**Dissertationes Forestales 222**

# Emulation of natural disturbances and the maintenance of biodiversity in managed boreal forests: the effects of prescribed fire and retention forestry on insect assemblages

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Academic dissertation

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## ABSTRACT

Intensive forest management and effective prevention of natural disturbances have caused major changes in forest ecosystems and many forest habitats and species are now threatened. Retention forestry and prescribed burning are methods that aim to bring the legacies of forest management closer to those of natural disturbances and to maintain biodiversity in managed forests. In this thesis, the effects of these two methods on biodiversity are explored by studying retention tree dynamics, and changes in the assemblages of beetles (Coleoptera) and flat bugs (Heteroptera: Aradidae, *Aradus*). The study is based on a 10-year long, replicated field experiment on boreal pine dominated forests in eastern Finland. The data includes 2758 individually marked retention trees on 24 sites, which were followed individually over a 10-year period. Species inventories from the experimental sites resulted in a dataset that included 468 species and 60,879 identified individuals.

Prescribed burning without logging, the method considered to be close to natural fire in a forest ecosystem, caused a long-term increase in species richness and differences in functional and phylogenetic compositions of saproxylic beetle assemblages compared to harvested stands. In the harvested stands, species richness increased strongly in the short-term but returned over the 10-year period to the pre-treatment level in the retention stands and to lower levels in the clear-cut stands. In the short-term, the functional-phylogenetic diversity of saproxylic beetles changed from a random to a clustered pattern after burning and retention harvests, whereas clear-cutting resulted in random communities. This implies that the species composition in retention harvests became phylogenetically more related and consisted of species with similar resource preferences, i.e. favoring open habitats and early decay stages. Ground beetles (Carabidae) are effective colonizers of open habitats, and their species richness increased after fire and logging. Applied retention tree levels (10 $m^3$ $ha^{-1}$ and 50 $m^3$ $ha^{-1}$, representing 3.5 % and 17 % of the pre-harvest volume, respectively) were not able to maintain ground beetle assemblages found in uncut forests. Burning increased species richness of pyrophilous and rare and Red-Listed (RRL) beetles and flat bugs but this effect was transient. Neither burning nor tree retention resulted in increased damage from pine-shoot beetles (*Tomicus* spp.) when compared with traditional clear-cutting.

The main findings of this thesis emphasize the difference between the assemblages of burned forests and the assemblages of clear-cut stands but shows that prescribed burning and retention forestry can be beneficial to conserve and maintain insect diversity. Furthermore, this thesis suggests that relatively high retention levels are needed due to the high post-harvest mortality of the trees. This is particularly important for the long-term availability of habitats that retention trees provide and low retention tree levels are unlikely to maintain diverse fauna on harvested sites.

**Keywords:** long-term effects; retention tree dynamic; saproxylic beetles; flat bugs; carabid beetles

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# LIST OF ORIGINAL ARTICLES

This thesis is a summary of the following papers referred to in the text by Roman numerals I-VI. The articles are reprinted here with the kind permissions of the publishers.

I Heikkala, O., Suominen, M., Junninen, K., Hämäläinen, A., Kouki, J., 2014. Effects of retention level and fire on retention tree dynamics in boreal forests. Forest Ecology and Management 328, 193-201. http://dx.doi.org/10.1016/j.foreco.2014.05.022

II Heikkala, O., Martikainen, P., Kouki, J., 2016. Decadal effects of emulating natural disturbances in forest management on saproxylic beetle assemblages. Biological Conservation 194, 39-47. http://dx.doi.org/10.1016/j.biocon.2015.12.002

III Heikkala, O., Seibold, S., Koivula, M., Martikainen, P., Müller, J., Thorn, S., Kouki, J., 2016. Retention forestry and prescribed burning result in functionally different saproxylic beetle assemblages than clear-cutting. Forest Ecology and Management 359, 51-58. http://dx.doi.org/10.1016/j.foreco.2015.09.043

IV Heikkala, O., Martikainen, P. Kouki, J. Prescribed burning is an effective and quick method to conserve rare pyrophilous forest-dwelling flat-bugs (Heteroptera: Aradidae). Manuscript.

V Martikainen, P., Kouki, J., Heikkala, O., 2006. The effects of green tree retention and subsequent prescribed burning on ground beetles (Coleoptera: Carabidae) in boreal pine-dominated forests. Ecography 29, 659-670. http://dx.doi.org/10.1111/j.2006.0906-7590.04562.x

VI Martikainen, P., Kouki, J., Heikkala, O., Hyvärinen, E., Lappalainen, H., 2006. Effects of green tree retention and prescribed burning on the crown damage caused by the pine shoot beetles (*Tomicus* spp.) in pine-dominated timber harvest areas. Journal of Applied Entomology 130, 37-44. http://dx.doi.org/10.1111/j.1439-0418.2005.01015.x

Contributions of the authors to the articles and to the manuscript. The authors are listed in the table in the same order than in the articles and in the manuscript.

| | Paper I | Paper II | Paper III | Paper IV | Paper V | Paper VI |
|---|---|---|---|---|---|---|
| Original idea / study or sampling design | KJ, JK | OH, JK | JM, JK | OH, PM, JK | PM, JK, OH | PM, JK, OH, EH |
| Data collection | OH, MS, AH | OH, PM | OH, PM | OH, PM | OH | OH |
| Species identification | --- | OH, PM | OH, PM | OH | OH | PM, OH, EH, HL |
| Data analysis | OH, JK | OH, JK | SS, ST, JM, JK | OH, JK | PM, JK, OH | PM, JK, OH |
| MS preparation | OH, MS, KJ, AH, JK | OH, PM, JK | OH, SS, MK, PM, JM, ST, JK | OH, PM, JK | PM, JK, OH | PM, JK, OH, EH, HL |

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# 1 INTRODUCTION

## 1.1 Background

Boreal forests compose one of the largest biomes in the world (Hansen et al. 2010) and are a major component of European forest ecosystems. Although these forests harbor a significant part of European biodiversity, the trend of global biodiversity decline is also evident in boreal forests and action to halt the decline is essential (Haila 1994; Esseen et al. 1997). In northern Europe, the current area of protected forests is too small and fragmented to be able to maintain forest biodiversity (Hildén et al. 2005; Angelstam et al. 2011). Furthermore, the establishment of sufficient additional set-aside areas and ecologically representative conservation areas is unlikely because of the lack of suitable natural forest stands and landscapes (e.g. Kouki et al. 2001; Richardson et al. 2007; Bouget et al. 2014). Thus, effective conservation methods are also needed in managed forests.

The boreal forest is not a naturally stable ecosystem, and this key finding can be used to develop forest management measures towards ecologically more sustainable activities (e.g. Attiwill 1994; Niemela 1997). Natural disturbances, such as fire, storm, insect outbreaks, diseases etc., which are subject to large spatial and temporal variation, have been a characteristic feature in boreal forests over the centuries. Repetitive cycle of disturbances and post-disturbance succession has been major driver in the development of the structure of natural boreal forests (Kuuluvainen 2009). Although large-scale stand-replacing disturbances by fire, windstorm and insect outbreaks cause the most dramatic changes in forest structure, also smaller-scale disturbances have played a major role in driving forest dynamics. Especially in forest areas with long fire cycle, the tree mortality has mainly been uneven and small-scale and caused by competition, fungi, insects etc., resulting in small-scale gap dynamics (Kuuluvainen 2009). The wide variability in the frequency and severity of natural disturbances is important for the maintenance of stand- and landscape-level heterogeneity in natural forests (Kuuluvainen 2002, 2009). Forest species have evolved with disturbances and a large proportion of them can utilize resources effectively in post-disturbance conditions. Thus, natural early-successional forests, which occur after stand-replacing disturbance and contain a large amount of diverse dead wood, are typically highly species-rich habitats (Kouki et al. 2001; Junninen et al. 2006; Swanson et al. 2011).

Wildfire is a major natural disturbance in boreal forests (Esseen et al. 1997; Pitkänen and Huttunen 1999; Wallenius et al. 2004). Thus, natural fires can also be used as a model to develop management actions, although this requires an in-depth knowledge of the behavior and effects of fires in forest ecosystems. The effect of fire on species assemblages in forest habitats is partly destructive, but also regenerative: many individuals are initially killed, but at the same time competition-free substrates and a large amount of diverse dead wood are generated by fire (Esseen et al. 1997; Franklin et al. 2000; Boulanger and Sirois 2007; Schowalter 2012). Several species have evolved to live in fire-related disturbances, and some of them are clearly dependent on burned habitats, i.e. pyrophilous (Wikars 1997). Furthermore, though the immediate impact of fire is often destructive for some species groups, such as plants, polypore fungi and epiphytes (Junninen et al. 2008; Hämäläinen et al. 2014; Johnson et al. 2014), the effect can turn positive in the longer-term. For example, the immediate decline in polypore fungi species richness on burned sites is quickly reversed, most likely due to increased quantities of available dead wood (Penttilä et al. 2013; Suominen et al. 2015).

Currently, intensive forest management has led to the suppression of natural fires, and clear-cutting has become the most common disturbance type in a large part of boreal forests, particularly in Fennoscandia (e.g. Linder and Ostlund 1998). Clear-cutting has been argued as an appropriate method for harvesting in fire-susceptible boreal forests that also naturally encounter recurrent stand-replacing disturbances (Mielikäinen and Hynynen 2003). There are, however, obvious differences in the structural and biological legacies of these natural and anthropogenic disturbances at both the stand- and landscape-levels (McRae et al. 2001; Siitonen 2001; Nitschke 2005; Junninen et al. 2006) and clear-cutting does not reflect the complexity of disturbance-succession cycle of natural forests (Kuuluvainen 2002; Bergeron and Fenton 2012). Large-scale natural disturbances typically leave a large and diverse volume of dying and dead wood, snags and coarse woody debris as legacies, but also living (injured) trees. Clear-cut stands appear quite different and the dead wood consists mostly of stumps and small size logging residues and living trees are totally absent (Franklin et al. 2000; Siitonen 2001; Swanson et al. 2011). At the landscape-level, wildfires cause naturally large numbers of small and small numbers of large disturbances with very variable frequency (McRae et al. 2001). Instead, the size of harvested units are usually small. Furthermore, harvesting frequencies are typically dictated by rotational age at a merchantable size, according to commercial optimization (McRae et al. 2001). Large scale application of clear-cutting and other intensive forest management practices, such as planting, thinning and removal of dead trees, together with the decrease of old-growth forests has led to an even-aged structure, and to the loss and fragmentation of biological legacies (Kouki et al. 2001; Olsson et al. 2012). Although the majority of boreal forest-dwelling species are likely to be able to tolerate major disturbances, they are not able to survive or recolonize post-disturbance forests if essential resources are insufficient or even absent (Thorn et al. 2015). Changes in post-disturbance legacies, particularly the decline of dead wood, have caused biodiversity loss in boreal forests and have threatened the existence of a large amount of forest-dwelling species (Tikkanen et al. 2006; Rassi et al. 2010; Stokland et al. 2012b). For example, forests are the main habitat for more than one third of all Red-Listed species (37.9% of 1880 species) in Finland. The main threats to these species are decreased amounts of dead wood, forest management practices in general, changes in tree species composition and reduction of old-growth forests (Rassi et al. 2010). Of these threats, the lack of dead wood is the most common cause of decline for threatened and near-threatened species in Finland (Rassi et al. 2010). Therefore, the maintenance of a sufficient volume of diverse dead wood in forests is a key element when aiming to sustain forest biodiversity. Currently there is a risk that the shortage of dead wood in forests becomes even worse, and thus increase the biodiversity loss, as harvesting of stumps and slash for fuel has become more common (Toivanen et al. 2012; Jonsell and Schroeder 2014).

## 1.2 Emulating natural disturbances in forest management – methods, benefits and risks

The application of harvesting methods that more closely emulate natural disturbances, instead of traditional clear-cutting, can be employed to prevent further species loss and to bring naturally occurring biological legacies into post-harvest forests. Retention forestry and prescribed burning are examples of such methods (Hunter 1993; Franklin et al. 1997). Gustafsson et al. (2012) defined retention forestry as the harvesting method that intentionally retains important structures and organisms such as living and dead trees and intact forest patches on site for the long term. The design and level of retention forestry differs considerably depending on the local environmental conditions, social acceptance and policy settings (Gustafsson et al. 2012).

Applying retention forestry instead of full clear-cutting has several potential beneficial effects on forest biodiversity. It can maintain structures and functioning of pre-harvest forests, enrich habitat types in the early-successional stages and enhance landscape connectivity and, thus, help species to “lifeboat” and re-colonize during the post-harvest years (Franklin et al. 1997; Gustafsson et al. 2010; Baker et al. 2013). Retention trees can provide shelter for species and buffer the microclimate, particularly if the size of the retention tree aggregates are large enough (Baker et al. 2013). For example, living retention trees provide valuable habitats for epiphytic bryophytes and lichens (Lõhmus et al. 2006; Caners et al. 2010; Gustafsson et al. 2013), forest birds and mammals (Lance and Phinney 2001; Gitzen et al. 2007; Zwolak 2009), corticolous arthropods (Halaj et al. 2009) and ectomycorrhizal fungi (Dahlberg et al. 2001) during the early-successional years. Post-harvest death of retention trees can maintain a supply of coarse dead wood, which benefits saproxylic species especially (e.g. Hyvärinen 2006; Hyvärinen et al. 2009), i.e. the species dependent on dead wood (Speight 1989). However, several species that demand intact forest as their habitat, are not able to survive in small-sized retention patches, but demand patches of several hectares of their sizes (Lee et al 2015).

Although retention forestry is a promising method for the emulation of natural disturbances, it still lacks some essential characteristics of natural disturbances. For example, combining retention with prescribed burning potentially adds a significant near-to-nature element to harvesting and can further decrease the negative effects on biodiversity. Burning has the potential to increase and diversify coarse dead wood by killing trees, and thus is able to generate new habitats for saproxylic species, and for pyrophilous ones in particular. Prescribed fire has been shown to have rapid positive effects on various taxa, particularly beetles (Saint-Germain et al. 2004; Hyvärinen et al. 2005; Hyvärinen 2006), but also flat-bugs (Johansson et al. 2010) and woodpeckers (Hutto 2008).

The succession-cycle of boreal forests is rather long and the growth of trees fairly slow. The development of trees from a set of young saplings to closed canopy takes decades and the trees can live for several hundreds of years. For example, in Fennoscandia the oldest recorded pine trees are 700-800 years old (Andersson and Niklasson 2004). It is clear that species assemblages undergo change throughout the succession. Therefore, if only the immediate and short-term effects of certain methods are studied, valuable insights into how these actions affect the forest throughout the succession cycle will be missed. To be able to evaluate the effect and benefits of retention forestry over the longer-term, extended analyses of species assemblages are needed. Similarly, it is essential to understand the dynamics of retained trees during the post-harvest years, as this determines their role as legacy structures. Previous studies have reported high windthrow mortality rates in retention trees during the initial post-harvest years (e.g. Hautala and Vanha-Majamaa 2006; Jönsson et al. 2007; Lavoie et al. 2012). Fire-caused tree mortality has been shown to be high in mature forests (Swezy and Agee 1991; Linder et al. 1998; Butler and Dickinson 2010). Studies that simultaneously analyze the effects of both fire and retention forestry on ecosystem characteristics (such as tree mortality) or species are rare.

One aim of natural disturbance emulation is to increase the amount of dead wood in the forest in order to provide habitats and resources for threatened biota. A potential side-effect, however, is that the increased amount of fresh dead wood also increases the risk of bark beetle (Coleoptera: Curculionidae, Scolytinae) outbreaks. In northern European boreal forests the risk of such outbreaks is high, especially in Norway spruce forests (*Picea abies* (L.) Karst.), where the *Ips*-species (and *Ips typographus* (L.) in particular) can potentially cause severe damage to the tree stand (Schroeder and Lindelöw 2002). In Scots pine (*Pinus sylvestris* L.) dominated forests, potential pest species are the pine shoot beetles; *Tomicus piniperda* (L.) and *Tomicus minor* (Hart.) (Långström 1983). Clearly, there is also a need to evaluate any potential and perhaps unwanted side-effects that new management measures may have on the tree stand.

### 1.3 Insects – study organisms

Insects are the most species-rich group of animals in the world, and account for more than half of the worlds known biodiversity. Beetles (Coleoptera) are the most species-rich group of insects (Foottit and Adler 2009) and are a highly suitable group for ecological studies, due to their high level of specificity to different ecological conditions and habitats. Beetles occupy virtually all terrestrial and fresh water habitats apart from Antarctica, and also include a high and ecologically diverse number of forest-dwelling species. There is a large amount of saproxylic species among beetles and dead wood is a very large and diverse resource base, which includes a large amount of different niches and microhabitats (Stokland et al. 2012a). Typically, saproxylic beetle species have specialized in the consumption of different fractions of this resource (Speight 1989; Grove 2002; Hjältén et al. 2012; Stokland et al. 2012a). Thus, saproxylic beetle diversity also acts as a good indicator of resource diversity. Furthermore, beetles have been shown to be adversely affected by intensive forestry (e.g. Grove 2002; Rassi et al. 2010), which emphasizes the suitability of this group for studies that aim to test ecologically sustainable methods for forestry.

Saproxylic beetles are significant contributors to ecosystem processes and functioning through the decomposition of wood (e.g. Angers et al. 2012; Jacobs and Work 2012; Ulyshen 2016). Thus, the analyzes of functional diversity and assemblage changes in saproxylic beetles widens our knowledge of whole ecosystem functioning.

In addition to saproxylic beetles, several other beetle groups are also indicative of the effect that forest management and natural disturbance emulation may have on biota. Ground beetles include several species associated with open habitats, but also species considered to favor closed forests (Koivula 2002; Niemelä et al. 2007). Several species have a poor dispersal ability. The forest-dwelling ground beetles are generally not associated with dead wood but rather with microclimatic conditions in the forest (Niemelä et al. 1992; Koivula 2002). Still, there are also some species, such as *Sericoda* spp and *Dromius* spp., which live almost completely on standing trees. Thus, the study of ground beetle assemblages provides useful information on the significance and effect of retention tree aggregates in saving the assemblages of closed forests. Several ground beetle species favor burned forests, including threatened species, such as *Sericoda bogemannii* (Gyllenhal) (Vulnerable, VU) and *Pterostichus quadrifoveolatus* Letzner (Near Threatened, NT), which emphasizes the suitability of this group for studies that explore the effects of fire (Lundberg 1984; Wikars 1992).

In addition to beetles, some other invertebrate groups play a key role in the evaluation of the effects of retention and prescribed burning. Flat bugs (Heteroptera: Aradidae, *Aradus*) is a poorly studied group of forest-dwelling insects. A total of 21 *Aradus*-species occur in Fennoscandia, of which 18 have been recorded in Finland (Rintala and Rinne 2010). Nearly all species are obligatory saproxylics, and seven of them are pyrophilous (Wikars 1997). As many as six of the 18 species are Red-Listed in Finland, and two of them classified as Regionally Extinct (RE) (Rassi et al. 2010). Both extinct species are pyrophilous. Thus, flat bugs comprise a very sensitive and informative group for studies that aim to explore the effects of prescribed burning on pyrophilous species.

### 1.4 Aims of the thesis

This thesis explores the effects of two near-to-nature methods; retention forestry and prescribed burning, on tree dynamics, forest invertebrate biodiversity and the risk of insect outbreaks. Post-harvest dynamics of retention trees were explored in a tree level study (I) that explored how the trees survive after logging and burning, and provide shelter and resources for species that require living and dead trees for their survival and recolonization. Biodiversity effects were explored by studying the assemblages of saproxylic beetles (II, III), saproxylic flat-bugs (IV) and ground beetles (V). Furthermore, the risk of insect outbreaks after the treatments was evaluated by studying the feeding intensity of pine shoot beetles at the study stands and in the adjacent forests (VI).

The main research questions were:

1. How do prescribed burning and retention level affect the mortality and tree fall dynamics of retention trees during ten post-harvest years? (I)
2. How do species richness and the assemblages of saproxylic beetles change over ten years after prescribed burning and retention forestry? (II)
3. What are the short-term effects of retention forestry and prescribed burning on the functional and phylogenetic diversity of saproxylic beetles? (III)
4. What is the short-term response of highly specialized and threatened insect genus; flat bugs, to prescribed burning and retention forestry? (IV)
5. How are the ground beetle assemblages affected by prescribed burning and retention forestry in short-term? (V)
6. Do retention trees or prescribed burning increase the risk of damage caused by pine shoot beetles (Tomicus spp) in adjacent forest stands? (VI)

## 2 MATERIAL AND METHODS

### 2.1 Study area and experimental design

This thesis is based on data collected over 11 years in a large-scale field experiment (Kouki 2013). The experimental area is situated in eastern Finland, in the municipalities of Lieksa and Ilomantsi, in the middle boreal vegetation zone (Fig. 1). The landscape of the study area consists mostly of mixed coniferous forests dominated by Scots pine and Norway spruce with a mix of deciduous trees, although swamps and small lakes are also common in the landscape.

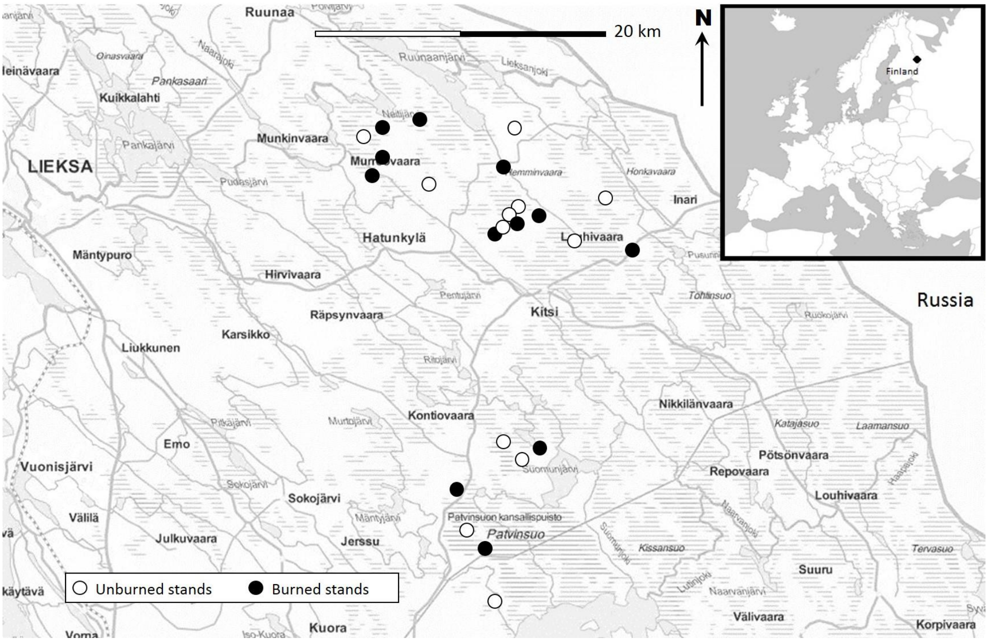

**Figure 1**. Map of the study area

Most of the forests in the region have been intensively managed, especially over the past 50-70 years, though some fragmented old-growth forests are still present. A total of 24 stands, each about 3-5 ha in area, were selected as experimental study sites. Those stands were initially about 150-years old forests (dominant canopy trees) that had been out of intensive forestry but showed signs of old selective cuttings. The average initial volumes of the growing stock and dead wood were 288 $m^3$ $ha^{-1}$ (S.D. = 71.1) and 41 $m^3$ $ha^{-1}$ (S.D. = 17.5), respectively. The dominant tree species was Scots pine (72% of total growing stock), and other common tree species were Norway spruce (22%) and birch (*Betula pendula* Roth and *Betula pubescens* Ehrh., 3% together). Furthermore, small numbers of other deciduous species, such as aspen (*Populus tremula* L.), grey alder (*Alnus incana* (L.)), goat willow (*Salix caprea* L.) and rowan (*Sorbus aucuparia* L.) were present. The experimental design consisted of two-factorial design, combining prescribed burning and four levels of harvesting: clear-cutting, 10 and 50 $m^3$ $ha^{-1}$ tree retention levels (representing 3.5 % and 17.4 % of total volume of living trees) and an unharvested control (Fig. 2). The logging treatments were defined on realistic forestry perspective. The lower retention level was chosen to represent the prevailing forestry practices in Fennoscandia (1-5% of pre-harvest volumes, Gustafsson et al. 2012), and the higher level to correspond the dead wood volume where the number of saproxylic beetles reaches its asymptotic value in mature forests (Martikainen et al. 2000). Each harvesting treatment was replicated six times, and half of those were subsequently burned. Consequently, there were eight treatment combinations with three replications of each (Figs. 2 and 4). The stands were harvested in winter 2000/2001 and burning took place in June 2001. Retention trees were mostly retained in circular aggregates,

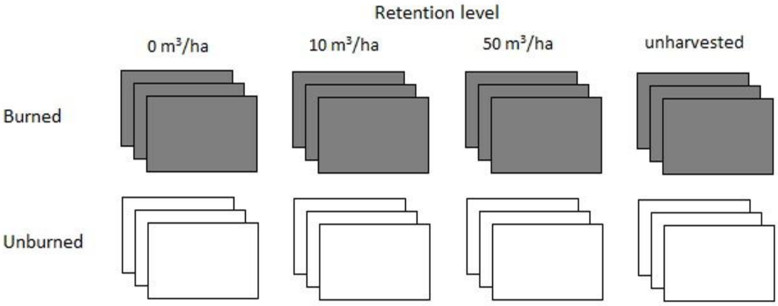

**Figure 2**. Experimental design consisting of burning treatment and four levels of logging intensity with three replications of each treatment combinations.

about 200-300 $m^2$ and 300-500 $m^2$ in area at the lower and higher retention levels, respectively. Implementation of burning is described in detail in Hyvärinen et al. (2005).

## 2.2 Data sampling and analysis

All retention trees were alive when the experiment was established in 2000. We followed the mortality and windfall rates in the retention trees over 10 post-harvest years by individually monitoring the trees in 2001, about one month after burning, and then again in 2005, 2008 and 2011, i.e. four, seven and ten years after the treatments (I).

Insect sampling was conducted with three methods: freely hanging window traps (FWT) were used for saproxylic beetles (II, III, VI), trunk attached window traps (TWT) for flat bugs (IV) and pitfall traps (PFT) for ground beetles (V) (Fig. 3; Table 1). The window traps consisted of two crossed plastic panes (40 cm x 60 cm) and a funnel under the panes that fed into a one-liter container filled with a solution of water, salt and detergent. FWTs were hung on strings between pairs of poles or trees. In total, 240 FWTs (2000-2003 and 2011) and 240 TWTs (2000-2003) were used; ten of both trap types were used at each stand. The PFTs consisted of 0.3 and 0.5 liter plastic cups, placed within each other, filled with a similar solution to that used in the window traps, and covered with a transparent roof that was set approximately 20-30 mm above the ground (Fig. 3). Four groups of five PFTs were set (only in 2002) at each stand, to give a total of 480 traps in 96 groups. In the stands with retention trees, two of the groups were located inside the tree groups and two in the open harvested area. Sampling seasons were similar for all trap types and lasted from mid-May to early September each year: 16.5.-1.9.2000; (II, III, IV, VI); 14.5.-7.9.2001 (IV, VI); 13.5.-12.9.2002 (II, III, IV, V, VI); 12.5.-10.9.2003 (IV) and 16.5.-7.9.2011 (II).

All the beetles were identified to the species level with a few exceptions (neither saproxylic nor ground beetles). Only saproxylic (II, III) and ground beetle (V) data were used in analyses. All adult flat bugs were identified to species level (IV). In paper VI, only *Tomicus*-species data were used. Furthermore, for an evaluation of the crown damage caused by pine-shoot beetles, fallen shoots were counted in 2003 and 2004 from linear transects established in the forests that surrounded the study stands, and by counting the breeding galleries of *Tomicus*-species in the trees killed by fire (VI).

**Figure 3.** The three trap types used in the thesis; freely-hanging window trap (FWT), trunk-attached window trap (TWT) and pitfall trap (PFT) from left to right respectively. Photos: Petri Martikainen and Jari Kouki

Since the experimental design was based on the classic two-factor factorial design, the main method of analyzes was the factorial analysis of variance (ANOVA). Effects of prescribed burning, retention level and time since harvesting on the mortality and tree fall rates of retention trees (I), species richness of saproxylic beetles (II) and flat bugs (IV) and on the average number of fallen shoots in the transects (VI) were tested with factorial repeated measures ANOVA. Similarly, the effects of burning and retention level on abundance, species richness and average size of ground beetles (V) were tested with factorial ANOVA. In addition to the ANOVA-based analyses, assemblage compositions of saproxylic beetles, flat bugs and carabid beetles were visualized with non-metric multidimensional scaling (NMDS) (II, IV, V). Article III focused on the functional structure of saproxylic beetle assemblages and, thus, a functional-phylogenetic approach, based on species phylogeny, biological traits and species-specific resource requirements, was applied (Cadotte et al. 2013). Statistical methods have been described in detail in the original articles I – VI.

# 3 MAIN RESULTS AND DISCUSSION

## 3.1 Fire increases mortality rates in retention trees, and leads to a diverse set of dead wood, although fire can also cause a lack of continuity in dead wood supply if the retention level is too low.

More than half of the total volume of retained trees died during the ten post-treatment years, although the pattern of tree mortality varied between treatments (I). Burning increased tree mortality rates at both retention levels. The majority of trees died in the burned stands and

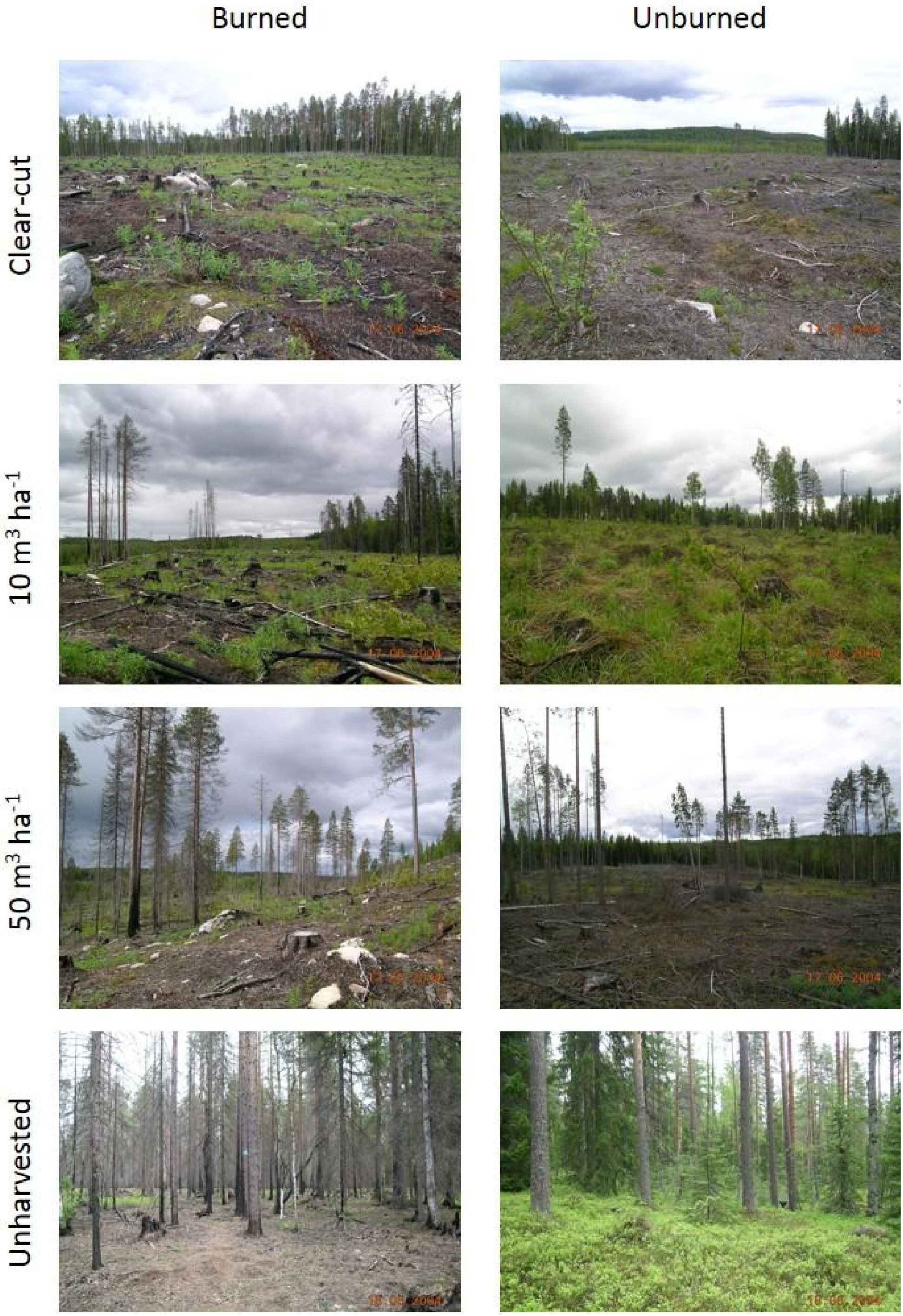

**Figure 4.** Photos of the eight different treatment combinations taken three years after the treatments. Photos: Jari Kouki

**Table 1.** Recapitulation of sampling methods, years and datasets in the original articles

| Method | Year replicates | Design per stand | Dataset | Paper |
|---|---|---|---|---|
| Retention tree monitoring | 2001, 2005, 2008, 2011 | Every tree individually monitored | Tree mortality | I |
| FWT | 2000, 2002, 2011 | 10 FWTs / stand | Saproxylic beetles | II |
| FWT | 2000, 2002 | 10 FWTs / stand | Saproxylic beetles | III |
| TWT | 2000, 2001, 2002, 2003 | 10 TWTs / stand | Flat bugs | IV |
| PFT | 2002 | 4 clusters of 5 traps / stand | Ground beetles | V |
| Fallen shoot counting transects | 2003, 2004 | 6 transects in uncut and 3 in harvested stands | Tomicus | VI |
| FWT | 2000, 2001, 2002 | 10 FWTs / stand | Tomicus | VI |

about one third in the unburned stands during the first ten post-harvest years. Fire-caused mortality of the trees was very high during or immediately after burning, especially at the lower retention level (10 $m^3$ $ha^{-1}$) where almost all trees died immediately; only one single pine was still alive four years after the fire. At the higher retention level (50 $m^3$ $ha^{-1}$), about half of the retained trees died immediately but many trees also survived, leading, over an extended period, to a diverse set of living, variably injured and dying trees, snags and fallen logs. The severity of fire on the logged areas was about the same at both retention levels, based on the amount of humus layer reduced in the fires (Laamanen 2002). However, the retention tree groups were slightly larger at the higher retention level, which led to decreased logging residues within the groups and likely resulted in individual trees that were located in the middle of the groups escaping the effects of flames. This led to lower immediate mortality rates (I). Some delay in mortality was also observed. Fire-injured trees are less able to resist insect outbreaks, diseases and desiccation due to their weakened physiological condition, which caused additional mortality (Dixon et al. 1984; Harrington 1993, 1996; Rasmussen et al. 1996). Severely injured trees, however, die within a couple of years after burning (DeBano et al. 1998). This also happened in this study, where peak mortality rates were observed in the first four years after the treatments (I). At the unburned sites, tree mortality was much lower and quite constant at both retention levels. There were no differences in proportional mortality between the retention levels at the unburned stands.

Burning strongly increased the volume of snags, whereas at the unburned stands it remained rather low throughout the monitoring period (I). Quite a few retention trees fell down immediately after the treatments, especially at the burned stands, although the fall-rate declined quickly in subsequent years (I). This is consistent with the findings of Busby et al. (2006) and Urgenson et al. (2013). The faster rates of tree fall at the burned stands compared to the unburned stands can, at least partly, be caused by weakened support of roots due to scorching of vegetation, humus and even the surface roots. However, the exact mechanism that causes this effect remained unclear.

Pines survived fire better than the other tree species (I), probably because its mean diameter was higher than that of the other species. Furthermore, the thick bark that covers the cambium, and the height of the crown bottom protects pines against scorching and damage (e.g. Ryan et al. 1988). Dead pines also remained standing for a longer period than the other tree species, so that the majority of snags in 2011 were pines (I).

The quick death of retention trees in the burned areas increases the amount of dead wood in the post-harvest early successional stages. Fire creates mortality patterns that are uneven in space and time and, thus, provide highly diverse substrates for wood-living species (I). By increasing dead wood diversity, saproxylic species diversity is also enhanced (II; III; IV). Dead wood quality and quantity will decline faster at lower retention levels, especially at burned sites, where the mortality of trees is high, leading to a gap in the continuity of dead wood later in the forest succession. Higher retention levels provide a longer-term supply of fresh dead wood and can also better maintain living trees.

### 3.2 Retention forestry and prescribed burning result in high saproxylic beetle species richness but also produce major changes in assemblage composition in early-successional forests. However, species richness remained unchanged only in unharvested forests but collapsed at harvested sites over the ten post-disturbance years.

Both fire and logging had major impacts on the species richness and the assemblage compositions of saproxylic beetles (II, III). Prescribed burning and all logging treatments increased saproxylic beetle species richness in the first post-treatment year (II; see also Hyvärinen et al. 2005). However, this effect was transient at all logged stands, and species richness had decreased to the pre-treatment level in the retention harvests and even lower in the clear-cut stands over ten years (II). At the unharvested stands, burning caused a long-term increase in species richness: after ten years saproxylic beetle species richness remained clearly higher than before burning, although it later declined slightly. A rapid increase in species was expected and was likely caused by increased resources for reproduction, such as fresh dead wood, especially stumps, logging residues and fire-killed retention trees.

The effects of the treatments were not similar in the different saproxylic beetle functional groups, i.e. early- and late-stage xylophagous, mycetophagous and predators (II). Burning of unharvested stands increased species richness of all functional groups in the ten-year period. In the harvested stands, species richness of predators increased after burning of the forest stand in the short-term, but the effect had disappeared over the following years. Burning did not affect species richness of any other functional groups in the harvested stands. Harvesting led to an increase in early- and late-stage xylophagous species in the first post-harvest year, although they were not affected by burning. Increased logging intensity led to a decrease in mycetophagous, early-stage xylophagous and predator species richness over the 10-year period. The results indicate especially clear-cutting to be harmful for these three groups, as their richness was reduces clearly below the pre-treatment level during ten years.

Dead wood on the study sites clearly decomposed in the 10-year period; stumps and logging residues became more decayed and dead trees were mostly devoid of bark (Fig. 5). Ten years after logging, no fresh dead wood was available in the clear-cut stands. High and

**Figure 5.** An example of a burned stand with retention level 50 $m^3$ $ha^{-1}$ three and 12 years after burning. Photos: Jari Kouki

rapid post-fire mortality of retention trees also resulted in an absence of fresh dead wood in the burned stands with retention trees over the long-term. Even at the higher retention level, the majority of retention trees had died and fallen during the ten post-treatment years at the burned stands (I, Fig. 5) and surprisingly, no difference was observed between the two retention levels in species richness of any of the functional groups (II).

Burning increased pyrophilous and rare and Red-Listed (RRL) species richness in the first post-treatment year (II). After ten years, species richness had increased at the burned unharvested stands, but had decreased at the logged stands compared to pre-treatment levels. At the burned unharvested stands, tree mortality had continued and new fresh dead wood was continuously available. This ensured a very diverse supply of dead wood, and thus provided habitats for species with variable resource preferences, and also provided RRL-species with a higher chance of survival (Saint-Germain et al. 2004; Boulanger and Sirois 2007; Hekkala et al. 2014). Pyrophilous species are usually only able to utilize burned trees for a short period after which they disappear within a few years from burned forests. These species require a continuous supply of new burned wood as was also shown in study IV (see also Wikars 1997; Toivanen et al. 2014).

The saproxylic beetle assemblages were affected by burning and harvesting and also by time (II). The assemblage shift caused by harvesting was stronger than that caused by burning. The assemblages of the burned unharvested stands clearly formed separate groups in both post-harvest years, and were situated closer to those of unburned controls in NMS. Retention trees brought assemblages closer to the controls at the unburned stands, but such a phenomenon was not visible in the burned stands. One year after the treatment, the assemblages of the stands differed clearly from the assemblages at the same stands nine years later. On the basis of these results, it is clear that ten years is too short a time for recovery of the assemblages of closed forests in logged areas.

### 3.3 Prescribed burning and retention forestry result in functionally and phylogenetically clustered communities of saproxylic beetles, whereas clear-cutting leads to random communities without clear species associations with certain resources

Fire and retention forestry led to increased species richness in the short term (Hyvärinen et al. 2005; II). Furthermore, these changes were accompanied by clear changes in assemblage compositions (II, III). Functional-phylogenetic diversity of saproxylic beetles decreased from a random to a clustered pattern after burning and retention harvests, indicating environmental filtering of both processes (III). This implies that the assemblages of retention harvests became more similar, consisting of species phylogenetically related to each other and/or with similar resource or habitat preferences. These effects became more pronounced with increasing logging intensity. Species-level traits that were favored by burning and tree retention were connected to open-habitat conditions and early decay stages, whereas clear-cutting revealed a random pattern without reference to specific resources. Thus, clear-cutting does not mimic the dynamics of wildfire, and results in different functional composition of species assemblages.

The immediate effects of fire on species assemblages are simultaneously destructive and regenerative. A major part of the original insect population can be killed, but new individuals rapidly colonize the burned forest (Wikars 1997; McCullough et al. 1998; Boulanger and Sirois 2007). The insects that colonize, however, include some very abundant species, species closely related with each other and species with similar traits and habitat preferences. Thus, fire functions as an environmental filter by clumping the functional and phylogenetic composition of species assemblages. Increased tree mortality rates following fire result in the generation and release of a large amount of new resources, and microclimate conditions are changed toward open canopy conditions (Moretti et al. 2010). Such phenomenon was observed in study III with prescribed burning and retention forestry. High immediate mortality of retention trees caused a major increase in fresh coarse dead wood (I), and provided a large amount of adequate habitats for fresh wood feeders and the species that prefer early decay stages of wood in general. Rapid colonization also increased the availability of prey and thus increased the populations of predators (II, III). Unexpectedly, fire also increased late-stage xylophagous species (III).

Although the functional diversity of saproxylic beetles on unharvested forests and clear-cuts did not differ (III), assemblage compositions were different (II). Clear-cutting led to a slight increase in fresh- and late-stage-wood feeders and mean body size was also increased (III). Dead wood consists mostly of old logs, stumps and logging residues and the supply of new dead wood is not continuous as in clear-cut stands. When retention forestry is applied, the amount of large-sized and fresh dead wood increases and the shadiness of the stand is decreased due to mortality of retained trees (I). This benefits light-associated species as well as species that prefer the early decay stages of dead wood (III). Due to high mortality and relatively small size of retention patches they were clearly not able to maintain closed-canopy forest conditions inside the patches (I; see also the response of carabid assemblages in study V). Harvesting at the higher retention level favored both fresh- and late-stage-wood feeders, while the lower retention level increased fresh-wood feeders only and led to a decrease in mycetophagous beetles (II, III). The phylogenetic and functional composition of beetle assemblages were more clumped at the lower retention level, indicating that a larger variability of resources was available at the higher level. The mean body size of saproxylic beetles increased in response to increased logging intensity (III). This was caused by the reduced proportion of small species in the habitats, as the amount of medium-sized species increased more than the amount of small species. Although small-sized species also increased after logging, numbers decreased with increasing logging intensity, indicating that the resources after intensive harvesting were more suitable for large species than for small species (III). One possible explanation for increasing amounts of medium-sized species could be their more strongly increased flying activity compared to smaller species at logged stands, but to verify this would need further research.

### 3.4 Pyrophilous flat bugs appear on burned sites immediately after fire but also disappear quickly within a few years.

Burning increased the number and abundance of pyrophilous flat bug species (IV). Two Red-Listed and very rare pyrophilous species; *Aradus angularis* J. Sahlberg (VU) and *A. laeviusculus* Reuter (NT), were observed in large numbers after burning: 31 and 43 specimens in total, respectively (IV). There are few previous records of these species in Finland (Heliövaara and Väisänen 1983; Lappalainen and Simola 1998; Rintala and Rinne 2010).

My results indicate that pyrophilous flat bugs are able to find and colonize burning or recently burned forests very effectively (IV). Schmitz et al. (2010) have shown that some pyrophilous flat bug species have similar infrared-sensitive sensilla to those previously found in a pyrophilous jewel beetle *Melanophila acuminata* DeGeer for example (Evans 1964). However, the effect of fire is transient at the stand level and the pyrophilous species disappear almost completely within two years (IV). For example, the records of *A. angularis* in study IV were almost all from 2001, immediately after burning. After that, the species was recorded only once in 2003. Clearly, in order to maintain these species recently burned forests should be continuously available at the landscape level.

Non-pyrophilous flat bugs disappeared during burning and were not recorded at all at the burned stands in 2001. However, they had recolonized the stands by the following year, and were more abundant than at the unburned stands by 2002. All the flat bug species recorded in study IV are mycetophagous species that forage for wood-living fungus (Heliövaara and Väisänen 1983; Rintala and Rinne 2010). The effects of burning combined with the removal of dead standing trees can be destructive for this kind of species in the short-term, as a proportion of old fallen dead wood and logging residues is burned and the rest is mostly scorched and charred. Furthermore, most of the original insect populations that live on the surface of the wood can be destroyed by fire, although the survival of wood-boring species inside large-diameter logs can be relatively high (Ulyshen et al. 2010). There is a collapse in wood-living fungus populations during burning and they can be almost absent immediately afterwards, but recover within a few years (Junninen et al. 2008; Penttilä et al. 2013). In the long-term, the effect of burning is positive for polypore fungi (Penttilä et al. 2013; Suominen et al. 2015), which most likely benefits non-pyrophilous flat bugs as well.

The results indicate that logging increased the abundance of flat bugs only when the retention trees were left during harvest (IV), although there were no differences between the two retention levels. Seibold et al. (2014) suggested large-diameter dead wood in sunny habitats is an important resource for flat bugs. In the retention harvests, the amount of coarse dead wood was also relatively high at the lower retention level due to high immediate mortality of the retention trees (I). Differences in species richness between the two retention levels may become visible in the longer-term, because the dead wood input is better maintained at the higher retention level. A lack of adequate resources for flat bugs in the clear-cut stands was likely, as the dead wood consisted mostly of stumps and logging residues and larger logs were absent.

## 3.5 Burning and logging increased carabid beetle species richness, but small sized retention tree aggregates were not able to maintain the assemblages of closed forests.

A total of 5770 ground beetles belonging to 63 species were collected in study V. One dominant species; *Pterostichus adstrictus* Eschscholtz with 3477 specimens, covered more than 60% of total catch. *P. adstrictus* was 21 times more abundant in the burned stands than in the unburned stands, although the pooled abundance of other species did not differ between the treatments. However, species richness in the first post-treatment year was clearly higher at the logged stands than at the unharvested stands, and burning increased species richness (V). Burning benefited species, such as *P. adstrictus, Sericoda quadripunctata* (DeGeer) and *Bembidion grapii* Gyllenhal, that are known to favor burned areas, but the majority of species that prefer open habitats were also clearly more abundant at burned rather than unburned stands. One Red-Listed and pyrophilous *P. quadrifoveolatus* (NT) specimen was observed at the burned stand at the lower retention level.

The increase in species richness of the ground beetles was expected after harvesting, as the species that prefer open habitats are known to colonize those areas (Heliölä et al. 2001; Koivula 2002). Burning decreased the mean size of species and increased the proportion of macropterous species (V). The proportion of macropterous species also clearly increased following harvesting. Similar findings have been reported previously by Holliday (1991) and Huber and Baumgarten (2005). Both the smaller size and the larger proportion of macropterous species at the burned stands suggest greater turnover of species at the burned stands. Large species are often brachypterous, which have a poor dispersal ability and thus are slower to recolonize stands.

Some environmental variables; the characteristics of ground-layer vegetation, soil conditions, the amount of living trees and abundance of red wood ants, showed correlations with ground beetle assemblages and with some individual species but assemblage-level effects were not always reflected at species level. For example, increased abundance of red wood ants decreased the abundances of carabids in general, but this was not observed for *Calathus micropterus* (Duftschmid) and *Notiophilus aquaticus* (Linnaeus). Why do these species seem not to avoid ants, remained unclear to me. Dead wood characteristics did not affect the carabid assemblages. These correlations were generally consistent with the previous findings of (Niemelä et al. 1992; Koivula and Niemelä 2003).

The retention tree aggregate areas at both retention levels were too small to maintain the assemblages of closed forests, which is consistent with the previous findings of Koivula (2002) and Gandhi et al. (2001). Retention tree aggregates can, however, provide better food, shade and shelter than open areas of the same stands, and serve as breeding habitats for wood living species, such as *S. quadripunctata*. The ground beetles favored tree groups at the burned stands, and the assemblages within the groups were intermediate between uncut forests and open areas (V). This was not observed at the unburned stands, where dense vegetation and logging residues occurred and also provided shade and shelter in open areas. Ground beetles appear to have a good tolerance to disturbance and they in fact may benefit frequent use of prescribed fire, possibly because this maintains open and sunny ground and field layer.

### 3.6 Retention forestry and prescribed burning do not result in increased damage from pine-shoot beetles in adjacent forests

Methods that emulate natural disturbances increase the amount of dead wood in stands (I). In managed forests, biotic disturbances, such as diseases and insect outbreaks are usually prevented by salvage logging, but in emulating natural disturbances an increase in the amount of dead wood is the goal, and salvage logging is therefore not performed. In pine-dominated forests the risk of insect damage is mainly caused by pine-shoot beetles. Paper VI of this thesis shows, however, that retention forestry and prescribed burning, regardless of the amount of dead wood present, does not result in significantly increased damage in adjacent forests from pine-shoot beetles. The numbers of fallen shoots increased in the closest part of the adjacent forests (mainly 10 – 20 m from the edge) in all harvesting treatments, returned to the background level at the clear-cut stands within three years, and remained at a somewhat increased level at the burned stand with retention trees. However, the number of fallen shoots remained at such a low level in all treatment combinations that foraging likely had only a negligible effect on the growth of trees. At the unharvested stands, burning increased the number of fallen shoots in only one stand where the intensity of the fire was sufficiently high to kill large pines, although the effect did not reach the unburned forest surrounding the burned area. Though the foraging of pine-shoot beetles increased somewhat after logging and burning in the surrounding forests, the effect was mostly restricted to the trees nearest the edge of the logged stands, and did not spread deeper into the adjacent forest. Similar effects have been later found in forest restoration by Komonen and Kouki (2008).

## 4 CONCLUSIONS AND IMPLICATIONS FOR FOREST MANAGEMENT

Based on my observations on trees and insects, traditional clear-cutting does not emulate the ecological effects of natural disturbances in boreal pine-dominated forest. My results, however, provide substantial new evidence that retention forestry is a method that can significantly improve the level of emulation and maintain the forest structures that are important for biodiversity. The results of my thesis suggests that retention forestry can be applied to maintain some elements of pre-harvest species richness over ten post-harvest years, but it also shows that major changes in species assemblages do occur. The burned unharvested forests, which can be considered as comparable to natural fire disturbance, hosted a different assemblage composition and increasing species richness of saproxylics throughout the post-disturbance years, whereas the increase of species richness turned out to be transient at the harvested forests. Furthermore, to achieve the benefits from retention trees, it is essential to apply sufficient levels of retention. Although my results do not provide an exact recommended retention level, the results strongly suggest that the retention levels currently used, especially in Fennoscandia (1-5 % of preharvest volume, Gustafsson et al. 2012), are too low to maintain diverse fauna and flora or to provide many of the objectives of retention. For example, larger retention volumes are needed to maintain the continuity of dead wood and living trees, and retention levels below 10 $m^3 ha^{-1}$ can only provide a limited amount of resources for species over the long-term. However, it is unlikely that sufficient amounts of trees will be retained in all harvesting areas. This may not be even necessary if retention can be planned at the landscape-level so that high-retention stands are continuously available at a regional scale and within dispersal distance of species (see also Runnel et al. 2013; Bouget and Parmain 2016). Further landscape-level research is, however, needed to explore the landscape-level effects on these factors. Furthermore, even at the higher levels of retention that were applied in my thesis the aggregates of retention trees were too small to enable maintenance of the assemblages of closed forests. Small-size aggregates operate under the edge effect and, thus, larger aggregates are clearly needed if the aim is to maintain closed forest assemblages (Aubry et al. 2004; Lee et al. 2015). However, even small sized aggregates can probably enhance species survival and re-colonization at least in the short-term and especially in areas that are naturally susceptible to large-scale disturbances (Baker et al. 2013).

Prescribed burning clearly benefits pyrophilous species, which have the ability to find burned areas. Thus, the availability of burned forests is important at the landscape-level, so that habitats for reproduction can be continuously found at distances that do not exceed the dispersal ability of species. The application of prescribed burning to retention forestry at a reasonable retention level provides a practical and feasible method to further enhance the emulation of natural disturbances, and leads to diverse assemblages of dead and living trees. Further research is needed to explore dispersal abilities of pyrophilous species but also saproxylics in general.

Finally, I was also able to show that these methods can be applied in northern European boreal pine-dominated forests without undue risks of insect pest damage. The risk of damage can be further reduced if the dead wood is generated after the swarming period of the pine-shoot beetles (VI). It should, however, be kept in mind that this result is applicable only in pine-dominated forests, and insect outbreaks in spruce forests were not evaluated in this thesis.

In terms of novelty, my thesis increases the knowledge of the forestry practices aiming to emulate natural disturbances, providing significant new information of the effects of prescribed burning and retention forestry on forest biodiversity. In particular, my results enlarge the knowledge of the response of saproxylic beetles, by extending time scale and bringing functional-phylogenetic perspective into analysis. Also the taxonomic coverage of my studies is broader than in many previous studies (e.g. Hyvärinen 2006) and covers also ground beetles and flat bugs. Furthermore, retention tree dynamics and the risk of pest invasion have now been investigated.

To conclude, the results from my thesis show that the principle of emulating natural disturbances in managed forests is an appealing method to reduce the negative effects of forest management on biodiversity. Traditional clear-cutting deviates considerably from natural disturbances and cannot be considered as an appropriate way to mimic those disturbances. Based on detailed tree- and species-level analyses, I propose that the inclusion of prescribed burning with a sufficient volume of retention trees adds significant ecological values to the emulation principle. Although economic aspects were not considered in my thesis, if these measures can be planned at the landscape scale and implemented on carefully planned and selected harvesting sites, it is quite likely that the economic effects on timber revenues would remain marginal. In that case, emulation of natural disturbances can also become a highly important tool in managed forests that can significantly complement the value that full set-aside areas have on biodiversity maintenance and may help overcome the lack of natural, protected forests. Although the “emulated” post-harvest young successional sites do not fully resemble natural forests, there are clear novel possibilities to enhance the biological characteristics and biodiversity of these sites through more careful and ecologically justified emulation of natural disturbances.

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## APPENDIX 1. List of saproxylic beetle species included in this thesis

Although burning was not yet implemented in 2000, the numbers of individuals have nevertheless been divided in columns according to upcoming fire-treatments. NT = Near Threatened; VU = Vulnerable; Pyr.= pyrophilous species (according to Wikars 1997).

| Species | | | Year | | | | | | Total |
|---|---|---|---|---|---|---|---|---|---|
| | | | 2000 | | 2002 | | 2011 | | |
| | | | Fire | No fire | Fire | No fire | Fire | No fire | |
| *Abdera affinis* | | | 1 | | | 4 | | 1 | 6 |
| *Abdera flexuosa* | | | | | | 1 | | | 1 |
| *Abdera triguttata* | | | 1 | 1 | 6 | 1 | 1 | 1 | 11 |
| *Acanthocinus aedilis* | | | | | | 2 | | | 2 |
| *Acmaeops marginatus* | NT | Pyr. | | | 15 | | | | 15 |
| *Acmaeops pratensis* | | | | | 840 | 90 | 124 | 8 | 1062 |
| *Acmaeops septentrionis* | NT | Pyr. | | | 12 | 2 | 1 | | 15 |
| *Acrulia inflata* | | | 3 | 4 | | | | 2 | 9 |
| *Agathidium discoideum* | | | 1 | 1 | 1 | 2 | | | 5 |
| *Agathidium nigripenne* | | | 2 | 7 | 2 | | 1 | | 12 |
| *Agathidium pisanum* | | | 35 | 55 | 6 | 7 | 2 | 2 | 107 |
| *Agathidium pulchellum* | VU | | | 1 | | | | | 1 |
| *Allandrus undulatus* | | | | | | 1 | 1 | | 2 |
| *Alosterna tabacicolor* | | | 18 | 5 | | 1 | 1 | | 25 |
| *Ampedus balteatus* | | | 10 | 18 | 794 | 341 | 768 | 403 | 2334 |
| *Ampedus erythrogonus* | | | 12 | 11 | 7 | 14 | 4 | 10 | 58 |
| *Ampedus lepidus* | VU | | | | | | | 1 | 1 |
| *Ampedus nigrinus* | | | 122 | 108 | 180 | 362 | 545 | 493 | 1810 |
| *Ampedus pomonae* | | | | | 22 | 6 | 6 | 1 | 35 |
| *Ampedus pomorum* | | | | | 2 | 1 | 2 | 3 | 8 |
| *Ampedus suecicus* | | | | | 6 | | 7 | 2 | 15 |
| *Ampedus tristis* | | | 9 | 7 | 350 | 107 | 216 | 100 | 789 |
| *Anaspis arctica* | | | 46 | 39 | 6 | 10 | 2 | 1 | 104 |
| *Anaspis bohemica* | | | 1 | 6 | 21 | 8 | 10 | 5 | 51 |
| *Anaspis frontalis* | | | | | 2 | 4 | 8 | 7 | 21 |
| *Anaspis marginicollis* | | | 522 | 411 | 42 | 137 | 182 | 120 | 1414 |
| *Anaspis rufilabris* | | | | | 1 | 1 | | | 2 |
| *Anidorus nigrinus* | | | | | 1 | | 2 | 4 | 7 |
| *Anisotoma axillaris* | | | 11 | 5 | 23 | 55 | 45 | 61 | 200 |
| *Anisotoma castanea* | | | 54 | 28 | 15 | 123 | 20 | 58 | 298 |
| *Anisotoma glabra* | | | 22 | 23 | 320 | 524 | 155 | 180 | 1224 |
| *Anisotoma humeralis* | | | 25 | 18 | 7 | 13 | 7 | 12 | 82 |
| *Anisotoma orbicularis* | | | 1 | 1 | | 1 | 5 | 13 | 21 |
| *Anobium rufipes* | | | | | | | | 1 | 1 |
| *Anobium thomsoni* | | | | | | 1 | 2 | 1 | 4 |
| *Anomognathus cuspidatus* | | | 1 | | 4 | 1 | 1 | | 7 |
| *Anoplodera maculicornis* | | | | | | | 1 | | 1 |
| *Anoplodera reyi* | | | 3 | 2 | 29 | 13 | 84 | 8 | 139 |
| *Anoplodera rubra* | | | | | | 2 | | 6 | 8 |

| Species | | Year | | | | | | Total |
|---|---|---|---|---|---|---|---|---|
| | | 2000 | | 2002 | | 2011 | | |
| | | Fire | No fire | Fire | No fire | Fire | No fire | |
| *Anoplodera sanguinolenta* | | 1 | 3 | 109 | 35 | 346 | 50 | 544 |
| *Anthaxia quadripunctata* | | | | 2 | 2 | | | 4 |
| *Aplocnemus nigricornis* | | | | | | | 1 | 1 |
| *Aplocnemus tarsalis* | | | 1 | | 16 | | 8 | 25 |
| *Arhopalus rusticus* | | | | 5 | 1 | | 2 | 8 |
| *Asemum striatum* | | 1 | 2 | 57 | 19 | 3 | | 82 |
| *Aspidiphorus orbiculatus* | | 5 | 5 | 6 | 5 | 3 | 6 | 30 |
| *Atheta boletophila* | | | 1 | | | | | 1 |
| *Atomaria abietina* | | | 1 | | | 2 | 1 | 4 |
| *Atomaria affinis* | | | 1 | | 1 | | | 2 |
| *Atomaria badia* | | 2 | 3 | 1 | | | | 6 |
| *Atomaria bella* | | 52 | 40 | 124 | 59 | 8 | 4 | 287 |
| *Atomaria elongatula* | | 2 | | | | 1 | 1 | 4 |
| *Atomaria subangulata* | | 2 | 6 | 8 | 7 | 3 | | 26 |
| *Atomaria umbrina* | | 2 | 3 | 3 | 7 | | | 15 |
| *Atrecus affinis* | | 4 | 4 | 6 | 6 | 11 | 3 | 34 |
| *Atrecus longiceps* | | 2 | 1 | | | | | 3 |
| *Atrecus pilicornis* | | 46 | 44 | 7 | 9 | 2 | 5 | 113 |
| *Batrisodes hubenthali* | | 1 | | 2 | | | | 3 |
| *Bibloporus bicolor* | | 4 | 3 | 2 | 5 | 3 | 3 | 20 |
| *Bibloporus minutus* | | 4 | 5 | 5 | 9 | 8 | 12 | 43 |
| *Bitoma crenata* | | | | 4 | 3 | 2 | 1 | 10 |
| *Bius thoracicus* | | | | 1 | 1 | 1 | | 3 |
| *Bolitochara mulsanti* | | 8 | 7 | | | 1 | 1 | 17 |
| *Bolitophagus reticulatus* | | 12 | 12 | 21 | 8 | 11 | 3 | 67 |
| *Buprestis haemorrhoidalis* | | | | | | 1 | | 1 |
| *Buprestis rustica* | | | | 2 | 10 | 13 | 9 | 34 |
| *Calitys scabra* | | | | 1 | | 3 | | 4 |
| *Callidium violaceum* | | | 1 | 2 | 1 | | 1 | 5 |
| *Calopus serraticornis* | | 2 | 2 | 8 | 2 | 1 | 3 | 18 |
| *Cardiophorus ruficollis* | | | | 120 | 15 | 199 | 40 | 374 |
| *Carphoborus rossicus* | | | | | | 1 | | 1 |
| *Cerylon deplanatum* | | | | 4 | 1 | | | 5 |
| *Cerylon fagi* | | 5 | 6 | 1 | 1 | | 3 | 16 |
| *Cerylon ferrugineum* | | 36 | 46 | 19 | 22 | 13 | 13 | 149 |
| *Cerylon histeroides* | | 34 | 27 | 23 | 26 | 13 | 19 | 142 |
| *Cerylon impressum* | NT | | | 4 | | | 1 | 5 |
| *Chrysanthia geniculata* | | | | 14 | 8 | 18 | 36 | 76 |
| *Chrysobothris chrysostigma* | | | | | 1 | | | 1 |
| *Cis bidentatus* | | | | 1 | | | | 1 |
| *Cis boleti* | | 14 | 12 | 26 | 25 | 8 | 8 | 93 |
| *Cis comptus* | | 2 | 2 | 2 | 2 | 15 | 6 | 29 |
| *Cis dentatus* | | | 1 | | | | | 1 |
| *Cis glabratus* | | 6 | 1 | 2 | | | 1 | 10 |
| *Cis jacquemartii* | | 6 | 7 | 11 | 3 | 4 | | 31 |
| *Cis lineatocribratus* | | 13 | 13 | 5 | 8 | 5 | 3 | 47 |

| Species | | | Year | | | | | | Total |
|---|---|---|---|---|---|---|---|---|---|
| | | | 2000 | | 2002 | | 2011 | | |
| | | | Fire | No fire | Fire | No fire | Fire | No fire | |
| *Cis micans* | | | 6 | 5 | 7 | 13 | 17 | 27 | 75 |
| *Cis punctulatus* | | | 8 | 6 | 11 | 22 | 21 | 3 | 71 |
| *Cis quadridens* | | | | | | 1 | | | 1 |
| *Clypastraea pusilla* | | Pyr. | | | 43 | 10 | | 1 | 54 |
| *Corticaria alleni* | VU | | | | | | 1 | | 1 |
| *Corticaria crenicollis* | | | 1 | | 3 | | | | 4 |
| *Corticaria foveola* | | | 1 | | | | | | 1 |
| *Corticaria lapponica* | | | 4 | 6 | 2 | 2 | 18 | 2 | 34 |
| *Corticaria lateritia* | | | 1 | | 9 | 1 | 3 | 1 | 15 |
| *Corticaria obsoleta* | | | | | 2 | | | | 2 |
| *Corticaria orbicollis* | | | 4 | 5 | 10 | 1 | 1 | 1 | 22 |
| *Corticaria polypori* | | | 1 | | | 2 | 1 | 2 | 6 |
| *Corticeus linearis* | | | | | 27 | 13 | | | 40 |
| *Corticeus longulus* | | | | | 1 | | | | 1 |
| *Corticeus suturalis* | | | | | 3 | 1 | 1 | | 5 |
| *Cryphalus saltuarius* | | | 11 | 5 | 1 | 1 | | 2 | 20 |
| *Cryptolestes abietis* | | | | | 6 | 1 | 2 | | 9 |
| *Cryptolestes alternans* | | | | 1 | 12 | | 4 | | 17 |
| *Cryptolestes corticinus* | | | | | 1 | 2 | 3 | 10 | 16 |
| *Cryptolestes weisei* | VU | | | | 4 | | | | 4 |
| *Cryptophagus corticinus* | | Pyr. | | | 7 | | | | 7 |
| *Cryptophagus parallelus* | | | | | 1 | | | | 1 |
| *Cryptophagus quadrihamatus* | | | | | 1 | | | | 1 |
| *Crypturgus cinereus* | | | | | | | 2 | 1 | 3 |
| *Crypturgus hispidulus* | | | 5 | 29 | 23 | 10 | 20 | 7 | 94 |
| *Crypturgus pusillus* | | | 2 | | 5 | 9 | 7 | 2 | 25 |
| *Crypturgus subcribrosus* | | | | 8 | 56 | 7 | 8 | 10 | 89 |
| *Curtimorda maculosa* | | | 3 | | 7 | 4 | 91 | 74 | 179 |
| *Dacne bipustulata* | | | 10 | 12 | 34 | 22 | 18 | 10 | 106 |
| *Dadobia immersa* | | | 5 | | 12 | 5 | 4 | 6 | 32 |
| *Dasytes niger* | | | 2 | 6 | 16 | 15 | 559 | 411 | 1009 |
| *Dasytes obscurus* | | | | | 96 | 54 | 1032 | 457 | 1639 |
| *Dendroctonus micans* | | | | | 1 | | | | 1 |
| *Dendrophagus crenatus* | | | 11 | 9 | 4 | 8 | | 4 | 36 |
| *Denticollis borealis* | | | | | 2 | 2 | 1 | 1 | 6 |
| *Denticollis linearis* | | | 7 | 7 | 3 | 5 | 3 | 6 | 31 |
| *Dexiogyia corticina* | | | | | 4 | | 1 | 1 | 6 |
| *Diaperis boleti* | | | | | 4 | | 3 | 1 | 8 |
| *Dictyoptera aurora* | | | 46 | 61 | 16 | 15 | 28 | 24 | 190 |
| *Dinaraea aequata* | | | 2 | 1 | 13 | 7 | 4 | 2 | 29 |
| *Dinaraea linearis* | | | 1 | 3 | 3 | 4 | 4 | 4 | 19 |
| *Dolichocis laricinus* | | | 1 | 3 | | | | | 4 |
| *Dorcatoma dresdensis* | | | 36 | 18 | 13 | 11 | 13 | 3 | 94 |
| *Dorcatoma punctulata* | | | 3 | 7 | 1 | | 8 | 3 | 22 |
| *Dorcatoma robusta* | | | 9 | | 9 | 6 | 11 | 8 | 43 |
| *Dryocoetes alni* | | | | | | | 3 | | 3 |

| Species | | | Year | | | | | | Total |
|---|---|---|---|---|---|---|---|---|---|
| | | | 2000 | | 2002 | | 2011 | | |
| | | | Fire | No fire | Fire | No fire | Fire | No fire | |
| *Dryocoetes autographus* | | | 310 | 396 | 1413 | 860 | 48 | 46 | 3073 |
| *Dryocoetes hectographus* | | | 38 | 61 | 29 | 16 | 41 | 18 | 203 |
| *Eblisia minor* | | | | | | 3 | 4 | 11 | 18 |
| *Enicmus fungicola* | | | 71 | 52 | 152 | 149 | 95 | 68 | 587 |
| *Enicmus planipennis* | | | 28 | 25 | 37 | 5 | 6 | 2 | 103 |
| *Enicmus rugosus* | | | 151 | 105 | 477 | 403 | 609 | 491 | 2236 |
| *Enicmus transversus* | | | | | 1 | 2 | 2 | 2 | 7 |
| *Ennearthron cornutum* | | | | 2 | | 2 | | 2 | 6 |
| *Episernus angulicollis* | | | 2 | | | | | | 2 |
| *Epuraea angustula* | | | 1 | 6 | 3 | 3 | 2 | 1 | 16 |
| *Epuraea biguttata* | | | 3 | 5 | 1 | 1 | 1 | 1 | 12 |
| *Epuraea boreella* | | | 6 | 13 | 13 | 2 | | 1 | 35 |
| *Epuraea contractula* | | | 2 | 3 | | | 5 | | 10 |
| *Epuraea deubeli* | | | | 1 | 10 | | | | 11 |
| *Epuraea fussii* | | | | | 3 | | | | 3 |
| *Epuraea hilleri* | | | | 1 | | | | 1 | 2 |
| *Epuraea laeviuscula* | | | 1 | | 16 | | | | 17 |
| *Epuraea longiclavis* | | | | | | | | 2 | 2 |
| *Epuraea marseuli* | | | 31 | 50 | 69 | 25 | 8 | 8 | 191 |
| *Epuraea muehli* | | | | 2 | 34 | | | | 36 |
| *Epuraea oblonga* | | | 2 | 4 | 8 | 3 | 1 | | 18 |
| *Epuraea pallescens* | | | 1 | 2 | 2 | | 1 | 3 | 9 |
| *Epuraea pygmaea* | | | 76 | 123 | 347 | 104 | 18 | 6 | 674 |
| *Epuraea rufobrunnea* | | | | | 2 | | | | 2 |
| *Epuraea rufomarginata* | | | 8 | 14 | 11 | 5 | 6 | | 44 |
| *Epuraea silacea* | | | 1 | | | | 2 | 3 | 6 |
| *Epuraea silesiaca* | NT | Pyr. | | | 1 | | 1 | | 2 |
| *Epuraea thoracica* | | | | | 8 | | | | 8 |
| *Epuraea variegata* | | | 2 | 4 | 3 | 1 | 4 | 1 | 15 |
| *Ernobius explanatus* | | | | 1 | 5 | 1 | 6 | | 13 |
| *Ernobius nigrinus* | | | 8 | 2 | 19 | 21 | 2 | 1 | 53 |
| *Eucilodes caucasicus* | | | 2 | 1 | | 1 | | | 4 |
| *Euglenes pygmaeus* | | | 1 | 1 | 15 | 6 | 15 | 4 | 42 |
| *Euplectus decipiens* | | | 2 | 5 | 1 | 1 | 1 | 3 | 13 |
| *Euplectus kirbii/nanus* | | | 1 | | | | 1 | 3 | 5 |
| *Euplectus mutator* | | | 2 | 4 | 9 | 6 | 13 | 5 | 39 |
| *Euplectus piceus* | | | 4 | | 1 | | 8 | 8 | 21 |
| *Euplectus punctatus* | | | 5 | 12 | 23 | 20 | 46 | 30 | 136 |
| *Euryusa castanoptera* | | | 5 | | 3 | 2 | 4 | 1 | 15 |
| *Gabrius expectatus* | | | 6 | 3 | 17 | 21 | 4 | 12 | 63 |
| *Gaurotes virginea* | | | | | 9 | 6 | | | 15 |
| *Glischrochilus hortensis* | | | 3 | 1 | 1 | 3 | 1 | 1 | 10 |
| *Glischrochilus quadripunctatus* | | | 9 | 9 | 29 | 10 | 2 | | 59 |
| *Globicornis emarginata* | | | | | 4 | 5 | 21 | 29 | 59 |
| *Gonotropis dorsalis* | NT | | | | 1 | | | | 1 |
| *Gyrophaena boleti* | | | | 1 | 1 | | 18 | 4 | 24 |

| Species | | Year | | | | | | Total |
|---|---|---|---|---|---|---|---|---|
| | | 2000 | | 2002 | | 2011 | | |
| | | Fire | No fire | Fire | No fire | Fire | No fire | |
| *Gyrophaena joyioides* | | | | 1 | | 2 | | 3 |
| *Gyrophaena poweri* | | | | 1 | | | | 1 |
| *Hadreule elongatula* | | | | 1 | 4 | 5 | 2 | 12 |
| *Hadrobregmus confusus* | | 2 | 2 | | 3 | 1 | 3 | 11 |
| *Hadrobregmus pertinax* | | 16 | 18 | 105 | 116 | 102 | 43 | 400 |
| *Hallomenus axillaris* | | 4 | 8 | 4 | 8 | 7 | 3 | 34 |
| *Hallomenus binotatus* | | 6 | 6 | 5 | 7 | 4 | 2 | 30 |
| *Harminius undulatus* | | 1 | 1 | 4 | | | | 6 |
| *Henoticus serratus* | Pyr. | | | 6 | | | | 6 |
| *Homalota plana* | | | | 2 | 1 | | | 3 |
| *Hylastes brunneus* | | 139 | 71 | 611 | 1111 | 83 | 166 | 2181 |
| *Hylastes cunicularius* | | 718 | 881 | 1471 | 1236 | 25 | 90 | 4421 |
| *Hylastes opacus* | | | 2 | 211 | 173 | 17 | 28 | 431 |
| *Hylecoetus dermestoides* | | 23 | 17 | 45 | 79 | 9 | 16 | 189 |
| *Hylobius abietis* | | 24 | 28 | 307 | 143 | 33 | 47 | 582 |
| *Hylobius piceus* | | | 2 | | 1 | | | 3 |
| *Hylobius pinastri* | | 1 | 1 | 3 | 2 | 3 | 4 | 14 |
| *Hylurgops glabratus* | | 40 | 72 | 6 | 6 | | | 124 |
| *Hylurgops palliatus* | | 82 | 52 | 20 | 6 | 3 | 9 | 172 |
| *Ipidia binotata* | | | 1 | 10 | 5 | 4 | | 20 |
| *Ips amitinus* | | | 1 | 155 | 64 | | | 220 |
| *Ips duplicatus* | | | | 1 | 1 | | | 2 |
| *Ips typographus* | | 1 | 1 | 100 | 12 | 1 | | 115 |
| *Ischnoglossa elegantula* | | 2 | | 2 | 3 | 1 | | 8 |
| *Ischnoglossa obscura* | | | | | | | 1 | 1 |
| *Judolia sexmaculata* | | 6 | 8 | 100 | 120 | 117 | 56 | 407 |
| *Lacon conspersus* | | 7 | 5 | 7 | 12 | 11 | 11 | 53 |
| *Lacon fasciatus* | | 1 | | 61 | 27 | 25 | 22 | 136 |
| *Laemophloeus muticus* | Pyr. | | | 8 | | 1 | | 9 |
| *Lasconotus jelskii* | | | 1 | 3 | 1 | | | 5 |
| *Latridius hirtus* | | 17 | 16 | 62 | 14 | 21 | 9 | 139 |
| *Leiestes seminigra* | | | | 1 | | 1 | | 2 |
| *Leptura melanura* | | 20 | 7 | 39 | 71 | 344 | 208 | 689 |
| *Leptura quadrifasciata* | | 3 | 5 | 21 | 34 | 41 | 9 | 113 |
| *Lepturobosca virens* | | 4 | 2 | 197 | 151 | 429 | 123 | 906 |
| *Leptusa pulchella* | | 65 | 44 | 21 | 13 | 2 | 5 | 150 |
| *Litargus connexus* | | | 1 | 48 | 5 | | | 54 |
| *Lordithon trimaculatus* | | 3 | | 2 | | | | 5 |
| *Lygistopterus sanguineus* | | | | 27 | 3 | 19 | 5 | 54 |
| *Magdalis carbonaria* | | | | 3 | 2 | | | 5 |
| *Magdalis duplicata* | | 6 | 7 | 36 | 44 | 2 | 2 | 97 |
| *Magdalis frontalis* | | | | 44 | 114 | 2 | 1 | 161 |
| *Magdalis linearis* | | | | | 1 | | | 1 |
| *Magdalis nitida* | | | | | 1 | | | 1 |
| *Magdalis phlegmatica* | | | 3 | 16 | 20 | | | 39 |
| *Magdalis ruficornis* | | | | | | 1 | | 1 |

| Species | | Year | | | | | | Total |
|---|---|---|---|---|---|---|---|---|
| | | 2000 | | 2002 | | 2011 | | |
| | | Fire | No fire | Fire | No fire | Fire | No fire | |
| *Magdalis violacea* | | | | 10 | 36 | | | 46 |
| *Malthinus biguttatus* | | 40 | 12 | 2 | 17 | 3 | 4 | 78 |
| *Malthinus flaveolus* | | | | | 1 | | 2 | 3 |
| *Malthodes brevicollis* | | 92 | 80 | 74 | 248 | 35 | 73 | 602 |
| *Malthodes crassicornis* | | 11 | 2 | 1 | 4 | 40 | 57 | 115 |
| *Malthodes flavoguttatus* | | | | 1 | 2 | | | 3 |
| *Malthodes fuscus* | | 15 | 18 | 85 | 50 | 21 | 42 | 231 |
| *Malthodes guttifer* | | 28 | 34 | 17 | 193 | 16 | 51 | 339 |
| *Malthodes marginatus* | | 16 | 30 | 3 | 26 | 5 | 9 | 89 |
| *Malthodes misellus* | | | | 72 | 14 | 53 | 25 | 164 |
| *Malthodes mysticus* | | | | | 2 | 7 | 3 | 12 |
| *Malthodes pumilus* | | 2 | | 10 | 9 | 15 | 13 | 49 |
| *Malthodes spathifer* | | 4 | | 3 | 4 | 2 | 2 | 15 |
| *Melanophila acuminata* | Pyr. | | | 9 | | | | 9 |
| *Melanotus castanipes* | | 448 | 348 | 874 | 467 | 930 | 694 | 3761 |
| *Micrambe longitarsis* | | 3 | 2 | 19 | 3 | | | 27 |
| *Microbregma emarginata* | | | | | 1 | | | 1 |
| *Microscydmus minimus* | | | | | 4 | 1 | 8 | 13 |
| *Microscydmus nanus* | | | | 9 | 20 | 2 | 12 | 43 |
| *Molorchus minor* | | 1 | 1 | 21 | 4 | | 3 | 30 |
| *Monochamus sutor* | | | | | 2 | 1 | 1 | 4 |
| *Mordellistena humeralis* | | 1 | | | | | | 1 |
| *Mycetochara flavipes* | | 13 | | 4 | 2 | 5 | 1 | 25 |
| *Mycetochara obscura* | | 22 | 7 | 4 | 10 | 16 | 15 | 74 |
| *Mycetophagus decempunctatus* | | | | 1 | | 1 | 1 | 3 |
| *Mycetophagus fulvicollis* | | 2 | | 1 | 3 | 2 | 2 | 10 |
| *Mycetophagus multipunctatus* | | 4 | 2 | | 1 | | | 7 |
| *Mycetophagus piceus* | | 3 | 2 | 51 | 23 | 7 | 2 | 88 |
| *Mycetophagus populi* | | | 3 | | 2 | 1 | | 6 |
| *Mycetophagus quadripustulatus* | | | | 2 | | 2 | | 4 |
| *Nepachys cardiacae* | | | | 7 | | 2 | | 9 |
| *Nudobius lentus* | | | | 14 | 31 | 2 | | 47 |
| *Octotemnus glabriculus* | | | 3 | 1 | 2 | 1 | | 7 |
| *Olisthaerus substriatus* | | 1 | 2 | 1 | 4 | 1 | | 9 |
| *Orchesia fasciata* | | 1 | 1 | 1 | | 3 | 1 | 7 |
| *Orchesia micans* | | 6 | 10 | 6 | 1 | | 1 | 24 |
| *Orchesia minor* | | | 1 | | | | 1 | 2 |
| *Orthocis alni* | | 15 | 8 | 7 | 6 | 9 | 8 | 53 |
| *Orthoperus corticalis* | | | | 5 | | 1 | | 6 |
| *Orthotomicus laricis* | | | | 19 | 21 | | 1 | 41 |
| *Orthotomicus proximus* | | | | 4 | 7 | 1 | | 12 |
| *Orthotomicus suturalis* | | 1 | 1 | 211 | 106 | 4 | 2 | 325 |
| *Ostoma ferruginea* | | 11 | 9 | 10 | 10 | 4 | 5 | 49 |
| *Oxymirus cursor* | | 15 | 15 | 7 | 26 | 10 | 11 | 84 |
| *Pachyta lamed* | | | | 82 | 40 | | | 122 |
| *Pachyta quadrimaculata* | | | | 1 | | | | 1 |

| Species | | Year | | | | | | Total |
|---|---|---|---|---|---|---|---|---|
| | | 2000 | | 2002 | | 2011 | | |
| | | Fire | No fire | Fire | No fire | Fire | No fire | |
| *Paranopleta inhabilis* | Pyr. | | 1 | 8 | 2 | | | 11 |
| *Pediacus fuscus* | | 1 | | 63 | 31 | 46 | 15 | 156 |
| *Peltis grossa* | | | | 5 | 2 | 9 | 3 | 19 |
| *Pentanota meuseli* | | | | 3 | | | | 3 |
| *Phloeocharis subtilissima* | | | | 1 | | 3 | | 4 |
| *Phloeonomus pusillus* | | 2 | 2 | 3 | 4 | 2 | 1 | 14 |
| *Phloeonomus sjobergi* | | 2 | 2 | 25 | 10 | | 1 | 40 |
| *Phloeopora concolor* | | | 1 | 14 | 7 | 3 | 3 | 28 |
| *Phloeopora corticalis* | | 1 | | 32 | 11 | 6 | 7 | 57 |
| *Phloeopora nitidiventris* | | | | 4 | | 1 | | 5 |
| *Phloeopora testacea* | | 4 | 2 | 11 | 1 | 1 | | 19 |
| *Phloeostiba lapponica* | | 1 | 2 | 31 | 2 | | 1 | 37 |
| *Phloeostiba plana* | | | | 5 | 2 | | | 7 |
| *Phloeotribus spinulosus* | | 11 | 11 | 2 | 10 | 10 | 13 | 57 |
| *Phyllodrepa clavigera* | | | | 14 | 22 | 5 | 4 | 45 |
| *Phyllodrepa linearis* | | 2 | 5 | 6 | 4 | 1 | 1 | 19 |
| *Phyllodrepa melanocephala* | | | 1 | | | | 1 | 2 |
| *Pissodes castaneus* | | | | 3 | 6 | 9 | | 18 |
| *Pissodes gyllenhalii* | | 5 | 14 | 8 | 33 | 2 | 1 | 63 |
| *Pissodes harcyniae* | | 2 | 2 | 3 | 4 | | 2 | 13 |
| *Pissodes pini* | | 1 | 1 | 8 | 13 | 2 | 2 | 27 |
| *Pissodes piniphilus* | | | | 3 | 1 | | | 4 |
| *Pityogenes bidentatus* | | 37 | 64 | 130 | 119 | 48 | 31 | 429 |
| *Pityogenes chalcographus* | | 9 | 19 | 1113 | 764 | 86 | 79 | 2070 |
| *Pityogenes quadridens* | | 3 | 2 | 29 | 38 | 4 | 5 | 81 |
| *Pityophagus ferrugineus* | | 5 | 10 | 169 | 119 | 5 | 8 | 316 |
| *Pityophthorus lichtensteinii* | | 68 | 53 | 7 | 10 | 2 | 1 | 141 |
| *Pityophthorus micrographus* | | 4 | 1 | 7 | 7 | | 1 | 20 |
| *Pityophthorus morosovi* | | | | | | | 1 | 1 |
| *Pityophthorus tragardhi* | | | 1 | | | | | 1 |
| *Placusa atrata* | | | 1 | 14 | 4 | | | 19 |
| *Placusa complanata* | | | | 4 | 1 | | | 5 |
| *Placusa depressa* | | | | 14 | 2 | | | 16 |
| *Placusa incompleta* | | | | 2 | | 1 | 1 | 4 |
| *Placusa tachyporoides* | | | | 2 | 2 | | 1 | 5 |
| *Platycerus caprea* | | 45 | 61 | 11 | 33 | 14 | 33 | 197 |
| *Platycis minuta* | | | 1 | | | 1 | 3 | 5 |
| *Platysoma angustatum* | | 1 | | 4 | 6 | | | 11 |
| *Platysoma deplanatum* | | | | | 1 | | | 1 |
| *Platysoma lineare* | | | 1 | 1 | | | | 2 |
| *Platystomos albinus* | | | | 8 | | | 1 | 9 |
| *Plegaderus vulneratus* | | 1 | | 4 | | 2 | 1 | 8 |
| *Pogonocherus decoratus* | | | | 1 | 1 | | 1 | 3 |
| *Pogonocherus fasciculatus* | | 29 | 14 | 25 | 27 | 3 | 2 | 100 |
| *Polygraphus poligraphus* | | | 5 | 400 | 9 | 24 | | 438 |
| *Polygraphus punctifrons* | | 9 | 5 | 1 | | | | 15 |

| Species | | | Year | | | | | | Total |
|---|---|---|---|---|---|---|---|---|---|
| | | | 2000 | | 2002 | | 2011 | | |
| | | | Fire | No fire | Fire | No fire | Fire | No fire | |
| *Polygraphus subopacus* | | | 4 | 22 | 41 | 3 | 3 | 9 | 82 |
| *Pseudocistela ceramboides* | | | | 1 | | | | | 1 |
| *Pteryngium crenatum* | | | 2 | | | | | | 2 |
| *Pteryx suturalis* | | | 2 | 2 | 3 | 1 | 3 | 3 | 14 |
| *Ptilinus fuscus* | | | | | 3 | | | | 3 |
| *Ptiliolum caledonicum* | | | | | 1 | | | | 1 |
| *Ptinella johnsoni* | | | | | 1 | | 1 | | 2 |
| *Ptinella limbata* | | | | | 2 | 5 | 2 | 5 | 14 |
| *Ptinus sexpunctatus* | NT | | | | | 3 | | | 3 |
| *Pyropterus nigroruber* | | | 3 | | 1 | | 2 | 5 | 11 |
| *Pytho abieticola* | VU | | | 1 | 1 | | | | 2 |
| *Pytho depressus* | | | | 2 | 14 | 4 | 2 | | 22 |
| *Quedius plagiatus* | | | 34 | 29 | 15 | 30 | 6 | 5 | 119 |
| *Quedius xanthopus* | | | 63 | 112 | 64 | 123 | 24 | 32 | 418 |
| *Rabocerus foveolatus* | | | 9 | 9 | 8 | 2 | | | 28 |
| *Rabocerus gabrieli* | | | | | | | 1 | | 1 |
| *Rhagium inquisitor* | | | 3 | 3 | 59 | 40 | | 3 | 108 |
| *Rhagium mordax* | | | 10 | 14 | 141 | 111 | 3 | 2 | 281 |
| *Rhizophagus cribratus* | | | 4 | 11 | 6 | | | 1 | 22 |
| *Rhizophagus depressus* | | | | 4 | 1 | | 1 | | 6 |
| *Rhizophagus fenestralis* | | | 8 | 32 | 38 | 6 | 3 | 3 | 90 |
| *Rhizophagus ferrugineus* | | | 92 | 114 | 933 | 208 | 19 | 14 | 1380 |
| *Rhizophagus grandis* | | | 1 | | | | | | 1 |
| *Rhizophagus nitidulus* | | | 10 | 10 | 1 | 2 | | 4 | 27 |
| *Rhyncolus ater* | | | | 1 | | | | | 1 |
| *Rhyncolus sculpturatus* | | | | 2 | 1 | 5 | 5 | 3 | 16 |
| *Salpingus planirostris* | | | 1 | | | | | | 1 |
| *Salpingus ruficollis* | | | 12 | 13 | 3 | | 4 | 1 | 33 |
| *Saperda carcharias* | | | | | | 1 | 1 | | 2 |
| *Scaphidium quadrimaculatum* | | | | | 1 | 1 | | 5 | 7 |
| *Scaphisoma assimile* | | | | | | 1 | 1 | 1 | 3 |
| *Scaphisoma boleti* | | | | 1 | | 1 | | | 2 |
| *Scaphisoma boreale* | | | 20 | 12 | 7 | 6 | 1 | 4 | 50 |
| *Scaphisoma inopinatum* | | | 1 | | 7 | 7 | 55 | 27 | 97 |
| *Scaphisoma subalpinum* | | | 6 | 7 | 9 | 8 | 4 | 2 | 36 |
| *Schizotus pectinicornis* | | | | 3 | 20 | 5 | 3 | 4 | 35 |
| *Scolytus ratzeburgii* | | | | | 3 | | | | 3 |
| *Scydmoraphes minutus* | | | | | 1 | | 1 | | 2 |
| *Silvanoprus fagi* | | | 25 | 28 | 114 | 35 | 10 | 10 | 222 |
| *Sphaeriestes bimaculatus* | | | 1 | 1 | 1 | 2 | | | 5 |
| *Sphaeriestes stockmanni* | | Pyr. | 1 | | 333 | 9 | | | 343 |
| *Sphindus dubius* | | | 4 | 2 | 8 | 14 | 29 | 18 | 75 |
| *Stagetus borealis* | | | 4 | | 23 | 36 | 101 | 30 | 194 |
| *Stenotrachelus aeneus* | | Pyr. | | | 8 | 1 | | | 9 |
| *Stephanopachys linearis* | NT | Pyr. | | | 16 | | 4 | | 20 |
| *Stephanopachys substriatus* | NT | Pyr. | 1 | | 7 | 1 | 2 | | 11 |

| Species | | Year | | | | | | Total |
|---|---|---|---|---|---|---|---|---|
| | | 2000 | | 2002 | | 2011 | | |
| | | Fire | No fire | Fire | No fire | Fire | No fire | |
| *Stephostethus pandellei* | | | | | | 2 | | 2 |
| *Sulcacis nitidus* | | | | 6 | 4 | 7 | 6 | 23 |
| *Synchita humeralis* | | | 3 | 6 | 3 | | | 12 |
| *Tachyta nana* | | | | 5 | 5 | 2 | | 12 |
| *Tetratoma ancora* | | | 1 | | | 1 | | 2 |
| *Tetropium castaneum* | | | | 17 | 5 | | | 22 |
| *Thanasimus femoralis* | | | | 8 | 5 | 2 | | 15 |
| *Thanasimus formicarius* | | 2 | | 34 | 18 | 1 | 2 | 57 |
| *Thiasophila wockii* | | | | 1 | | 2 | 2 | 5 |
| *Tomicus minor* | | 1 | 1 | 4 | | 3 | 1 | 10 |
| *Tomicus piniperda* | | 3 | | 2 | 1 | 2 | 1 | 9 |
| *Tomoxia bucephala* | | | | 9 | 4 | 23 | 16 | 52 |
| *Trichius fasciatus* | | 9 | 5 | 149 | 89 | 104 | 39 | 395 |
| *Triplax aenea* | | 6 | 3 | | 1 | | 2 | 12 |
| *Triplax rufipes* | | 4 | | | 3 | 4 | 8 | 19 |
| *Triplax russica* | | 157 | 127 | 36 | 65 | 74 | 64 | 523 |
| *Triplax scutellaris* | | 8 | 4 | 1 | 3 | | 1 | 17 |
| *Tritoma bipustulata* | | | | | | 3 | 3 | 6 |
| *Trypodendron laeve* | | | 10 | 23 | 2 | | 1 | 36 |
| *Trypodendron lineatum* | | 30 | 51 | 321 | 17 | 3 | 17 | 439 |
| *Trypodendron signatum* | | 55 | 50 | 18 | 1 | 3 | | 127 |
| *Trypophloeus asperatus* | NT | | | 2 | | | | 2 |
| *Trypophloeus bispinulus* | | | | | | | 1 | 1 |
| *Tyrus mucronatus* | | | | 4 | 3 | 14 | 6 | 27 |
| *Upis ceramboides* | NT | | | | 2 | | | 2 |
| *Xyleborus dispar* | | 6 | 5 | | | 1 | | 12 |
| *Xylechinus pilosus* | | 59 | 70 | | 21 | 12 | 21 | 183 |
| *Xyletinus fibyensis* | | | | | | 1 | 1 | 2 |
| *Xyletinus pectinatus* | NT | | | | | | 1 | 1 |
| *Xylita laevigata* | | 51 | 59 | 226 | 112 | 50 | 42 | 540 |
| *Xylita livida* | | | 2 | | 1 | | 3 | 6 |
| *Zilora ferruginea* | | | | | | 1 | | 1 |
| Grand total | | 5029 | 5075 | 16954 | 11454 | 9205 | 6168 | 53885 |
| Species number | | 208 | 212 | 309 | 277 | 255 | 240 | 393 |

# APPENDIX 2. List of ground beetle species included in this thesis

NT = Near threatened; Pyr. = pyrophilous species (according to Wikars 1997)

| Species | Year 2002 | | Total |
|---|---|---|---|
| | Fire | No fire | |
| *Agonum fuliginosum* | 3 | 9 | 12 |
| *Agonum sexpunctatum* | 18 | 1 | 19 |
| *Amara brunnea* | 3 | 3 | 6 |
| *Amara communis* | 7 | 1 | 8 |
| *Amara famelica* | 1 | | 1 |
| *Amara gebleri* | | 1 | 1 |
| *Amara lunicollis* | 22 | 20 | 42 |
| *Amara nigricornis* | 42 | 5 | 47 |
| *Amara ovata* | 1 | | 1 |
| *Amara plebeja* | | 1 | 1 |
| *Amara praetermissa* | 43 | 1 | 44 |
| *Amara quenseli* | 13 | | 13 |
| *Bembidion bruxellense* | 1 | | 1 |
| *Bembidion gilvipes* | 1 | | 1 |
| *Bembidion grapii* | 43 | | 43 |
| *Bembidion lampros* | 154 | 2 | 156 |
| *Bembidion mannerheimii* | 1 | | 1 |
| *Bembidion quadrimaculatum* | 2 | | 2 |
| *Bradycellus caucasicus* | 4 | 1 | 5 |
| *Calathus melanocephalus* | | 1 | 1 |
| *Calathus micropterus* | 189 | 383 | 572 |
| *Carabus cancellatus* | 2 | | 2 |
| *Carabus glabratus* | 11 | 51 | 62 |
| *Carabus violaceus* | | 2 | 2 |
| *Cicindela campestris* | 21 | | 21 |
| *Cicindela sylvatica* | 26 | | 26 |
| *Clivina fossor* | 9 | | 9 |
| *Cychrus caraboides* | 2 | 27 | 29 |
| *Cymindis macularis* | 1 | | 1 |
| *Cymindis vaporariorum* | 8 | | 8 |
| *Harpalus affinis* | 3 | | 3 |
| *Harpalus latus* | 2 | | 2 |
| *Harpalus quadripunctatus* | 76 | 10 | 86 |
| *Harpalus solitaris* | 18 | 1 | 19 |
| *Harpalus tardus* | 1 | | 1 |
| *Leistus terminatus* | 1 | 1 | 2 |
| *Microlestes minutulus* | 2 | | 2 |
| *Miscodera arctica* | 42 | 1 | 43 |
| *Notiophilus aquaticus* | 20 | 3 | 23 |
| *Notiophilus biguttatus* | 122 | 49 | 171 |
| *Notiophilus germinyi* | 44 | 4 | 48 |
| *Notiophilus palustris* | 17 | 15 | 32 |
| *Notiophilus reitteri* | | 1 | 1 |
| *Patrobus assimilis* | | 5 | 5 |

| Species | | | Year 2002 | | Total |
|---|---|---|---|---|---|
| | | | Fire | No fire | |
| *Patrobus atrorufus* | | | 1 | | 1 |
| *Platynus mannerheimii* | | | | 2 | 2 |
| *Pterostichus adstrictus* | | | 3319 | 158 | 3477 |
| *Pterostichus crenatus* | | | 3 | | 3 |
| *Pterostichus diligens* | | | 5 | 2 | 7 |
| *Pterostichus melanarius* | | | | 2 | 2 |
| *Pterostichus minor* | | | 1 | | 1 |
| *Pterostichus nigrita* | | | 2 | 3 | 5 |
| *Pterostichus oblongopunctatus* | | | 156 | 392 | 548 |
| *Pterostichus quadrifoveolatus* | NT | Pyr. | 1 | | 1 |
| *Pterostichus rhaeticus* | | | 2 | 8 | 10 |
| *Pterostichus strenuus* | | | 16 | 17 | 33 |
| *Pterostichus versicolor* | | | 42 | 1 | 43 |
| *Sericoda quadripunctata* | | Pyr. | 54 | | 54 |
| *Synuchus vivalis* | | | | 1 | 1 |
| *Trechus rivularis* | | | | 1 | 1 |
| *Trechus secalis* | | | 1 | | 1 |
| *Trichocellus cognatus* | | | 3 | | 3 |
| *Trichocellus placidus* | | | 1 | 1 | 2 |
| Grand Total | | | 4583 | 1187 | 5770 |
| Species number | | | 53 | 38 | 63 |

## APPENDIX 3. List of flat bug species included in this thesis

Although burning was not yet implemented in 2000, the numbers of individuals have nevertheless been divided in columns according to upcoming fire-treatments. NT = Near Threatened; VU = Vulnerable; Pyr.= pyrophilous species (according to Wikars 1997).

| Species | | | Year | | | | | | | | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | 2000 | | 2001 | | 2002 | | 2003 | | |
| | | | Fire | No fire | Fire | No fire | Fire | No fire | Fire | No fire | |
| *A. angularis* | VU | Pyr. | | | 30 | | | | 1 | | 31 |
| *A. betulae* | | | 8 | 4 | | 23 | 96 | 52 | 60 | 107 | 350 |
| *A. betulinus* | | | 1 | 3 | | 3 | 7 | 5 | 26 | 29 | 74 |
| *A. brevicollis* | | | | | | | 4 | 4 | 3 | | 11 |
| *A. cinnamomeus* | | | | | | | 4 | 2 | 2 | 3 | 11 |
| *A. corticalis* | | | | | | | 18 | 15 | 7 | 10 | 50 |
| *A. crenaticollis* | | Pyr. | | | 5 | 17 | 168 | 6 | 32 | | 228 |
| *A. depressus* | | | 1 | 1 | | 3 | 3 | 1 | | 3 | 12 |
| *A. laeviusculus* | NT | Pyr. | | | 19 | | 20 | | 4 | | 43 |
| *A. lugubris* | | Pyr. | | | 28 | | 5 | | 5 | | 38 |
| *A. obtectus* | | | 43 | 31 | | 12 | 126 | 50 | 67 | 41 | 370 |
| *A. signaticornis* | | Pyr. | | | | | 6 | | | | 6 |
| Grand Total | | | 53 | 39 | 82 | 58 | 457 | 135 | 207 | 193 | 1224 |
| Species number | | | 4 | 4 | 4 | 5 | 11 | 8 | 10 | 6 | 12 |