The results concerning the silvicultural burnings can also be applied to predict the long-term effects of restoration. Although the species richness decreases steeply with time due to the closure of the sites and depletion of resources, burnt sites remained as more species-rich sites than unburnt ones. In restoration actions mimicking the natural disturbance dynamics of boreal forests, the volume of tree retention (both dead and alive) is much larger than in ordinary forest management and thus it can be expected that the restored sites retain their species richness for a longer time.

Finally, restoration can not be seen to cause a risk of bark beetle –induced forest damage in the surrounding commercial forests in Finland. Fire seems to be the “safest” way to create large quantities of dead wood because it decreases the resource quality for the most likely pest species.

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YHTEENVETO (RÉSUMÉ IN FINNISH)

Metsien ennallistamisen merkitys kovakuoriaislajiston monimuotoisuudelle

Metsien häiriödynamiikassa tapahtuneet muutokset ja lahopuun väheneminen ovat tärkeimpiä Suomen metsälajiston uhanalaistumiseen johtaneita syitä. Harvinaistuneen lajiston elinolosuhteita voidaan parantaa metsien ennallistamisella, jossa pyritään luomaan monimuotoisuuden kannalta tärkeitä resursseja ja metsän rakennepiirteitä. Metsien ennallistaminen perustuu Suomessa tavallisesti luontaisen häiriödynamiikan jäljittelyyn, käytetyimpiä keinoja ovat metsän poltto ja lahopuun lisääminen.

Väitöskirjatutkimuksessani selvitin metsän ennallistamistoimien vaikutuksia kovakuoriaislajiston, erityisesti lahopuusta riippuvaisten lajien, monimuotoisuuteen. Väitöskirjan osajulkaisuista kolme pohjautuu Lammin Evolle vuonna 2002 perustettuun ennallistamiskokeeseen, jossa ennallistamiskäsittelyinä olivat kuusivaltaisen talousmetsän poltto sekä metsän osittainen harvennus yhdistettynä järeän lahopuun tuottoon. Neljännessä osajulkaisussa tutkin, miten nykyisten metsänhoitosuositusten mukaiset toimenpiteet, hakkuualueiden kulotus ja säästöpuiden jättö hakkuualueille, vaikuttavat kovakuoriaisten monimuotoisuuteen ja miten lajiston sukkessio etenee hakkuun jälkeisinä vuosina.

Kovakuoriaisten laji- ja yksilömäärät olivat suurempia poltetuilla ennallistamiskohteilla ja poltto muutti selkeästi myös kovakuoriaisyhteisön rakennetta. Harvinaisten lahopuusta riippuvaisten lajien ja uhanalaisten lajien määrät kasvoivat polton seurauksena. Myös metsän osittainen harvennus lisäsi kovakuoriaisten laji- ja yksilömääriä, mutta harvennetuille aloille tuotetun lahopuun määrällä ei ollut selkeää vaikutusta. Poltto paransi myös lahopuuresurssin laatua lisäten yksittäisten kuolleiden puiden kovakuoriaislajiston monimuotoisuutta, mutta polton vaikutus oli erilainen eri puulajeilla. Lahoavia koivuja suosiva lajisto hyötyi selvästi poltosta, mutta polton vaikutukset lahoavilla kuusilla elävään lajistoon eivät olleet yhtä selkeitä, ja erityisesti monet pioneerilajit suosivat palamattomia kuusia. Tuholaislajeina pidettyjen kaarnakuoriaisten määrät lisääntyivät ennallistamiskohteilla, mutta poltto huononsi lahopuuresurssin laatua näiden lajien kannalta. Kaarnakuoriaisten leviäminen ennallistamiskohteita ympäröiviin metsiin oli vähäistä, joten ennallistaminen ei näyttäisi lisäävän metsätuhoriskiä talousmetsissä.

Kulotetuilla hakkuualoilla tavattiin enemmän kovakuoriaislajeja kuin kulottamattomilla ja erityisesti harvinaisten ja uhanalaisten lajien määrät olivat kulotusaloilla korkeammat. Säästöpuiden määrä vaikutti positiivisesti kulotusalojen kovakuoriaislajiston monimuotoisuuteen ja lisäksi niillä alueilla, joille ei ollut jätetty riittävästi säästöpuita, ei kulotuksesta ollut hyötyä. Kovakuoriaisten lajimäärät olivat korkeimmillaan välittömästi hakkuun tai polton jälkeen ja vähenivät ajan myötä, poltetuilla aloilla lajisto säilyi kuitenkin polttamattomia aloja runsaampana.

Tulokset osoittavat, että metsien ennallistamispoltto lisää kovakuoriaislajiston monimuotoisuutta ja että poltolla voidaan luoda elinympäristöjä ja resursseja erikoistuneille lajeille. Ennallistaminen hyödyttää todennäköisesti eniten lajeja, joilla on hyvä leviämiskyky, ja jotka pystyvät näin nopeasti hyödyntämään poltossa syntynyttä suurta lahopuun määrää ja paahteisia oloja. Sen sijaan vanhan metsän pienilmastoa vaativiin, leviämiskyvyltään heikompiin lajeihin ennallistamisella lienee vaikeampi vaikuttaa. Häiriöympäristöjä suosivat lajit hyötyvät myös ennallistamistoimista, joissa metsän osittainen harvennus yhdistyy lahopuun tuottoon, mutta ennallistamisaloille tuotetun lahopuun määrällä ei lyhyellä aikavälillä näytä olevan merkitystä. Koska lahopuun määrän on kuitenkin todettu olevan yksi tärkeimmistä metsälajiston monimuotoisuuteen vaikuttavista tekijöistä, lahopuun tuoton lopullisten vaikutusten selvittäminen vaatii ehdottomasti pitkäaikaista seurantaa. Metsätaloudellista kulotusta voidaan pitää talousmetsien monimuotoisuutta lisäävänä toimenpiteenä, mutta tämä edellyttää, että riittävä määrä säästöpuita jätetään kulotusaloille. Lisäksi kulotetut alat säilyvät arvokkaina elinympäristöinä vain rajoitetun ajan.

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