

**The Conservation of Saproxylic
Beetles in Boreal Forest: Importance
of Forest Management and Dead
Wood Characteristics**

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Abstract

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Forest management has altered the age structure, tree species composition and dead wood availability of Swedish boreal forests. As a consequence, many saproxylic (wood living) insect species have decreased in abundance and many species are threatened. New conservation-oriented forestry uses management measures to favour saproxylic species in managed forests. In my thesis, I evaluated the importance of these measures for saproxylic beetles and possible improvements by using a large-scale field experiment at ten sites in northern Sweden. The substrate types used in the experiment included burned and shaded logs, logs inoculated with two species of wood-decaying fungi, untreated control logs, created snags and the tops of the snags. The experiment was performed in three stand types: clear-cuts, mature managed stands and old-growth stands. Additionally, I performed attraction experiments to examine the attraction of saproxylic beetles to sporocarps and mycelia-infected wood of wood-decaying fungi in landscapes with different proportions of old spruce forest.

Saproxylic beetles were affected by both forest management and dead wood characteristics. Snags differed from lying untreated logs and tops and supported different assemblages of saproxylic beetles and significantly higher numbers of several bark beetle and predator species. Tops attracted different assemblages from both snags and untreated logs. Burned logs supported a lower abundance of saproxylic beetles, particularly fire-favoured species and cambium consumers (especially *Dryocoetes autographus*, *Hylurgops palliatus*, *Hylurgops glabratus* and *Hylastes cunicularius*) and different assemblages of fire-favoured beetles, cambium consumers and predators from the untreated logs, probably because burning makes the cambium less suitable as food for bark beetles. However, some species were attracted to the burned logs. Log exposure proved to be important, especially on clear-cuts where shaded logs supported different assemblages of saproxylic beetles, particularly predators, from untreated logs. Shaded logs on clear-cuts also hosted different saproxylic beetle assemblages from untreated logs in mature managed and old-growth stands, suggesting that shaded logs on clear-cuts do not provide suitable substrate for all shade-demanding species. Sporocarps and mycelia-infected wood attracted some beetle species; *Lordithon lunulatus* was attracted to *Fomitopsis pinicola* sporocarps and *D. autographus* to *Fomitopsis rosea* mycelium-infected wood.

Forest management affected the saproxylic beetle fauna and landscapes with lower proportions of old spruce forest supported depauperate saproxylic beetle assemblages compared with landscapes with higher proportions of old spruce forest. Clear-cuts supported different assemblages of saproxylic beetles, and all functional groups, compared with mature managed and old-growth stands. The assemblages of saproxylic beetles and predators also differed between old-growth and managed stands.

Properties of the substrate are important for saproxylic insects and many species have specific substrate demands. To conserve functionally intact beetle assemblages in an area with intense forestry, both old-growth forest reserves and measures in the managed forest, such as the creation of a variety of dead wood substrates, is needed.

Keywords: dead wood, saproxylic beetles, conservation, Sweden, boreal forest, substrate characteristics, forest management, functional groups.

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Appendix

Papers I-VI

My thesis is based on the following papers, which I refer to by roman numerals.

- I. Hjältén, J., Johansson, T., Alinvi, O., Danell, K., Ball, J. P., Pettersson, R. B., Gibb, H. and Hilszczański, J. The importance of substrate type, shading and scorching for the attractiveness of dead wood to saproxylic beetles. (Accepted for publication in *Basic and Applied Ecology*).
- II. Johansson, T., Gibb, H., Hilszczański, J., Pettersson, R. B., Hjältén, J., Atlegrim, O., Ball, J. P., and Danell, K. 2006. Conservation-oriented manipulations of coarse woody debris affect its value as habitat for spruce-infesting bark and ambrosia beetles (Coleoptera: Scolytinae) in northern Sweden. *Canadian Journal of Forest Research* **36**: 174-185.
- III. Johansson, T., Gibb, H., Hjältén, J., Hilszczański, J., Alinvi, O., Ball, J. P., and Danell, K. The effects of substrate manipulations and forest management on predators of saproxylic beetles. (Submitted manuscript).
- IV. Johansson, T., Hjältén, J., Gibb, H., Hilszczański, J., Stenlid, J., Ball, J. P., Alinvi, O., and Danell, K. 2006. Variable response of different functional groups of saproxylic beetles to substrate manipulation and forest management: implications for conservation strategies. (Submitted manuscript).
- V. Johansson, T., Olsson, J., Hjältén, J., Jonsson, B.-G., and Ericson, L. Beetle attraction to sporocarps and wood infected with mycelia of decay fungi in old-growth spruce forests of northern Sweden. (Submitted manuscript).
- VI. Olsson, J., Johansson, T., Ericson, L., and Hjältén, J. The amount of old spruce forest in the landscape affect the richness and composition of beetle assemblages attracted to wood-decaying fungi. (Manuscript).

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Introduction

The importance of dead wood in forest ecosystems has been emphasised worldwide (Harmon *et al.* 1986, Hale, Pastor & Rusterholz 1999, McGee, Leopold & Nyland 1999, Siitonen 2001). In natural forest ecosystems, dead wood is continuously created by a combination of small scale gap dynamics and reoccurring catastrophic events, such as fires and storms, on a larger scale (Engelmark 1999, Siitonen 2001). This means that complexity of dead wood substrates builds up over time (Hansen *et al.* 1991).

Prior to the introduction of modern forestry and fire protection programmes in the nineteenth century, fire was one of the major processes that shaped the Fennoscandian boreal forest landscape and determined the structure and composition of forest vegetation (Zackrisson 1977, Engelmark 1999). Fire creates substrate for a wide range of organisms, including several insect and wood fungi species (Wikars 2001, Saint-Germain, Drapeau & Hébert 2004). Thus, many species in the boreal forest are adapted to and even dependent on fire for their long term survival (Wikars 1997). Pyrophilous insects often have adaptations to find suitable burned areas, for example a good dispersal capacity and special organs to orientate towards a fire (Hart 1998). Fire is also important for a broader range of organisms because it both creates dead wood in open areas and removes competition (McCullough, Werner & Neumann 1998). Furthermore, a burned area contains large volumes of dying and weakened trees that support saproxylic organisms with substrate over a long period (Ås 1993, Wikars 1997).

Thus, dead wood is one of the most important substrates for maintaining biodiversity in forest ecosystems (Esseen *et al.* 1997, Siitonen 2001), and a substrate that is strongly negatively impacted by human activities (Grove 2002). Forest management generally leads to a decrease in dead wood volume and quality (Fridman & Walheim 2000, Gibb *et al.* 2005). In Western Europe, this process has reached its greatest extent, resulting in the loss of almost all natural forests from the landscape (Grove 2002). This has influenced the abundance and distribution of many dead wood dwelling (saproxylic) organisms.

Ecology of saproxylic insects

Because dead wood provides a wide range of possible habitats, the insects using the wood comprise a diverse fauna in terms of their nutritional ecology (Esseen *et al.* 1997). Cambium consumers, dominated by bark beetles, include both primary and secondary species. Primary cambium consumers utilize the cambium on recently dead, dying and sometimes living trees; secondary cambium consumers only use dead trees (Knizek & Beaver 2004, Sauvard 2004); fungivorous species bore into the sapwood and grow fungi that provides food for the larvae, (Borden 1988, Paine, Raffa & Harrington 1997) or they live in fruit bodies or mycelia of wood decaying fungi (Jonsell & Nordlander 1995, Økland 1995, Jonsell, Nordlander & Jonsson 1999, Komonen 2001). All these consumers constitute food for predators, such as beetles from the families Cleridae, Rhizophagidae and

Trogossitidae (Kenis, Wermelinger & Grégoire 2004), wood peckers (Murphy & Lehnhausen 1998, Fayt 1999) and parasitic wasps (Kenis, Wermelinger & Grégoire 2004, Hilszczański *et al.* 2005). In later stages of decay, carpenter ants and several other insect species use the wood for nests and shelter (Ehnström & Waldén 1986, Esseen *et al.* 1997).

Dead wood provides habitat for both insects and fungi and interactions are thus important: insects act as vectors for fungi and fungi serve as food for the insects (Gilbertson 1984). Many bark beetles transmit blue stain fungi (Paine, Raffa & Harrington 1997) and it has been suggested that they also act as vectors for wood decay fungi, e.g. *Fomitopsis pinicola* (Harrington, Furniss & Shaw 1981, Pettey & Shaw 1986) and ascomycete fungi, e.g. *Daldinia loculata* (Johannesson 2000, Wikars 2001, Guidot *et al.* 2003). The type of rot occurring in the wood also influences the composition of the insect assemblages that colonize the wood (Araya 1993b, 1993a). Fruiting bodies of wood decay fungi are important microhabitats and many fungi species host unique insect faunas (Økland 1995, Komonen 2001, Komonen *et al.* 2004).

Bark beetles (Curculionidae: Scolytinae) is the most numerous taxon in the early successional stages of dead wood. Although most bark beetle species use the cambium on dead trees, some species can infest and kill living trees. These species can become severe pests and in some areas trees worth millions of SEK are lost every year due to pest bark beetle outbreaks. For example the spruce bark beetle, *Ips typographus*, is a major pest on Norway spruce in large parts of Europe (Wermelinger 2004) and the mountain pine beetle, *Dendroctonus ponderosae*, annually kills large areas of forest in North America each year (Raffa 1988). Pest species and their associates have been the target of much research during the 20th century, however, far less is known about bark beetles not considered as pest species. It has been hypothesised that high abundances of non-pest bark beetles could support populations of predatory beetles that also control pest populations (Martikainen *et al.* 1999). Natural enemies of bark beetles can significantly decrease offspring production of pest bark beetles (Schroeder & Weslien 1994), however the relative importance of natural enemies, dead wood availability and non pest bark beetles in the control of pest bark beetle populations needs further examination.

Very few saproxylic species can be regarded as potential pests and many other species are important from a conservation perspective. In Fennoscandia, many insects associated with dead wood are decreasing in number (Berg *et al.* 1994) and 471 beetle species associated with forest habitats are included on the Swedish red list (Gärdenfors 2005). Some of these species were common before large scale forest management while others, e.g. several predator and parasitoid species, naturally occur in small populations. Species that are initially rare in the landscape rapidly become increasingly rare with fragmentation (Golden & Christ 1999, Komonen *et al.* 2000, Kruess & Tschardt 2000). The ecology of these species is, to a large degree, unknown, because of the large sampling effort that is demanded to obtain sufficiently large samples.

Forest management and biodiversity

During the last few decades, forestry in Fennoscandia have been intensive, including large scale logging, site preparation, thinning and active prevention of natural disturbances. Previously, forests were used for small scale logging and cattle grazing and large areas were covered by old-growth forests (Linder & Östlund 1992, Linder & Östlund 1998). Forests in the northern parts of Fennoscandia were largely unaffected by human activities on the landscape scale before and during the nineteenth century (Östlund, Zackrisson & Axelsson 1997). As a result of the intensive forestry, the major parts of the Fennoscandian boreal forest have a simplified tree species composition, reduced stand age and are dominated by even-aged monocultures (Uuttera, Maltamo & Kuusela 1996, Östlund, Zackrisson & Axelsson 1997, Uotila *et al.* 2001, Uotila *et al.* 2002). The change and intensification in usage has had severe effects on flora and fauna because the area of old-growth forest has decreased dramatically and the remaining 5 % are highly fragmented and mainly concentrated in the mountain region (Fridman 1999). Forestry has negatively affected the frequency of natural disturbances such as fire and the occurrence of habitat elements important to many species e.g. dead wood, especially coarse wood and wood in later decay stages, old trees, deciduous trees and swamp forests (Linder & Östlund 1998, Rouvinen, Kuuluvainen & Karjalainen 2002). The total amount of dead wood has decreased from between 30 and 90 m³ per hectare in old growth forests to about 6 m³ per hectare in the managed forest (Fridman & Walheim 2000). This has resulted in a decreased distribution of many wood-decay fungi and today 561 fungi species associated with forest habitats are red-listed in Sweden (Gärdenfors 2005). Many of these red-listed fungi support unique insect faunas and the decrease in the fungi population is thus likely to result in a decrease in populations of several insect species. For example, *Amylosticta lapponica* and *Fomitopsis rosea* are both old-growth forest species that host unique insect assemblages (Komonen 2001, Komonen, Siitonen & Mutanen 2001). These assemblages are also negatively affected by forest fragmentation, with species in the top of the food chain being most affected (Komonen *et al.* 2000).

Until the 1980's, forest management in Scandinavia was mainly concentrated on high timber production and the avoidance of pest outbreaks (Lämås & Fries 1995). Hence, large areas were subjected to ditching and treatment with herbicides and dead wood and deciduous trees were removed from the forest, resulting in a paucity of these substrates. However, the new Swedish forestry act (Anonymous 1994) places environmental protection on level with production in Swedish forestry and an important environmental goal is to conserve all native species in Sweden (Anonymous 2006). To achieve these goals, and to fulfil the demands from the forest certification system (FSC) a number of conservation measures are taken in the managed forest, e.g. creating snags, burning clear-cuts and leaving retention trees (Anonymous 2000, Larsson & Danell 2001). Attempts have been made to evaluate these measures (Wikars 2002, Jonsell, Nittérus & Stighäll 2004, Hyvärinen *et al.* 2005) but there is still a lack of knowledge about how much and what kind of dead wood should be created to support functionally intact beetle assemblages whilst keeping the risk of pest outbreaks low. Furthermore, forest

companies require guidelines if they are to reach their environmental goals in an economically efficient way.

The large, controlled, long-term experiment, described in this thesis provides a powerful test of the value of a range of potential methods for improving the quality of dead wood substrates for saproxylic species. There is lack of knowledge about the many biotic interactions that occur in dead wood ecosystems; to fully understand the effects of conservation-oriented measures in forest management, we need to develop deeper understanding of these interactions. Previous research on saproxylic insects has focused mainly on insect groups containing many pest species, such as Curculionidae and Cerambycidae and their associated fauna (Annala *et al.* 1972, Lekander *et al.* 1977, Weslien 1992, Weslien & Schroeder 1999, Öunap 2001, Kenis, Wermelinger & Grégoire 2004). In recent years, studies of beetle communities have become more common (e.g. Martikainen *et al.* 2000, Gibb *et al.* 2006a), but groups such as Staphylinidae and Nitidulidae, which include many predatory and fungivorous beetles are still underrepresented and knowledge about substrate demands for many of these species is scarce. Furthermore, conservation oriented measures often conflict with forest protection (i.e. protection of the trees from damage of pest insects) and the forestry act (Anonymous 1994) only permits 5 m³ per hectare and year of fresh conifer wood to be left in the forest. In a landscape dominated by managed forest with low amounts of dead wood, it is possible that the risk of pest outbreaks is lower than previously thought, especially in the northern parts of Fennoscandia where the climate is cooler.

Objectives

In this thesis, I examine the value of the conservation measures taken today, i.e. mainly the creation of snags on clear-cuts, and possible improvements of these measures. The rationale of the tested improvements is as follows. Prescribed burning of clear-cuts and forest stands to favour species depending on fire is performed in Swedish forestry today. However, it has been proposed that smaller prescribed burnings (0.1-1 ha), with the advantage of being cheaper than the burning of larger areas, could possibly favour some fire favoured insects and may serve as an alternative or complement to traditional burnings (Andersson 2001). To test this idea, we included burned logs in the experiment. Furthermore, since shading and the presence of wood fungi are known to be important in determining which beetles colonise the wood (Jonsell, Schroeder & Weslien 2005, Lindhe, Lindelöw & Åsenblad 2005), fungi-inoculated and shaded logs were also included in the experiment. Snags were included because they are the most common conservation measure performed in forestry today. I examined the remaining top of the snags to estimate their value for conservation compared with snags. The age and history of the forest stands are also important factors (Martikainen *et al.* 2000, Similä *et al.* 2002, Similä, Kouki & Martikainen 2003) that were included in the experiment by comparing the beetle assemblages on dead wood in clear-cuts,

mature managed and old-growth stands. The different stand types have previously been shown to support different insect assemblages (Kaila, Martikainen & Punttila 1997, Martikainen *et al.* 1999, Similä *et al.* 2002), but little is known about how stand type interacts with dead wood quality to influence the composition of the saproxylic community. This design gives the opportunity to examine and compare the effects of different kinds of created dead wood in stand types that are abundant in Swedish forests and to examine the interactions between these factors. My thesis mainly concerns early successional beetles on spruce and consequently bark beetles and their associated fauna dominate in the studies. From a conservation point of view, early successional assemblages, including many non threatened species, e.g. bark beetles, are important because they may affect the later succession. Some of these species can also act as keystone species, causing disturbances that drive forest succession (Martikainen *et al.* 1999, Safranyik *et al.* 2004).

The odours emitted from wood and wood decay fungi are important in host location by many beetle species. Knowledge about host selection, host specificity and the assemblage composition on different species of wood fungi is of major importance for the conservation of saproxylic beetle assemblages because of the many interactions that occur between dead wood, fungi and insects (Gilbertson 1984, Blackwell & Jones 1997). I tested if beetles could distinguish between fruit bodies and mycelia of different fungi species as well as between fruiting bodies and mycelia of the same fungi species. Furthermore, because forest fragmentation has negative effects on many species (Abildsnes & Tömmersås 2000, Komonen *et al.* 2000, Rukke 2000, Kouki *et al.* 2001), I tested if the composition of the landscape i.e., the proportion of old spruce forest, affects the beetle assemblage that is attracted to wood-decaying fungi.

Specifically, I addressed the following questions:

1. How does the composition of assemblages of saproxylic beetles differ between different forest types (clear-cut, mature managed and old-growth)? (I, II, III, IV)
2. How are assemblages of saproxylic beetles affected by substrate manipulations? (I, II, III, IV)
3. How is attraction and production of saproxylic beetles affected by the presence of wood fungi? (III, V, VI)
4. How could forest management practices be improved to favour beetle species that are negatively affected by forestry? (I, II, III, IV)

Material and methods

Study area

All study sites were situated in the middle boreal zone (Ahti, Hämet-Ahti & Jalas 1968) in the provinces of Västerbotten, Ångermanland and Lapland in northern Sweden (Figure 1). The altitude of the sites ranged from 100 to 550 m a.s.l. All study sites were in forests dominated by Norway spruce (*Picea abies*) and the ground cover was of a moist to mesic *Vaccinium myrtillus* L. type, i.e., mosses and *V. myrtillus* dominated the field layer (Ebeling 1978).

In the log manipulation experiment, I included ten groups of stands, each containing one old-growth stand, one mature managed stand and one clear-cut area. The stands were similar in terms of productivity class (G15-G23), number of stems per hectare, volume of living wood per hectare, average stem diameter and average tree height. The old-growth stands were mostly nature reserves and were older and contained more dead wood than the mature managed stands and clear-cut areas (Table 1). In the old-growth stands very few stumps could be found, indicating low historical use. In the mature managed stands, evidence of past selective logging (i.e. cut stumps), for trees of larger diameter could be found but the stands have never been clear-cut (Gibb *et al.* 2005).

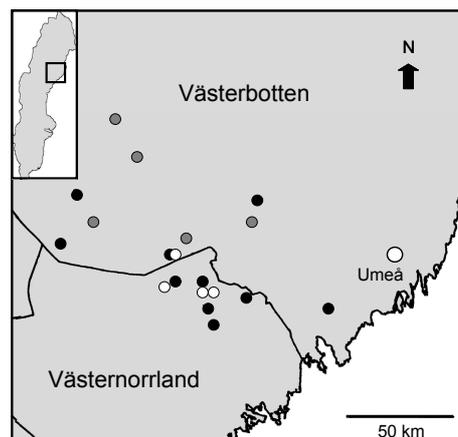


Figure 1. The study area. Black dots = the log manipulation experiment, white dots = the fungi attraction experiment in 2003, grey dots = the fungi attraction experiment in 2004.

The study sites in the fungi attraction experiment in 2003 were all old-growth spruce forests, selected because they contained large amounts of dead wood providing suitable habitats for both wood-decaying fungi, including the species used in the experiment, and saproxylic beetles. In 2004, I used five pairs of sites. The sites within each pair were located relatively close to each other and were chosen to differ in the proportion of old spruce forest (>80 years) in the surrounding landscape i.e. one site in each pair had a significantly higher proportion of old spruce forest than the other (for details see Edman *et al.* 2004).

Table 1. Mean age and CWD content of the stands included in the log manipulation experiment. From Gibb et al. (2005).

Stand type	Mean age	Lying CWD ($\text{m}^3 \text{ha}^{-1}$)	Standing CWD ($\text{m}^3 \text{ha}^{-1}$)
Clear-cut		5.91±1.88	3.79±1.32
Mature managed	108	6.60±1.63	11.40±3.48
Old-growth	151	23.48±6.81	40.73±11.56

Experimental design

The log manipulation experiment (Papers I-IV)

In each of the experimental stands, three blocks (five in Långrumpskogen (Paper I)) containing six spruce logs (4 m long) and a created snag (3 m high) were placed in a randomised block design (Hurlbert 1984). The blocks were placed 25-50 m apart and within each block, there was at least 3 m between the logs. Each block included an untreated log (hereafter referred to as a control), a burned log, an untreated log placed in natural shadow and one in artificial shadow, a log inoculated with the brown rot fungus *Fomitopsis pinicola* (Swartz: Fries) Karst., a log inoculated with the white rot fungus *Resinicium bicolor* (Alb. & Schwein.) Parmasto, a created snag and the remaining top of the snag (Figure 2).

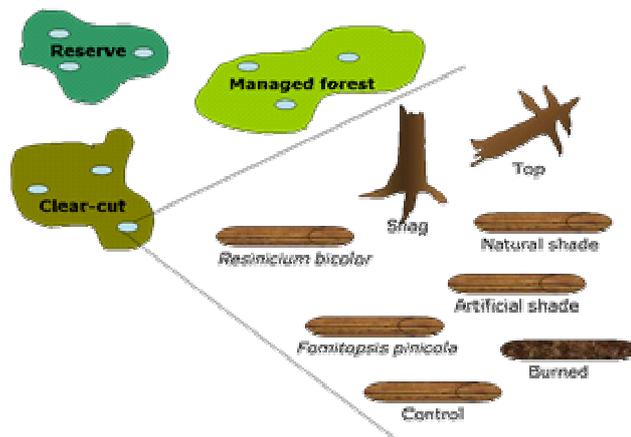


Figure 2. Design of the log manipulation experiment. The same set up was replicated on ten sites.

Burning of the surface of one log in each block was performed with a LPG-burner to simulate the effect of a wild fire. One log on each block was inoculated with fungi by filling twelve 10 mm holes with mycelium grown on spruce sawdust. The effect of the inoculations was confirmed after one year and proved to be successful (Paper IV). To create artificial shade, we stapled polypropylene weed barrier to a wooden frame approximately 30 cm above one log in each block. The naturally shaded log was placed in a suitable shaded place, i.e., a place less exposed to the sun than the control log in each block. The snag was created by cutting a living tree at a height of about 3 m. On the clear-cuts, I used logs created during the felling operation. The logs in Långrumpskogen were put out in early

spring 2001 while logs on the other nine sites were put out during the autumn/winter 2001-2002. This means that the logs in Långrumpskogen have been available for insect colonisation one year more than the logs on the other nine sites and are therefore not directly comparable to them. Because of this, Långrumpskogen was excluded from the analyses in Papers II-IV.

The fungi attraction experiments (Papers V-VI)

The 2003 experiment was set up in a randomized block design in four old-growth spruce dominated forest sites. I used eight substrate types per block and a total of five blocks per site. The substrate types were: control (empty mesh bag), sterilised wood, *Fomitopsis pinicola* sporocarp, *F. pinicola* mycelium-infected wood, *Fomitopsis rosea* sporocarp, *F. rosea* mycelium-infected wood, *Phellinus chrysoloma* sporocarp, and *Phlebia centrifuga* mycelium-infected wood. In 2004 I set up an experiment with five pairs of sites and four substrate types in three blocks per site. The substrates were: control (empty mesh bag), sterilised wood, *F. pinicola* mycelium-infected wood, and *F. rosea* mycelium-infected wood.

The mycelium substrates in both 2003 and 2004 consisted of dikaryotic mycelium grown on 0.8 cm thick discs of Norway spruce (*P. abies*), with a diameter of 7 - 8.5 cm. Similar discs were used as the wood substrate. The sporocarp baits (2003 only) consisted of fresh fruit bodies, with a diameter of 6-8 cm, of the studied species. The sporocarps were sampled one day before they were put out in the forest and kept separated in paper bags at low temperature in a cooling bag during transport.

Insect sampling

I used two types of traps to collect insects on the experimental logs; trunk window traps, which provide a measure of insects attracted to the different treatments (Papers I, II); and trunk eclector traps which give a measure of the production of insects in the logs (Papers II, III, IV). See Paper II for detailed descriptions and pictures of the traps.

In the fungi attraction experiments (Papers V, VI), the beetles were collected in flight intercept traps consisting of a thin transparent piece of plastic (15*25 cm) attached to wooden poles with a diameter of 5 cm, approximately 50 cm above ground. The plastic was bent and attached on both sides next to the top of the pole and another piece of plastic (5*10 cm) was nailed to the top of the pole to prevent insects from entering the trap from above. The different substrates were put into fine mesh bags and attached with a staple inside the plastic window to allow odours out but stop insects from feeding on the bait. I attached an aluminium tray (11 x 15 cm; 5 cm deep) half-filled with 50 % propylene glycol and a trace amount of detergent under the plastic window to collect the insects.

Functional groups

I selected saproxylic species according to the definition by Speight (1989) i.e., species that are dependent on dead wood during some part of their life cycle. The

species were further divided into the nutritional functional groups based on knowledge from the literature (e.g. Saalas 1923, Palm 1948, Koch 1989) and personal observations by R. Pettersson, J. Hilszczański and S. Lundberg. The functional groups included in my analysis were: cambium consumers, detritivores, fungivores, predators, and wood borers (see Paper IV for explanations). I selected species favoured by fire according to Lundberg (1984).

Results and discussion

Effects of substrate characteristics

Snags, logs and tops

The abundance, species richness and assemblage composition of saproxylic beetles, particularly the abundances of many bark beetles and predators differed significantly between snags and logs. Snags attracted significantly higher numbers of the bark beetles *Crypturgus subcribrosus*, *Hylurgops palliatus*, *Polygraphus punctifrons* and *Pityogenes chalcographus* as shown by window traps (Paper II) and had a higher production of *C. subcribrosus* (Paper II) and the predators *Eपुरaea boreella* and *E. angustula* (Paper III) than the logs, shown by catches in eclector traps. In contrast, two bark beetle (Paper II) and three predator species (Paper III) showed the opposite pattern. The consistence between the patterns in window and eclector traps for *C. subcribrosus* and *Polygraphus punctifrons* suggests that the patterns are not only a result of different flying height of the different beetle species, but that these species actually use the logs as a breeding substrate (Paper II). The assemblages of saproxylic beetles attracted to the experimental logs differed when we compared snags, tops and logs (Paper I, see also Gibb *et al.* 2006a). The saproxylic beetles contributing most to the differences in assemblage between snags, logs and tops were *Dryocoetes autographus*, and *E. marseuli*, which preferred logs, *Tetropium fuscum* and *Molorchus minor*, which preferred snags and *Ips typographus* and *Pityogenes chalcographus*, which preferred tops (Paper I).

The explanation for the observed pattern might be that snags differ from lying wood in orientation i.e., snags are vertical and logs horizontal. Because of this snags are more exposed to sun and wind than logs and tops. Additionally, snags are connected by roots to the ground, which probably affects the decay process and makes it different from the decay process of logs. Tops differ from snags in orientation and from both snags and logs because they have intact branches preventing them from direct contact with the ground. The branches probably protect the bark area of the tops so that they dry out more slowly than the branch-free snags. Branch-free logs with ground contact probably stay moist even longer. Furthermore, the logs are covered by snow in winter, in contrast to snags and tops that are more exposed to damage from wood-peckers (pers. obs.). My results are consistent with earlier studies (Jonsell & Weslien 2003, Hedgren & Schroeder

2004, Hilszczański *et al.* 2005, Gibb *et al.* 2006a) showing that snags and lying wood support different insect faunas. Thus, to conserve intact insect assemblages in boreal forest, it is of major importance to provide both standing and lying dead wood. Additionally, my results suggest that lying trees with intact branches attract unique assemblages, highlighting the importance of leaving intact fallen trees for saproxylic beetles.

Burning

Burned logs attracted higher numbers of saproxylic beetle individuals and fire-favoured species and individuals than untreated control logs when I examined beetles caught in window traps (Paper I). However, the eclector trap catches showed the opposite pattern with a lower abundance of species and individuals of fire-favoured species, cambium consumers and total saproxylic beetles (only on clear-cuts) produced on the burned logs (Paper III). Individual bark beetle species showed the same pattern (Paper II).

The reason for the negative effect of burning on several groups and species of beetles is probably that the burning dried out the cambium and made it less suitable as food for cambium consumers (Saint-Germain, Drapeau & Hébert 2004), which consequently reduced food availability for predatory beetles. In addition to Wikars (2002), results from my study show that not only primary bark beetle species but also secondary species e.g. *Dryocoetes autographus* (Paper II) and beetle assemblages (Paper IV) are negatively affected by burned wood, i.e., the burned logs supported depauperate saproxylic beetle assemblages. The attraction of some beetles to burned wood (Paper I) suggests that, even though these species may not breed in the wood, they use the smell of burning as a cue when locating a suitable substrate. Furthermore, ascomycete fungi appear to colonize burned wood better than fresh wood (Johannesson 2000, Wikars 2002), which could favour mycetophagous insects (Wikars 2002). This suggests that we could expect to catch more such beetles in the eclector traps later because several fungivorous species (Lundberg 1984, Wikars 2002), e.g. *Corticaria gibbosa*, *Atomaria bella*, *Epuraea pygmaea* and *Corticaria rubripes*, were attracted to the burned logs, and some (*C. rubripes* and *E. pygmaea*) appeared to emerge more frequently from the burned logs (Paper I). Some wood fungi e.g. *Daldinia loculata*, support a specific fauna of fire dependent insects and it is possible that the wood fungi that will occur on the burned logs in my experiment will also support faunas that are connected to burned forest. However, there are quite few species that demand burned wood or fire scorched trees for their survival (pyrophilous species see Wikars 1997). A burned area provides large amounts of wood with different degrees of burning and sun-exposure. The fire also provides habitat for deciduous trees that support a specific beetle fauna and, because many insects are killed in the fire, competition is reduced on a burned area (McCullough, Werner & Neumann 1998). The effect of very small burnings (0.1-0.5 ha) to limit the cost of fully scaled prescribed burnings has been tested and the results indicate that, although some fire favoured species were found at the burned sites, there were no occurrences of pyrophilous species, suggesting that the species that are dependent on fire for their long term survival require larger burnt areas

(Andersson 2001). Even though some beetles were attracted to the burned logs, my results suggest that burning of single logs is probably not sufficient to provide the beetle fauna with the high diversity of substrates created by a wild fire. To conserve fire favoured species in the boreal forest landscape, more drastic measures, including the burning of clear-cuts and forest stands, are needed.

Shading

Shading of logs, both natural and artificial shade, had the strongest effect on saproxylic beetles on clear-cuts. My results suggest that the level of shading is important for many saproxylic organisms, consistent with e.g. Sverdrup-Thygeson & Ims (2002) and Lindhe, Lindelöw & Åsenblad (2005). The clearest effects were found when species were analysed individually, but nutritional functional groups were also affected, e.g. shading of logs lowered the abundance of wood borers. The assemblage composition of total saproxylic beetles and predators in elector traps differed significantly between shaded logs on clear-cuts and control logs on clear-cuts, and in mature managed and old-growth stands (Paper IV). The shaded logs on the clear-cuts supported an assemblage partly overlapping with control logs in mature stands and partly overlapping with control logs on clear-cuts, suggesting that generalist forest species may be favoured by shading of logs on clear-cuts but that more specialist forest dwelling species need substrate located deeper inside forest stands. Several bark beetle and predator species were affected by shading and the artificially shaded logs attracted significantly more *Trypodendron lineatum* and *Hylurgops palliatus* than the control logs (Paper II). The predator *Ampedus tristis* showed the opposite pattern (Paper III). The naturally shaded logs in this study were mainly placed under trees along the clear-cut edge or under a group of trees out on the clear-cut. Shaded logs on clear-cuts are less exposed to sun than the control logs on clear-cuts but they are still affected by the clear-cut edge in terms of increased wind and less stable microclimate. This is reflected in the saproxylic beetle assemblages that differed both between shaded and control logs on clear-cuts and between shaded logs on clear-cuts and control logs in mature managed and old-growth stands (Paper IV). These results are consistent with Peltonen and Heliövaara (1998) and Peltonen and Heliövaara (1999), suggesting that edge effects (Ries *et al.* 2004) affect the whole assemblage of early successional saproxylic beetles. Thus, shaded logs on clear-cuts can not be considered a substitute for dead wood deeper inside forest stands, but may be used as a complement. To conserve intact beetle assemblages in boreal forest, dead wood with variable degree of shading/exposure is needed.

Fungi inoculations of logs and attraction to wood fungi

There was no difference in total beetle abundance or species richness among the substrates examined in the attraction experiments (Papers V and VI). However, individual species (*Dryocoetes autographus*, *Lordithon lunulatus* and *Hylastes cunicularius*) showed significant attraction to fungi substrates and the control. Similar patterns were also found for species that were not common enough to be analysed individually e.g. *Lordithon speciosus*. *Dryocoetes autographus* was significantly more abundant on *F. rosea* mycelium than on the controls or other fungus substrates. Furthermore, *D. autographus* was more abundant on wood than

on the empty bag control and less abundant on the *P. chrysoloma* sporocarps, *F. pinicola* mycelia and *F. rosea* sporocarps than on the sterilised wood. *Lordithon lunulatus* was mainly attracted to the *F. pinicola* sporocarps compared both with the control and the sterilised wood and seemed to be generally more abundant on the fungus substrates than on the sterilised wood and control. In 2004 (Paper VI) *H. cunicularius* was more abundant in the control traps than in traps baited with *F. pinicola*. This pattern is hard to explain: maybe this species avoids *F. pinicola*.

The common bark beetle *D. autographus* was attracted to mycelia of *F. rosea* (Papers V, VI) which is a rare wood decay fungi connected to old-growth forests (Renvall 1995, Larsson 1997). This pattern is noteworthy since *D. autographus* is a rather common bark beetle that attacks recently dead spruce trees or downed logs in shady habitats (Lekander *et al.* 1977, Ehnström & Axelsson 2002) and *Fomitopsis rosea* is a rare fungus, confined to old-growth spruce forests (Renvall 1995, Larsson 1997). It is possible that *D. autographus* uses by-products, e.g. ethanol or monoterpenes, from the decay process as cues to find a supply of suitable substrate and that the *F. rosea* mycelium produces ethanol when the wood discs are decaying. Earlier studies have shown that many early successional saproxylic beetles are attracted to ethanol (Schroeder & Lindelöw 1989, Schroeder 1993, Jonsell, Schroeder & Larsson 2003). Furthermore, *F. rosea* was a common wood decay fungus before large-scale forest management (Renvall 1995, Larsson 1997), so it is possible that *D. autographus* still uses smell from *F. rosea* mycelium as a cue to find suitable substrate.

As adults, the staphylinids *L. lunulatus* and *L. speciosus* are generalist predators on fungivorous insects (Koch 1989, Fäldt *et al.* 1999) and in my experiments (Papers V, VI), they were clearly more attracted to the fungus substrates than to the control or the wood. Among the fungus substrates, *L. lunulatus* showed a strong preference for sporocarps of *F. pinicola*. *L. speciosus* was more attracted to the mycelia of *F. rosea* and *F. pinicola* than to sterilised wood and control in 2004. My results are consistent with earlier studies suggesting that predatory beetles from the families Staphylinidae and Rhizophagidae use the hymenium of polypores as a hunting ground (Hågvar & Økland 1997, Hågvar 1999) and confirm the habitat characteristics suggested earlier for *L. lunulatus*, i.e. the sporocarps of common wood fungi (Koch 1989, Økland & Hågvar 1994). Our data also indicate that *L. lunulatus* can discriminate between the smell from sporocarps and that from mycelia. Earlier studies have shown that *L. lunulatus* are attracted to general fungal odours, i.e. various octanols (Fäldt *et al.* 1999), compounds emitted from mycelia are apparently different. On the other hand, *L. speciosus* also seems to be attracted to mycelia, indicating that this species may use volatiles from the mycelia as a cue to locate sporocarps.

Earlier studies have shown that substrate preferences differ between insect species living in sporocarps of the same fungi species and found that preferences vary depending upon successional stage, sun exposure, height above ground and fruit body size (Fossli & Andersen 1998, Guevara *et al.* 2000, Jonsell, Nordlander & Ehnström 2001). My results suggest that the presence of fungi in a log is important already prior to the development of fruiting bodies (Papers V, VI).

These results are to some degree in contrast with the results from Paper IV, where no effects of the fungi inoculation treatments could be detected. However, Paper IV only considered eclector traps and it is possible that some beetle species were more attracted to the fungi inoculated logs than to the control logs but that they have not yet had time to fulfil their life cycle, emerge and be trapped in the eclector traps. I did not see any effect of the fungi inoculations of the experimental logs on the species richness and abundance of the functional groups or individual species (Papers III, IV). Clearer patterns would may have been obtained if only logs with successful inoculations had been included in the study, this was however not possible because only 10 logs from each fungi species were sampled for mycelia of the inoculated species. However, fungi may play a more important role at later decay stages. Because many early successional beetles bring their own fungi, the effect of the fungi inoculation may be limited, especially because the inoculated fungi probably need more time to colonise the whole log and to develop different types of rot. Furthermore, there will be a succession in the fungal flora (Renvall 1995) that will probably be affected by the inoculations and make the inoculated logs different from the control logs in later decay stages. In later decay stages the occurrence of fungal mycelia is shown to be important for determining the species composition of beetles on snags (Jonsell, Schroeder & Weslien 2005), and the same pattern could be expected for the experimental logs in my study.

I expected more pronounced effects of fungi species on the beetle assemblage because several beetle species are known to be attracted to sporocarps of one specific fungus, e.g. *Cis quadridens* and *C. glabratus*, are attracted to *F. pinicola* (Jonsell & Nordlander 1995). In my experiment these fungivorous species were caught in very low numbers (Paper V). One reason for this could be that I used fresh sporocarps and that these species prefer dead or dying sporocarps. Another explanation is that these species may have their main flight period later during the summer and hence were not flying at the time of our study.

In conclusion, fungi inoculation of logs had small effects on the saproxylic beetle fauna in early decay stages of dead wood. However, the smell from sporocarps and mycelia of wood-decaying fungi attracted some specific beetle species, indicating that the occurrence of wood fungi is important in later decay stages.

Effects of forest management

Saproxylic beetles, including all functional groups and several individual species, were affected by forest management (Papers I, II, III, IV). In total, the clear-cuts supported fewer saproxylic beetle species but a higher total abundance (only significant for the control) than the mature managed and old-growth stands. However, higher abundance was mainly the result of high densities of *Pityogenes chalcographus* (Paper IV). Clear-cuts differed from mature managed and old-growth stands both in assemblage composition for all functional groups and in the species richness and abundance of detritivores, fungivores and predators, which were less abundant and species rich in clear-cuts than in the other stand types. In

contrast, wood borers and cambium consumers showed the opposite pattern (Paper IV) while fire favoured species were more abundant on clear-cuts than in mature managed and old-growth stands (Paper IV). This could be expected because many species that are favoured by fire, e.g. *Pityogenes chalcographus*, are early successional species that are good dispersers and have a high ability of finding newly created substrate. They are also favoured by other disturbances, such as storm fellings (Wermelinger, Duelli & Obrist 2002). The patterns for fire favoured species and cambium consumers were confirmed when the most common bark beetles and predators were analysed individually (Paper II, III).

Mature managed and old-growth stands supported higher abundance and different assemblage composition of fungivores compared with clear-cuts (Paper IV), in contrast to Komonen and Kouki (2005). Fungivores could be expected to be more abundant in older forests due to high diversity and availability of substrates, because many fungi species are favoured by a moist and shaded habitat (Rayner & Boddy 1988) and respond negatively to the dry environment of clear-cuts (Bader, Jansson & Jonsson 1995, Lindblad 1998). For species living on these fungi, less substrate is available in intensively managed forest. Fungivores are probably more negatively affected by forestry than e.g. cambium consumers, because their habitats are lost when clear-cuts and young stands are created.

Species at higher trophic levels are thought to be more sensitive to forest management than their prey (Speight 1989, Komonen *et al.* 2000, Hilszczański *et al.* 2005), so my finding that predators are more common in mature managed and old-growth stands, mainly reflected in the higher abundances of *Phloeonomus sjoeborgi* and *Quedius plagiatus* in these stand types (Papers III, IV), is not surprising. Stands with tree cover offer a more stable microclimate than the exposed clear-cuts and the supply of suitable substrate is also more continuous, resulting in richer assemblages of prey species. However, individual predator species responded differently to stand type and *Ampedus tristis* and *Nudobius lentus* were more abundant on clear-cuts than in the other forest types, suggesting that these species are adapted to disturbances such as forest fires and that they can respond quickly to increased volume of fresh dead wood and increased prey abundances. These species are also classified as fire favoured by Lundberg (1984). Furthermore, *Ampedus tristis* was less common on the naturally shaded logs than on the control logs, possibly reflecting a preference for open, sun exposed habitats. Several predators also responded to dead wood availability and prey abundance indicating complex interactions between predators, prey and habitat availability (Paper III).

I detected few differences in species richness, abundances or beetle assemblage composition between mature managed and old-growth stands, although managed stands are thought to support a lower diversity of saproxylic beetles (Martikainen *et al.* 2000). However, old-growth stands supported significantly more species of cambium consumers than the mature managed stands. In addition, the assemblages in mature managed and old-growth stands differed with respect to the composition of total saproxylic beetles and predators (Paper IV). This indicates that mature managed forests probably contain enough suitable substrate at least for early

successional saproxylic beetles. Furthermore, the mature managed stands in this study show evidence of past selective logging, but they have never been clear-cut. However, while there is no significant difference in the amount of wood in decay stage one, the mature managed stands contains less wood in later decay stages than the old-growth stands (Gibb *et al.* 2005), suggesting that although these forests are suitable habitats for early successional beetles, greater differences in beetle assemblages could probably be expected in later decay stages. Such a tendency for increasing differences between mature managed and old-growth stands can to some degree be seen already; there were no differences between mature managed and old-growth stands in 2001 (Paper I) or 2002 (Paper II, see also Gibb *et al.* 2006a), but some differences were apparent after an additional year, i.e. in 2003 (Paper IV). Because these forests have had a continuity of tree cover, and have been dominated by natural gap dynamics after the last selective felling they probably still support a large part of the fauna that are threatened by more intense forest measures like clear-cutting. Furthermore, large parts of the Scandinavian boreal forests show evidence of an extinction debt (Tilman *et al.* 1994, Hanski, Moilanen & Gyllenberg 1996), which means that the populations of many species are too small to be viable in a long term perspective and will eventually go extinct with continued intensive forest management.

The proportion of old spruce forest in the landscape proved to be important in determining which species were attracted to mycelium-baited traps (Paper VI). The assemblages of saproxylic beetles and the assemblages of fungivores and predators differed between the landscape types, mainly due to lower species richness and abundance of saproxylic beetles and fungivores in landscapes with lower proportions of old spruce forest. This suggests that forest fragmentation and habitat loss have resulted in depauperate beetle faunas in landscapes with smaller proportions of old spruce forest. My results highlight the importance of conducting studies assessing the effects of habitat fragmentation and habitat loss on saproxylic beetles at multiple scales (Paper VI).

In conclusion, my results suggest that forest management has pronounced effects on the saproxylic beetle fauna but that the effects vary between species and nutritional functional groups. Forest management also has indirect effects, for example by changing the availability and composition of available substrate and by affecting interactions between species. To limit the negative effects of forest management on many species, knowledge about these interactions are of major importance.

Management and conservation

The results of my study proved that characteristics of the substrate are important for the assemblage composition of saproxylic beetles and that many beetle species have specific substrate demands (Papers II, III, IV, V) as suggested earlier (see e.g. Palm 1948, Koch 1989, Koch 1992, Jonsell, Weslien & Ehnström 1998),

highlighting the importance of providing different kinds of dead wood in all stand types. Standing and lying wood, as well as wood with different levels of exposure, proved to be especially important for early successional beetles. The occurrence of wood fungi and, consequently, different rot types, are probably more important later in the succession, when it is possible that not only the fungi inoculated logs, but also burned logs, shaded logs and snags will support different fungal floras and hence different beetle assemblages.

The main effect of the burned log treatment was a reduced production of bark beetles. It is possible that the burned logs in this experiment only represent a small fraction of the diversity of substrates created in an area exposed to a wild fire. This is also supported by the results from Andersson (2001) who found few positive effects of small burnings and Wikars (2002) who found that burned logs supported fewer primary bark beetles than unburned logs. Based on my results, I conclude that burning of logs cannot replace burning of clear-cuts and standing forest in conserving insects favoured by fire. To conserve pyrophilous insects there is a need of prescribed burnings of larger areas resulting in a diversity of dead wood. Burning of clear-cuts is probably not enough because fire intensity and the volume and diversity of the created substrate are lower on burned clear-cuts than in burned forests (Hyvärinen *et al.* 2005). Thus, burning of intact stands is also needed. One way to achieve this is to save all wood in the stands subjected to natural forest fires and then add prescribed burnings of clear-cuts to reach the goals of the FCS-regulations (Anonymous 2000).

The Swedish forestry aims at conserving naturally occurring species, including species threatened by forestry, whilst simultaneously minimizing the risk of pest outbreaks. In an old-growth forest, secondary bark beetles are much more abundant than primary ones, suggesting that, in the absence of major disturbances, the populations of potential pest species will stay at non-epidemic levels (Martikainen *et al.* 1999). Intensive forest management, changing a landscape dominated by old-growth forest to one dominated by young monocultures has a severe impact on the bark beetle fauna. Even if there is not necessarily a difference in species richness or abundance of beetles, there is little overlap between the species assemblages (Martikainen *et al.* 1996). This shift from a community including many secondary bark beetles and predatory beetles to a community dominated by a few primary beetles and low abundance of predators could potentially increase the risks of pest outbreaks. One way of preventing this outcome is to try to manage the forest so that natural enemies of potential pest species are favoured and kept in high populations. Keeping predators in high populations could for example be achieved by favouring non pest bark beetles like *D. autographus*, as indicated by the results from the studies presented here.

The results from Paper II suggest that the risk of severe pest outbreaks is low in northern Sweden, indicating that conservation-oriented management could be emphasised more in this region, while in areas with higher risks of outbreaks, more caution should be taken. Furthermore, northern Sweden has a shorter history of forestry than southern Sweden and there are still mature managed stands that have never been clear-cut, although they have been selectively logged. Still many

of these mature managed forests contain old-growth forest characteristics like old trees, high volumes of dead wood and red listed species. I show that these forests can be valuable for the conservation of early successional insects because they support quite intact early successional saproxylic beetle assemblages (Paper IV, see also Gibb *et al.* 2006a). However, with continued traditional management for timber and pulpwood these forests are at great risk of losing much of their capacity to support intact insect assemblages. One way to increase the chance of these forests to keep the structures important for maintaining biodiversity is to increase the length of the rotation periods, possibly resulting in dead wood accumulation in the stands, giving more species the chance to colonise. Because many beetles seem to be largely affected by the proportion of old forest in the surrounding landscape (Paper VI, Gibb *et al.* 2006b), it may be more effective to allocate substrate created to support saproxylic species to stands in close vicinity to stands where these species occur in viable populations and to landscapes that contain high proportions of old-growth forest. Furthermore, leaving large amounts of dead wood close to reserves and key biotopes that already contain large amounts of dead wood could possibly increase the effective size of the reserves and provide an opportunity to maintain at least some of the more specialized species (see also (Martikainen *et al.* 2000).

Future research

The long term nature of the research project where my work is included and the fact that the experimental logs are still in the first decay stage highlights the importance of following these logs over a longer time period. The effects of the substrate manipulations will probably change over time and the composition of the fungal flora will become more important for determining the composition of the insect communities. Furthermore, there will be a succession of both fungi and insects on the logs which has rarely been studied with this kind of large-scale controlled experiment. Later decay stages host larger numbers of threatened beetle species, further emphasising the importance of long-term research projects in this system.

There are still many interactions between insects and fungi that have not been thoroughly investigated. For example, volatiles emitted by different fungal species and their effects on the attraction of insects need further research. Present knowledge includes the community structure of the insect assemblages on a number of wood fungi species (Jonsell, Nordlander & Ehnström 2001, Komonen 2001, Jonsell & Nordlander 2004) and the response to volatiles from *F. pinicola* and *F. fomentarius* on their associated insects (Fäldt *et al.* 1999). The ecology of insects and fungi that are considered economical pest species is quite well understood (e.g. Paine, Raffa & Harrington 1997), but the interactions of insects and fungi on wood in later decay stages deserves more attention. There is a gap in knowledge about the extent to which insects act as vectors of old-growth forest fungi and about the volatiles of these fungi and their function as insect attractants.

The threats against many old-growth forest species cannot be reduced if our knowledge about the complex interactions between the species involved is lacking.

The ecology of insects connected to dead wood and dead wood fungi is likely to be affected by climate change. It is important that research is carried out on the effects of climate change on potential pest species, on associated species and on rare species that may be at greater risk of extinction. In Sweden, climate models predict that annual precipitation and temperature as well as the spatial and temporal variation in local climate will increase, with the most pronounced changes in winter (Katz & Brown 1992, Mearns, Rosenzweig & Goldberg 1997, Przybylak 1997, Räisänen & Alexandersson 2003). We need to understand the effects of these changes on the insect fauna in order to adapt measures for increasing biodiversity, whilst minimizing the risk of pest outbreaks. With a warmer climate, and maybe more pest problems as indicated by e.g. Virtanen *et al.* (1996), there is a risk that conservation-oriented measures may be pushed aside in endeavours to achieve production goals and reduce the risk of pest outbreaks. To avoid these problems, we have to understand the ecology of both pest and non pest species and their interactions. Applied experiments testing different strategies to combine these goals are therefore needed.

The Swedish model for conservation, with a combination of reserves and conservation-oriented measures in the managed forests aims at conserving all species native to the boreal forest (Anonymous 2006), but the efficiency of these measures are still poorly known. One problem is that the substrate demands for many species, including several threatened ones, are to a large degree unknown and much of the available data are anecdotal. There is a need for research programmes aiming to determine thresholds for the minimum volume of dead wood required to maintain intact insect assemblages in managed forests. Studies on the landscape level, comparing today's measures with alternative strategies, are necessary. Both the amount and the allocation of conservation-oriented measures need to be tested experimentally, for example with even distribution of measures in some landscapes and clustered distributions in other. Probably, restoration of structures such as dead wood, old trees and landscapes (e.g. increased proportion of deciduous trees and burned areas) is necessary to maintain viable populations of many saproxylic species that are threatened today. The effects of such measures need to be evaluated to find both economically and ecologically sustainable ways of managing the Swedish boreal forests.

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