# Response of Saproxylic Insect Communities to Forestry: Implications for Conservation

Fredrik Stenbacka
*Faculty of Forest Sciences*
*Department of Wildlife, Fish, and Environmental Studies*
*Umeå*

Doctoral Thesis
Swedish University of Agricultural Sciences
Umeå 2009

Acta Universitatis Agriculturae Sueciae
2009:69

Cover: Large flight-intercept trap at Stenbithöjden clear-cut.
(photo: F. Stenbacka)

ISSN 1652-6880
ISBN 978-91-576-7416-6

Print: Arkitektkopia AB, Umeå 2009

# Response of Saproxylic Insect Communities to Forestry: Implications for Conservation.

## Abstract

In boreal Fennoscandia clear-cutting practices and fire suppression have drastically reduced dead wood amount and diversity, deteriorating the sapoxylic fauna (species associated with dead wood). More effective conservation measures are urgently needed, which requires more empirical data on many saproxylics in managed forest landscapes. In this thesis I have studied both the immediate and more long-term effects of clear-cutting on saproxylic insect communities (beetles, parasitic wasps and flat bugs), by comparing species richness, abundance and assemblage composition in the whole successional range of existing spruce dominated forests. My thesis also provides data on substrate requirements of red-listed beetles, response of flat bugs to forest fires, and complementarity of sampling methods for assessing data on rare and threatened species.

Old-growth forests supported the most intact communities and the highest densities of saproxylic insects and are probably very important as source habitats, especially for red-listed species. Mature managed forests were very similar in assemblage composition, strongly suggesting a high conservation value of these forests. Surprisingly, many saproxylic beetles adapted to late successional stages were present in thinned middle-aged forests, suggesting a significant conservation potential of these forests, provided that sufficient amounts and qualities of dead wood are retained. In contrast, unthinned forests held assemblages more similar to clear-cuts, which both were low in occurrence of red-listed beetles. Re-growth forests had a sparse dead wood supply compared to the older forests, especially reserves, and my results suggest that dead wood retention should include both snags and logs as these support different saproxylic assemblages. Finally, prescribed burnings are necessary for the survival of pyrophilus flat bugs.

Window and eclector traps collected different assemblages of both red-listed saproxylic beetles and parasitoids. Window traps gave a better measure of the local species pool, while eclector traps provided more detailed information on substrate requirements, host choice and hatching periods. For more precise parasitoid-host relationships, debarking of logs can be a useful method. Thus, the trap types used should be carefully selected depending on the specific questions addressed in each study.

*Keywords:* Coleoptera, Hymenoptera, Heteroptera, saproxylic, red-listed, dead wood, habitat and substrate requirements, parasitoid-host associations, sampling method, forest management, conservation.

*Author's address:* Fredrik Stenbacka, Department of Wildlife, Fish and
Environmental Studies, SLU, SE-901 83 Umeå, Sweden.
*E-mail:* Fredrik.Stenbacka@vfm.slu.se

# Dedication

Till Mamma och Pappa för det gedigna naturintresse ni gett mig som fört mig fram till detta mål!

*Nog finns det mål och mening i vår färd, men det är vägen som är mödan värd.*

Karin Boye

# Contents

# List of Publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I Hjältén, J., Stenbacka, F., Pettersson, R. B., Gibb, H., Johansson, T., Danell, K., Ball, J. P. and Hilszczański, J. Saving the rarest: habitat and substrate associations and stand specific production of red-listed saproxylic beetles (submitted manuscript).

II Stenbacka, F., Hjältén, J., Hilszczański, J., Ball, J. P., Gibb, H., Johansson, T., Pettersson, R. B. and Danell, K. Complementarity of sampling methods in assessing effects of forestry on parasitoids (Hymenoptera, Incheumonoidea) of saproxylic beetles (submitted manuscript).

III Stenbacka, F., Hjältén, J., Hilszczański, J. and Dynesius, M. Old species in new habitats: succession of beetle assemblages in managed boreal forest landscapes (submitted manuscript).

IV Johansson, T., Hjältén, J., Stenbacka, F. and Dynesius, M. (2009). Responses of eight boreal flat bug (Heteroptera: Aradidae) species to clear-cutting and forest fire (*Journal of Insect Conservation*, Online first, DOI 10.1007/s10841-009-9218-1).

Paper IV is reproduced with the kind permission of the publisher.

# 1 Introduction

Habitat loss and degradation due to human activities is the most severe threat to biodiversity worldwide. Thus, human presence must be incorporated into conservation planning, along with the view of ecological systems being dynamic and non-equilibrial through evolutionary change (Meffe *et al*., 2006). Conservation biology is based on the values (intrinsic and instrumental) of biodiversity (Callicott, 2006), and the relationship between biodiversity and ecosystem functioning must be acknowledged in management and policy making (Loreau *et al*., 2001; Spence, 2001; Elmqvist *et al*., 2004). That is: "biodiversity influences the stability of dynamic patterns and ecological resilience, ensuring persistence of functions in the presence of disturbance" (Jentsch *et al*., 2002).

Avoiding depletion of natural biodiversity means maintaining viable population sizes above critical threshold values where extinctions are likely to occur. This may vary considerably between habitats and species, and for most species we still lack empirical data to determine when critical thresholds are reached, e.g. minimum viable population size or minimum habitat area (With and Crist, 1995; Kinzig and Harte, 2000). Especially for species of conservation concern, e.g. rare or threatened species, and species of higher trophic levels, we urgently need to improve our knowledge in order to develop effective conservation measures. Because such species may occur in low population sizes and patchy distributions, it is also important to find efficient methods for assessing quantitative data for making qualitative and reliable estimates about their survival in the face of anthropogenic disturbance (Martikainen and Kouki, 2003). In this thesis I have therefore assessed, with different methods, habitat and substrate requirements of saproxylic insect communities in disturbed boreal forest landscapes.

## 1.1 Boreal forest landscapes

Deforestation of natural forests is a global concern and has resulted in negative and long-lasting effects in many forest ecosystems (Esseen *et al*., 1997; Bawa and Seidler, 1998; Siitonen, 2001; Grove, 2002a; Millennium Ecosystem Assessment, 2005). In some countries the dramatic expansion of agriculture along with human settlements has turned large virgin forest areas into open crop fields or grazing land (Tilman *et al*. 2001). In other areas natural forests have been replaced by various plantations of commercial interest, e.g. rubber trees, oil palms or faster-growing exotic tree species (Richardson and Rejmánek, 2004; Aratrakorn *et al*., 2006; Turner and Foster, 2009). This complete change of native ecosystems and the often unforeseen, but devastating effects of invasive species, have in particular lead to massive species extinctions in tropical areas (Dale *et al*. 1994, Turner *et al*. 1994).

Boreal regions have also experienced an expansion of colonization and cultivation during the last millennium, and in Fennoscandia, tar and potash production, along with timber use for shipbuilding developed during the last ~500 years (Östlund, 1993; Anonymous, 1999). Still, the greatest changes have taken place during the 19th and 20th centuries, when the scale of forestry impacts increased dramatically due to the industrialization (sawmills and pulp factories) of forestry (Östlund et al., 1997; Anonymous, 1999; Kouki *et al*., 2001). In the boreal forests of Fennoscandia, clear-cutting forestry has prevailed for half a century, producing even-aged homogenous monocultures, and impoverishing the conditions for many organisms (Larsson and Danell, 2001; Siitonen, 2001). This intensive forest management, along with heavy fire suppression, has strongly modified stand and landscape structure (Östlund et al., 1997; Linder and Östlund, 1998). At present, about 95% of the productive forestland in Sweden is commercially used and because most of the protected areas are concentrated in the northwest mountain chain, the boreal forests of Sweden are strongly dominated by managed forest stands of varying age with scattered small patches of protected old-growth forest reserves.

In virgin boreal forests natural disturbances and successional processes maintain structural and functional heterogeneity (Kuuluvainen, 2002; Bengtsson *et al*., 2003), thus maintaning biodiversity. For example, spatial and temporal diversity of important structural features like dead wood is created and maintained by, for example, gap disturbances and natural fire regimes (Kuuluvainen, 2002). However, such features and processes have been lost in the fragmented managed boreal landscapes and restoration of these forests, along with setting aside key habitats, is needed to reduce landscape-level species losses. Ecological sustainable forestry is embedded both in the Swedish Forestry Act and in environmental certification demands (Anonymous, 2007a; Anonymous, 2008) and general management guidelines mimicking natural disturbances have been implemented (Larsson and Danell, 2001; Spence 2001; Lindenmayer *et al.*, 2006). Most of these conservation measures are, however, confined to final harvest and are largely untested empirically.

Many species are not negatively affected by intense forest management, but these are mainly early successional or often generalist species and thus unlikely to be threatened. Instead, conservation efforts should focus on species intolerant to clear-cutting, e.g. rare and threatened species adapted to old-growth conditions (Berg *et al.*, 1995; Spence *et al.*, 1996; Niemelä, 1997; Grove, 2002a). Such species are likely to become increasingly isolated in reserves in fragmented managed forest landscapes (Kouki *et al.*, 2001; Siitonen, 2001). For successfully preserving these species we need to improve our knowledge about their resilience following clear-cutting (see Grove, 2002a; Buddle *et al.*, 2006; Dynesius and Hylander, 2007; Caruso *et al.*, 2008; Dynesius *et al.*, 2009). Moreover, we need to identify which assemblages or communities are sensitive to modern forestry and the underlying causes why this is so. This is becoming increasingly important as the proportion of stands regenerated after clear-cutting is increasing steadily: in Sweden, 37% of the unprotected productive forestland is covered by 20-60 year old forests, and an additional 22% is of even younger forests or recent clear-cuts (Anonymous, 2009). As these forests have been intensively managed from the beginning, most of them lack continuity of important structures like dead wood (Martikainen *et al.*, 2000; Siitonen, 2001).

## 1.2 Dead wood as key habitat

Dead wood and its characteristics are among the most important factors in maintaining high biodiversity, explaining both species richness and presence of red-listed species (e.g. Berg *et al.*, 1994, 1995; Økland *et al.*, 1996; Jonsell *et al.*, 1998; Nilsson *et al.*, 2001; Siitonen, 2001; Grove, 2002b, Tikkanen *et al.*, 2006). For example, ~60% of Sweden’s forest-living red-listed species are dependent on dead wood (Dahlberg and Stokland, 2004), i.e. are saproxylic species (Speight 1989). The rareness of many saproxylics is a result of the drastic reduction in the amount and quality of dead wood substrates due to modern forestry practices (Fridman and Walheim, 2000; Siitonen, 2001; Gibb *et al.*, 2005). Studies have also shown that dead wood diversity, continuity and connectivity are probably more crucial for the survival of saproxylic insects than dead wood volume (Schiegg, 2000; Siitonen, 2001; Similä *et al*., 2003). Regarding these deficits in managed forests, many saproxylic species specialized on rare substrates (e.g. large-diameter or well-decomposed wood) can only sustain viable populations in protected old-growth forests, which might lead to a disappearance of over 50% of the saproxylic species pool (Siitonen, 2001).

Dead wood management is, however, complicated because the dead wood habitat is complex and understanding the ecology of saproxylic species (including interactions) is not easy (see Jonsson *et al*., 2005). More precisely, dead wood offers a range of different habitats and the substrate requirements of saproxylic species varies strongly regarding tree species, standing or lying dead wood, degree of sun-exposure, decomposition class, diameter, burned dead wood, associated species, etc. (e.g. Jonsell *et al*., 1998; Martikainen *et al*., 2000; Siitonen, 2001; Jonsell and Weslien, 2003; Dahlberg and Stokland, 2004; Lindhe *et al*., 2005; Gibb *et al*., 2006a; Jacobs *et al*., 2007a). However, the retention of trees and dead wood on clear-cuts has improved the conditions for saproxylic insects, mainly for species associated with sun-exposed dead wood, for aspen-associates, but also for some fire-favoured species (e.g. Kaila *et al*., 1997; Martikainen, 2001; Gibb *et al*., 2006a). Still, little is known about the recovery of saproxylic species in stands regenerating after clear-cutting. The amount and input of dead wood in these forests is, however, very low (Sippola *et al*., 1998; Ranius, *et al*., 2003; Jonsson *et al*., 2005) and it is therefore reasonable to believe that they are poor in saproxylic species and that they might need active measures to avoid further landscape level species losses.

## 1.3 Study organisms in focus

Saproxylic species include all species that are dependent on dead wood, or on other dead wood species, during some part of their lifecycle (Speight, 1989). There are two levels of dead wood dependence: obligate saproxylics that are totally dependent on dead wood for their survival, and facultative saproxylics that are partly dependent or associated with dead wood (Dahlberg and Stokland, 2004). Data on substrate requirements have been compiled for about half of the ~7000 saproxylic species in Sweden, where insects comprise the largest group of organisms, but our knowledge is still very incomplete (Anonymous, 2007b; Dahlberg and Stokland, 2004)

Beetles (Coleoptera) are one of the most species-rich insect orders in the world (Gaston, 1991) and they are a relatively well-studied group (both saproxylics and non-saproxylics) in respect to disturbance by forestry (e.g. Niemelä *et al*. 1993; Grove, 2002a; Similä *et al*., 2002). Beetles are a major part of the saproxylic fauna and especially in boreal areas their abundance, species richness and species composition varies most strongly with amount and diversity of dead wood (Jonsell *et al*., 1998; Martikainen *et al*., 2000; Siitonen, 2001; Jonsell and Weslien, 2003; Dahlberg and Stokland, 2004; Gibb *et al*., 2006a, b; Jacobs *et al*., 2007a). In Sweden, Coleoptera is the biggest species group of all saproxylic organisms and also contain most red-listed saproxylics: i.e. >1300 saproxylic beetles of which 501 red-listed (Dahlberg and Stokland, 2004). Further, the saproxylic beetle community includes many functional groups, e.g. cambium consumers, detritivores, fungivores, wood borers, predators, fire-favoured (Saalas, 1923; Palm, 1948; Lundberg, 1984; Koch, 1989), which respond differently to environmental disturbances because of their various substrate and habitat associations (Gibb *et al*., 2006a; Johansson *et al*., 2007). Beetles are therefore a highly suitable group to study in relation to anthropogenic disturbances and dead wood characteristics (Paper I and III).

I also studied parasitic wasps (Hymenoptera, Ichneumonoidea, Ichneumonidae / Braconidae) of saproxylic beetles (Paper II). Although parasitic Hymenoptera is a species rich group (Gaston, 1991) that is very important in terrestrial ecosystems, they have been severely neglected in a conservation perspective (Shaw and Hochberg, 2001). Their role as natural enemies of pest insects has mainly been acknowledged in agricultural biological control programs (e.g. Neuenschwander, 2003; Mills, 2005), but these parasitoids also deserve more attention as possible indicator species of ecosystem changes. Their specialization at a high trophic level, which may result in low and variable population sizes, make parasitoids vulnerable and even extinction prone as a result of environmental disturbances (LaSalle and Gauld, 1993; Kruess and Tscharntke, 2000; Shaw and Hochberg, 2001), e.g. by modern forestry. However, none of the >3800 species of Ichneumonoidea found in Sweden have yet entered the red-list, mainly because of lack in species information (Gärdenfors *et al*., 2003; Gärdenfors, 2005). These parasitoids are divided into idiobionts (wider host range) and koinobionts (more host-specific) according to their different life strategies, i.e. mainly ectoparasitic and endoparasitic lifestyle, respectively (Haeselbarth, 1979; Askew and Shaw, 1986; Fitton *et al*., 1988). However, more knowledge is needed on their distribution, interactions and survival in managed boreal forests.

Finally, I studied boreal flat bugs (Heteroptera, Aradidae) (Paper IV), another little-known group of forest insects. Globally, flat bugs (or fungus bugs) is a small family including only about 1900 species (Kormilev and Froeschner, 1987). In boreal forests most species are considered mycophagus and live under the bark of dead trees or on polypore fungi, and some species are strongly associated with burned forest (Heliövaara and Väisänen, 1983; Coulianos, 1989; Wikars, 1992; Hjältén *et al*., 2006). Thus, most flat bugs are probably negatively affected by the forestry practices (including fire suppression) of Fennoscandia, and of the 22 known species in Sweden (20 *Aradus* sp., one *Aneurus* sp., one *Mezira* sp.) nine are nationally red-listed (Gärdenfors *et al*., 2003; Gärdenfors, 2005). This is a disturbingly high proportion and more knowledge is needed regarding their habitat requirements and distributions for more effective conservation actions. This is especially true for the red-listed species of which several are pyrophilus.

## 1.4 Objectives

To ensure the persistence of functional forest ecosystems we need to determine which parts of the ecological communities are resilient to disturbance and which are not. In the latter case we also need information regarding the proximate reasons for this, e.g. changes in abiotic factors, reduction in suitable substrates or hosts (for parasitic wasps), changes in biotic interactions, etc. Based on this we can identify resource-efficient ways to minimize overall species loss. The following main questions were addressed in the consecutive papers:

1. What are the habitat and substrate requirements of red-listed saproxylic coleopterans and how do we best obtain data on these aspects?

2. What is the best method for sampling saproxylic parasitoids? Are these species especially sensitive to disturbance by modern forestry?

3. What is the situation regarding dead wood and saproxylic beetles in young managed forests regenerated after clear-cutting compared to older, naturally developed forests? Which species or groups of species are negatively affected by clear-cutting and when do they recover?

4. How do flat bugs respond to natural and non-natural disturbances, fire and forestry, respectively?

# 2 Material and methods

## 2.1 Study areas

The main part of the study (Paper I, II, III and parts of IV) was conducted in the middle boreal forest zone (Ahti *et al*., 1968) in northern Sweden. The study areas were dominated by Norway spruce (*Picea abies* (L.) Karst.), mixed with Scots pine (*Pinus sylvestris* L.), some birch (*Betula pendula* Roth. and *B. pubescens* Ehrh.) and some aspen (*Populus tremula* L.). The understorey vegetation was mainly of moist to mesic *Vaccinium myrtillus* L. type (Ebeling, 1978) and the altitude ranged from 100 to 550 m a.s.l. Parts of Paper IV was performed in the northern boreal forest zone (Ahti *et al*., 1968) in a pine (*P. sylvestris*) dominated area of dry to mesic ground that had been exposed to a large-scale forest fire. All areas have a long history of forest management and fire suppression, resulting in a rather typical production forest landscape with a matrix of managed forests of different age classes and patches of protected old-growth forests.

## 2.2 Experimental design and trapping methods

In Papers I-II, I used a large-scale field experiment on dead wood initiated in 2001. The basic set up consisted of ten study areas, each including three stand types belonging to different age classes: an old-growth forest in or in direct association with a nature reserve or national park (mean forest age of ~160 years), an unprotected mature forest (mean age ~120 years), and a clear-cut area (cut in 2000 or 2001) (see Fig. 1). On each of these 30 experimental sites a randomized block design (Hurlbert, 1984) were applied, with three blocks per site and six different dead wood types of spruce in each block: an untreated control log, a burned log, a naturally shaded log, two fungi-inoculated logs (*Fomitopsis pinicola* (Swartz ex Fr.) Karst. and *Resinicium bicolor* (Alb. & Schwein) Parmasto), and a snag. The fungi-inoculations proved to be successful (Johansson *et al*., 2007). This experimental set-up enables determination of habitat- and substrate requirements of saproxylic beetles and their associated parasitoids. Maybe more importantly, comparing saproxylic species and communities in the different stand types may allow us to detect short-term effects from clear-cutting forestry.

To sample insects both trunk eclector traps (emergence traps) and trunk window traps (flight intercept traps) were used. The eclector traps measure the production of saproxylic insects in dead wood and were attached at random position along the log/snag. The eclector traps were designed to catch all emerging insects from a section of dead wood by wrapping a polypropylene weed barrier of 30 cm in width around the logs/snags (see Johansson *et al*., 2006a and Alinvi *et al*., 2007 for further details). A translucent 250 ml plastic bottle, half-filled with 50% propylene glycol with a small amount of detergent to reduce surface tension was attached to the trap to collect the insects (Southwood and Richard, 1978; Schiegg, 2001). The window traps were attached at a random position on the logs and at breast height on the snags. The window traps give a measure of which insects are attracted to a certain dead wood type, but do not ensure that the logs or snags are, in fact, the source for emerging insects as do the eclector traps. The window traps consisted of a transparent polycarbonate window (10 x 15 cm) that was attached vertically to each log/snag as flight intercept. To collect the insects, an aluminum tray (11 x 15 x 5 cm), also half-filled with glycol solution, was attached under the polycarbonate window (see Johansson *et al*., 2006a and Alinvi *et al*., 2007 for further details).

In paper II, I also debarked logs to more precisely determine parasitoid-host associations. In two of the ten study areas above, I distributed ten fresh one meter spruce bolts (i.e. 10 x 1 m) in the reserve, ten in the mature managed forest and ten on the clear-cut (i.e. six experimental sites and a total of 60 bolts). After colonization, the bolts were debarked in the search for all possible stages of parasitoids (mainly cocoons) and possible remains (i.e. head capsules) of their saproxylic hosts. All detected cocoons, including surrounding bark with host-galleries and remains, were moved to Petri dishes. To rear the parasitoid cocoons the samples were kept moist at room temperature and in a dark place (for further details about rearing of parasitoids see Shaw, 1997).

*Figure 1*. The studied forest types: a) an old-growth spruce forest, b) a mature managed spruce forest, c) a thinned spruce forest, d) an unthinned spruce forest, e) a clear-cut, and f) a burned pine forest. (Photos: F. Stenbacka)

In Paper III and IV, I used nine of the ten above study areas as basis, and added two more age-classes to the design: a middle-aged recently commercially thinned stand (mean age 53 years, representing the oldest available forests resulting from modern forestry, i.e. clear-felling) and a young unthinned (although in most cases pre-commercially thinned) stand (mean age 30 years) (see Fig. 1). Altogether, this added up to 45 experimental sites. These five stand types (old-growth, mature, thinned, unthinned, clear-cut) allow comparisons of beetle assemblages in the full range of the currently existing spruce forest types of northern Europe. In Paper IV, two more study areas were included to evaluate the effect of fire, i.e. a burned and an unburned pine forest (140-170 years old) each including six sampling sites (a total of 12 experimental sites).

In these studies I used a standardized design of three large free-hanging flight intercept traps (IBL2 traps) per site. These triangular window traps, with a thin semi-transparent plastic flight intercept of about 0.35 m$^2$, were attached between trees approximately 1.5 m above ground. Window traps have proven efficient for trapping beetles and are highly suitable for comparisons between different forest environments (e.g. Økland, 1996; Alinvi *et al*., 2007; Sverdrup-Thygeson and Birkemo, 2009). Beetles were collected in 600 ml plastic bottles 1/3 filled with 50% propylene glycol and a small amount of detergent. A rain water drainage module was attached between the trap and the bottle to avoid overfilling of the bottle and dilution of the glycol solution.

## 2.3 Dead wood survey

Dead wood was assessed in each stand type in the ten study areas, using four line-transects, 100 m long and 5 m wide (i.e. in total 0.2 ha). The protected old-growth forests, unprotected mature forests and clear-cuts were surveyed in September 2003 and this data was also used in Gibb *et al*. (2005), while the data for unthinned and thinned stands was collected specifically for this study in July-August 2006 (Paper III). No suitable unthinned and thinned stand was found for the study area of Rödberget. The transects in each site headed north, south, east and west from a midpoint selected between the three traps. Within the transect we recorded lying dead wood (logs) with a minimum diameter of 10 cm and a minimum length of 1.3 m, and standing dead wood (snags and high stumps) with a minimum diameter at breast height (dbh = 1.3 m above ground) of 10 cm. On logs we measured maximum and minimum diameters, as well as their length within the transect. For standing dead wood we measured dbh and height. For each dead wood object we recorded decomposition stage using a simplified classification system with four classes (derived from Söderström, 1988) and tree species. The volume of dead wood objects was calculated using a formula for a truncated circular cone:

$$V = (\pi h / 3)\,(r_1^2 + r_1 r_2 + r_2^2)$$

where h = height or length and $r_1$ = maximum radius and $r_2$ = minimum radius. For standing dead wood we calculated maximum and minimum radii (species-wise) using the change in radius per meter derived from logs longer than 3 m in the transect. For further details on the collection of and calculations on dead wood data I refer to Gibb *et al.* (2005). Dead wood volumes differed greatly between the sites (Fig. 2) and the different successional stages (Table 1).

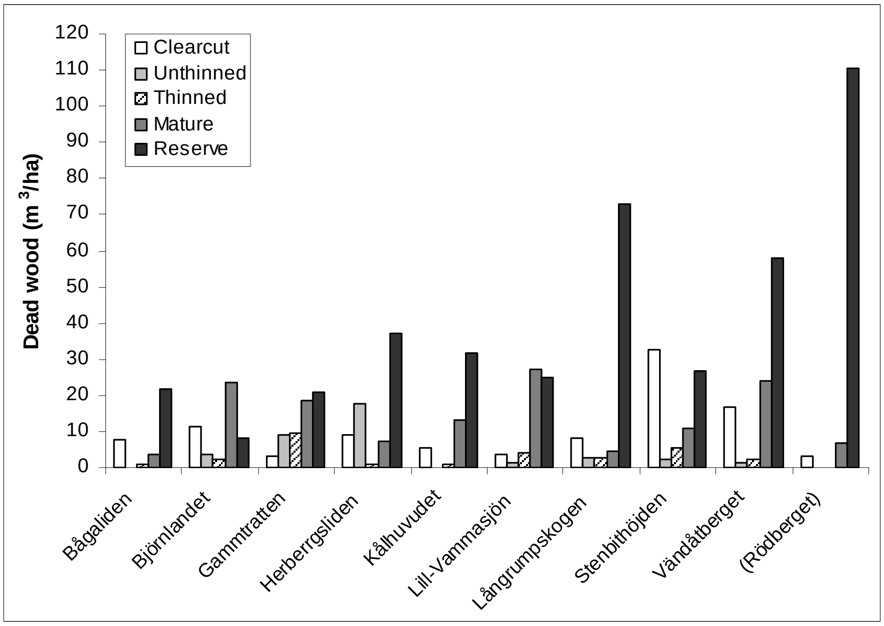

*Figure 2*. Natural dead wood volume per hectare in each forest type in each of the ten study areas. Note: no data for unthinned and thinned stands at Rödberget.

*Table 1*. Mean ± SE natural dead wood volumes of different tree types, tree species divided into coniferous and deciduous, decay classes and size classes in five spruce dominated forest types in Northern Sweden. Note: Rödberget not included in these comparisons as there were no available unthinned and thinned forests at this locality.

| Characteristic | | Clear-cut | Unthinned | Thinned | Mature | Reserve |
|---|---|---|---|---|---|---|
| Total | | 10.86 ± 3.06 | 4.27 ± 1.91 | 3.20 ± 0.93 | 14.74 ± 2.94 | 33.69 ± 6.68 |
| Treetype | Logs | 8.93 ± 2.81 | 4.13 ± 1.87 | 2.47 ± 0.61 | 9.53 ± 2.31 | 20.52 ± 4.39 |
| | Snags | 1.93 ± 0.60 | 0.14 ± 0.07 | 0.72 ± 0.49 | 5.21 ± 1.50 | 13.17 ± 3.26 |
| Species | Coniferous | 7.66 ± 2.33 | 3.32 ± 1.35 | 1.70 ± 0.46 | 11.08 ± 2.17 | 28.92 ± 6.85 |
| | Deciduous | 2.88 ± 0.85 | 0.95 ± 0.72 | 1.49 ± 0.57 | 3.19 ± 1.37 | 4.71 ± 1.65 |
| Decay class | 1 | 4.14 ± 1.37 | 0.03 ± 0.02 | 1.00 ± 0.28 | 4.03 ± 1.01 | 10.28 ± 2.71 |
| | 2 | 2.48 ± 0.65 | 0.17 ± 0.09 | 1.04 ± 0.75 | 3.10 ± 1.47 | 9.92 ± 2.89 |
| | 3 | 1.57 ± 0.74 | 0.71 ± 0.34 | 0.31 ± 0.14 | 2.47 ± 0.71 | 6.17 ± 1.36 |
| | 4 | 0.37 ± 0.20 | 3.12 ± 1.57 | 0.12 ± 0.11 | 3.19 ± 1.44 | 3.42 ± 1.03 |
| Diameter | 10-14 cm | 2.82 ± 0.71 | 0.52 ± 0.18 | 1.22 ± 0.25 | 2.43 ± 0.72 | 4.07 ± 1.44 |
| | 15-19 cm | 2.10 ± 0.61 | 0.38 ± 0.14 | 1.07 ± 0.33 | 2.57 ± 0.31 | 5.81 ± 1.20 |
| | 20-29 cm | 3.29 ± 1.02 | 1.97 ± 0.96 | 0.81 ± 0.36 | 5.85 ± 1.34 | 12.97 ± 3.45 |
| | >30 cm | 2.64 ± 1.22 | 1.40 ± 0.93 | 0.10 ± 0.10 | 3.89 ± 1.31 | 10.83 ± 2.82 |

# 3 Results

In total, 38 red-listed saproxylic beetles and 436 individuals were caught using both trunk eclector and trunk window traps over four trapping seasons (Paper I), and 43 species and 1456 individuals of saproxylic parasitic wasps by the same trapping methods over one season (Paper II). The large flight-intercept traps used in Paper III collected 35 024 individuals of saproxylic beetles belonging to 429 species over one season, of which 33 species and 401 specimens were red-listed. In Paper IV, we only caught 8 aradid-species and 119 individuals, again by using large flight-intercept traps. See Table 2 for a summarizing overview.

## 3.1 Habitat and substrate associations of red-listed saproxylic beetles (Paper I)

Red-listed saproxylic beetle total abundance and species richness (eclector and window traps pooled) differed both among substrates ($p = 0.003$) and forests types ($p < 0.001$), but no significant interaction was found between these factors (Table 1 in Paper I). Snags held the highest total abundance and number of species, while among forest types clear-cuts had a significantly lower abundance and species richness than mature managed forests and reserves. However, when eclector and window traps were analyzed separately, we found no significant differences between substrates for eclectors, but in window traps snags still had significantly higher abundance and species richness than the other substrates. Differences among forest types remained the same for both trap types, i.e. clear-cuts had lower abundance and species richness than the other forest types. Removing the dominant species *Epuraea longipennnis* from the analyses did not change the overall patterns.

The volume of spruce dead wood of decay class one was significantly highest in reserves ($p = 0.013$), thus the calculated estimated abundance per hectare of red-listed beetles in natural dead wood was also higher in reserves than in clear-cuts and mature managed forests ($p = 0.041$).

The total species assemblages (traps pooled) also differed between both substrates and forest types ($p = 0.0002$ for both) (Table 2 in Paper I): snags held different assemblages than all other substrate types, whereas clear-cuts had different assemblages than mature managed forests and reserves. Mature forests and reserves did not differ significantly and no significant interactions between substrate and forest type were detected. However, analyzing the trap types separately, revealed a significant interaction between substrate and forest types for eclectors. These effects were found in reserves, where snags and *Fomitopsis pinicola* logs differed significantly from several of the other substrates, e.g. controls and burned logs. Clear-cuts had generally different assemblages in eclectors than mature managed forests and reserves. However, this was not significant for all substrates. The assemblages in window traps differed between snags and the other substrate types. There was also a marginally significant difference between burned and shaded logs. Clear-cuts had different window trap assemblages than the other forest types.

## 3.2 Sampling and distribution of saproxylic parasitoids (Paper II)

Window traps collected more parasitoid species than eclector traps ($p = 0.023$), whereas total abundance did not differ between the trap types. However, of the four dominant species *Ontsira antica*, *Bracon obscurator*, *Cosmophorus regius* and *Helconidea dentator*, the first three were more abundant in eclector traps (Table 1 in Paper II). Along with *Bracon hylobii*, these species contributed most to the detected significant differences in species assemblages ($p = 0.0026$) between the trapping methods (Table 2 in Paper II). No significant interactions between trap type and stand type were detected in any analyses.

Species richness and total abundance did not differ among stand types. However, there was a significant effect of stand type on the abundance of different groups of saproxylic parasitoids: idiobionts ($p = 0.002$) were more abundant on clear-cuts than in mature managed forests and reserves, while koinobionts ($p = 0.012$) were more abundant in mature managed forests and reserves than on clear-cuts. The two dominant species of each life strategy (i.e. idiobionts *O. antica* and *B. obscurator*; koinobionts *C. regius* and *H.*

*dentator*) also followed these patterns. This segregation between the groups were also evident in the detected assemblage differences ($p$ = 0.0002) between clear-cuts and the other stand types (Table 2 in Paper II), where the main contribution to the differences were by the four most common species mentioned above.

By debarking logs for analyzing parasitoid cocoons and host remains, we recorded *Pissodes gyllenhalii/harzyniae* as a new host for *B. obscurator* and confirmed *Eubazus pallipes* as parasitoid on weevils (*Pissodes* spp.).

## 3.3 Succession of beetle assemblages in managed forest landscapes (Paper III)

The abundance ($p$ = 0.0001) and species richness ($p$ < 0.0001) of saproxylic beetles, including red-listed species, increased with forest successional age (Fig. 4a-b in Paper III). Both abundance and species richness were clearly higher in old-growth and mature forests than in clear-cuts and unthinned stands (Table 1 in Paper III). However, thinned stands were not significantly separated from the two older forest types. When analyzing the red-listed saproxylic beetles separately, the overall patterns in abundance ($p$ < 0.0001) and species richness ($p$ = 0.0002) among forest types were similar (Fig. 4c-d & Table 1 in Paper III). However, the dominance of old-growth and mature forests in supporting more species were proportionally even higher for red-listed beetles: i.e. 71% of all red-listed individuals and 74% of all red-listed species (Appendix A in Paper III). In addition, there was a trend for a lower occurrence of red-listed species in thinned than in old-growth forests. Further, the species richness of non-saproxylic beetles did not respond to forest type ($p$ = 0.996), but the abundance ($p$ = 0.034) was affected with lowest numbers in clear-cuts and highest in mature forests (Fig. 4e-f & Table 1 in Paper III).

Interestingly, for all three groups of beetles (saproxylic, red-listed saproxylic, non-saproxylic), the assemblage compositions were similarly affected by forest type ($p$ = 0.0002 for all groups). For all three beetle groups, clear-cuts differed from all other forest types (Fig. 5 & Table 2 in Paper III). In addition, unthinned forests also held different species assemblages than old-growth and mature forests for all species groups. Thinned forests were surprisingly similar, although to some extent differed from the two older forest types in assemblage compositions. Among saproxylics, the species that contributed most to assemblage differences between forest types were clearly either associated with open habitats or older closed forest (Appendix B in Paper III). For red-listed species the old-growth specialists were even more important, while for non-saproxylics the open habitat species had a bigger impact.

## 3.4 Response of flat bugs to clear-cutting and forest fire (Paper IV)

The flat bugs were most abundant in old-growth stands (30 individuals) and least abundant in young unthinned stands (9 individuals). However, neither the total abundance (89 individuals) nor species richness (5 species) was significantly different between stand types (Table 1 in Paper IV). Looking at individual species, only *Aradus depressus* (61 individuals) and *Aradus betulinus* (16 individuals) were statistically analyzed. The former was significantly ($p = 0.027$) more abundant in old-growth, mature, and thinned stands than on clear-cuts. *A. betulinus*, on the other hand, seemed to be indifferent to stand-age although it was most abundant on clear-cuts ($p = 0.106$). The other species were caught in very low numbers: *Aradus betulae* (4 individuals on clear-cuts), *Aradus corticalis* (3 on clear-cuts, 1 in thinned), and *Aradus cinnamomeus* (1 on clear-cut, 2 in thinned, 1 in mature).

Turning to the effect of burning, both species richness (5 species) and total abundance (30 individuals) were significantly ($p = 0.002$ for both) higher in burned forest compared to unburned control (Table 2 in Paper IV). In fact, no flat bugs were caught in the unburned control areas. For individual species, the difference was significant for *Aradus brevicollis* and *Aradus lugubris* ($p = 0.002$ and 0.021, respectively).

*Table 2*. Summarizing data on the sampled insects in each study, where the groups in focus highlighted in bold. In Paper III, both saproxylic beetles in general and as red-listed were in focus, thus numbers given for each group, respectively, in the different stand types.

| | **Paper I** | | **Paper II** | | **Paper III** | | **Paper IV** | |
|---|---|---|---|---|---|---|---|---|
| | Coleoptera | | Hymenoptera | | Coleoptera | | Heteroptera | |
| | Species nr. | Abundance | Species nr. | Abundance | Species nr. | Abundance | Species nr. | Abundance |
| Total | 800 | 281891 | **43** | **1456** | 657 | 42457 | **8** | **119** |
| Saproxylics | 496 (62%) | 259979 (92%) | 100% | 100% | **429 (65%)** | **35024 (82%)** | 100% | 100% |
| Red-listed | 40 | 488 | 0%* | 0%* | 34 | 466 | 0% | 0% |
| RL saproxylics | **38 (4.8%)** | **436 (0.2%)** | | | **33 (5%)** | **401 (0.9%)** | | |
| Stand type | | | | | | | | |
| Clear-cut | 20 | 59 | 32 | 501 | 244 / 14 | 4336 / 31 | 4 | 16 |
| Unthinned | | | | | 259 / 12 | 5042 / 33 | 2 | 9 |
| Thinned | | | | | 278 / 17 | 7475 / 57 | 4 | 16 |
| Mature | 27 | 206 | 27 | 536 | 274 / 19 | 8592 / 122 | 2 | 18 |
| Old-growth | 24 | 171 | 27 | 419 | 301 / 19 | 9579 / 158 | 2 | 30 |
| Burned | | | | | | | 5 | 30 |
| Unburned | | | | | | | 0 | 0 |
| Trap type | | | | | | | | |
| Eclector | 23 | 227 | 20 | 655 | | | | |
| Window | 32 | 209 | 40 | 520 | | | | |

* No saproxylic hymenopterans are currently red-listed in Sweden, which is mainly due to a lack of information on species within this group (Gärdenfors, 2005).

# 4 Discussion

My thesis provides some important new information on saproxylic insect communities in managed boreal landscapes, which I discuss in this section. First, I look into the direct effects of clear-cutting on saproxylic species of conservation concern, i.e. red-listed saproxylic beetles and saproxylic parasitoids (Paper I & II), but my thesis also includes data on saproxylic insect communities in ageing forests following clear-cutting (Paper III & IV). This includes habitat associations of saproxylic beetles (including red-listed) and flat bugs in the whole range of ages for spruce dominated stands of northern Sweden. Additionally, the response of flat bugs to disturbance by fire in pine dominated forests is presented. Finally, I discuss the importance of sampling method for assessing quantitative data and providing information on different aspects of insect biology. This in particular reference to rare and threatened species, i.e. red-listed saproxylic beetles and saproxylic parasitoids (Paper I & II).

## 4.1 Saproxylic insects in boreal forests

### 4.1.1 Importance of old-growth and mature forests

The prerequisites for saproxylic species in managed boreal landscapes are clearly shown by the dead wood situation in different stand types (Table 1). My results show that old-growth forests by far contain the highest amount and diversity of dead wood (Table 1; see also Fridman and Walheim 2001; Siitonen *et al.*, 2000; Gibb *et al.*, 2005), hence is the habitat most likely to support the most species rich and intact saproxylic insect communities, as well as other saproxylic groups like fungi and also non-saproxylic species (Spence *et al.*, 1996; Penttilä *et al.*, 2004). As shown by the calculated beetle abundance per hectare in relation to dead wood amount in Paper I, these naturally developed forests are also likely to be source habitats for many saproxylic species. In particular, many red-listed beetles were strongly connected to the protected old-growth forests, e.g. *Monochamus urussovi* and *Enicmus apicalis* (Paper I & III). My results confirm that many of these species are largely confined to stable habitats of late successional stages as they rely on rare substrates such as large-diameter or well-decomposed wood, or are involved in tight interactions with certain wood-fungi (Hammond *et al*., 2004; Johansson *et al*., 2006b). For example, the flat bug *Aradus depressus* (Paper IV) is associated with polypores on deciduous trees (Heliövaara and Väisänen, 1983; Coulianos, 1989) and was most common in the old-growth stands, where the amount of deciduous dead wood was highest (Table 1). Similar patterns of preference for undisturbed habitats were also seen for the saproxylic parasitoids, where the more specialized koinobionts were more common in old-growth forests than on clear-cuts (Paper II). It is likely that these more host-specific parasitoids connected to late successional stages are more vulnerable to forest management as they rely on intact food chains (Komonen *et al*., 2000).

The need for old-growth forests to maintain forest biodiversity is indisputable (Angelstam and Andersson, 2001). However, as they are just a small fraction of the Swedish forest landscape and are additionally unevenly distributed, it is questionable if these small and often isolated reserves in themselves can sustain viable populations of some saproxylic species in the long term. Hence, it was to some degree promising and somewhat surprising, that the results in all four studies in my thesis were consistent when comparing saproxylic communities in the protected old-growth forests with mature managed forests; i.e. no significant differences were found. My results strongly suggest that less intensive forest management has generally much lower negative impacts on natural ecosystems and biodiversity (see also Berg *et al*., 1995; Grove, 2002a). Namely, the mature managed stands in this study have only been selectively logged in the past (never clear-felled), which could explain why they still support more or less the same saproxylic communities as the reserves, including red-listed species. One additional explanation could be that at the time of past selective loggings, the boreal landscape was still relatively unexploited by forestry, which may have allowed re-colonization from surrounding areas. Regarding saproxylic beetles in general, similar patterns have been reported earlier in the same study areas (e.g. Gibb *et al*., 2006a, Hjältén *et al*., 2007, Johansson *et al*., 2007). In addition, other studies have also found mature managed forests to be suitable for many red-listed bryophyte and lichen species (Gustafsson, 2002; Gustafsson *et al.*, 2004). This does not mean that we can neglect the importance of protected old-growth forests, as these are still important source habitats for many rare and threatened species dependent on rare dead wood substrates, e.g. red-listed saproxylic fungi was much more common in the reserves than in the mature managed forests (Olsson, 2008). Instead, dead wood amount and diversity in present mature managed forests seem to exceed critical thresholds for maintaining viable populations of saproxylic species, which offers an opportunity to counteract further fragmentation of protected old-growth forests. However, these forests are not renewed and as they also are very valuable for forestry, a high proportion is exploited each year probably resulting in further species losses. This must be regarded as an alarming issue as boreal forests already are supposed to experience future species losses due to delayed effects of past habitat loss/fragmentation, i.e. an extinction debt (Tilman *et al.*, 1994; Hanski *et al.*, 1996). Thus, the negative effects of forestry must be minimized by implementing effective conservation measures in managed stands.

### 4.1.2 Short-term effects of clear-cutting

Environmental and microclimatic conditions on clear-cuts are unfavourable for many saproxylic species, especially those associated with older forests, which was shown by the very different assemblage composition on clear-cuts compared to old-growth forests (Paper I & III). For saproxylic species clear-cutting practices, including soil scarification, also result in a considerable decrease in dead wood amount and diversity (Table 1; Paper III; Fridman and Walheim, 2001; Gibb *et al.*, 2005). As a consequence, the species richness and abundance of saproxylic beetles (in particular red-listed) were much lower on clear-cuts than in old-growth and mature managed forests (Paper I & III). Moreover, many of the species found on clear-cuts were common generalist species that can utilize the fresh dead wood (Paper III), but also some species of conservation concern were more abundant on clear-cuts, e.g. the red-listed *Platysoma minus* and *Denticollis borealis* (Paper I & III). Both species are associated with sun-exposed wood, birch and aspen respectively, and other studies have reported such species utilizing retained deciduous trees on clear-cuts (e.g. Kaila *et al.*, 1997; Martikainen, 2001; Sverdrup-Thygeson and Birkemo, 2009). Still, more red-listed species were found in old-growth and mature forests, which emphasizes that these habitat types are fundamental for biodiversity conservation in present managed forest landscapes.

As a compensatory measure, snags/high stumps, usually of spruce, are created at clear-cuts. However, based on species richness and abundance in the different substrates in Paper I, I can not argue that retention of any particular spruce substrate on clear-cuts would be preferable for the conservation of red-listed beetles. It should be noted though, that snags held and attracted different assemblages of red-listed beetles than the substrate logs and thus providing both standing and lying dead wood is essential for maintaining complete saproxylic communities. Other studies have also showed the supplementary function of standing and lying dead wood for the assemblage composition of saproxylic insects (e.g. Jonsell and Weslien, 2003; Hedgren and Schroeder, 2004), and earlier studies on our experimental logs have also detected such differences both for beetles and their associated parasitoids (Hilszczański *et al*., 2005; Gibb et al., 2006a; Hjältén *et al*., 2007). However, for the idiobiontic parasitoids that were dominating on clear-cuts (Paper II), snags were of less importance according to Hilszczański *et al*. (2005). Instead they found high occurrence of koinobionts on snags in forested habitats (following host abundance), which implies both high habitat and host specificity for these more specialized parasitoids.

We did not find any effect of burning single logs on clear-cuts (Paper I). Clear-cuts can, however, to some degree resemble the open and sun-exposed habitats created by fire disturbance and can hence attract some fire-favored species, e.g. *Denticollis borealis* and *Aradus betulae* (Paper III & IV; Kaila *et al*., 1997; Wikars, 2002; Gibb *et al*., 2006a). However, for conservation of more pyrophilic species, e.g. several flat bug species (Paper IV), prescribed burning of clear-cuts where an adequate amount of dead and dying trees is created would be favourable (Toivanen and Kotiaho, 2007).

### 4.1.3 State of re-growth forests

Conservation measures taken at final cuttings also have a more long-term importance of setting the basis for young forests following clear-cutting. In a dead wood perspective, retention of both dead and living trees, as well as prescribed burnings of clear-cuts, will improve the living conditions for saproxylic species by adding structural heterogeneity and dead wood continuity into future re-growth forests (e.g. Siitonen, 2001; Hyvärinen *et al*., 2006; Jacobs *et al*., 2007b; Toivanen and Kotiaho, 2007). However, 20-60 year old Fennoscandian boreal forests (unthinned-thinned) originate from a period of forest management with very little conservation concern. My results clearly show that these forests are very poor in dead wood

(Table 1; Paper III), which might be due to that past retention of dead wood was insignificant and wind felled trees were taken out to avoid pest insect outbreaks. Put differently, these forests lack diversity, input and continuity of dead wood (Paper III; see also Sippola *et al*., 1998, Ranius *et al*., 2003; Similä *et al*., 2003).

The differences in saproxylic and non-saproxylic beetle assemblages found in Paper III, clearly shows that the unthinned forests still experience the effects of open habitat (see also Spence *et al*., 1996; Similä *et al*., 2002). Although the amount of dead wood of later decay classes was higher than of early stages (Table 1), the saproxylic assemblages were more similar to clear-cuts than of older forests, i.e. dominated by species associated with disturbed habitats and early successional stages. As discussed above, such saproxylics often live on fresh or sun-exposed wood, of which the supply in the studied unthinned forests was very sparse, which probably also explained the lower abundance and species richness of saproxylics in these forests. This emphasizes the importance of green tree retention to sustain dead wood continuum in these stands, but it is also important to find a cost-efficient retention level and this subject deserves more attention (see however Hyvärinen *et al*., 2005; Jacobs *et al*., 2007b).

In contrast, the amount of fresh dead wood was higher in thinned forests (but still low), which was mainly due to the input of small diameter logging residue. Also, the mean tree height was approximately 13 m in these stands providing a more closed canopy, and the beetle assemblages were in fact more similar to mature and old-growth forests than to unthinned forests and clear-cuts (Paper III). Although of much lower abundances, surprisingly many late successional species were present in thinned forests. The red-listed *Agathidium mandibulare* was even as abundant in thinned stands as in older forests even though the species has very specific wood and fungi requirements typical of old-growth forests (Ehnström, 2002). These are new and important findings indicating a surprisingly positive situation for saproxylic beetles in managed forests regenerated after clear-cutting. The large flight-intercept traps used in Paper III do not, however, show if the beetles originate from dead wood in these stands and the potential input of "tourist species" in the samples must be considered (see trap type discussion below). Still, my results show that these young forests at least can serve as passages/corridors between source habitats (see Niemelä, 2001) and could probably also serve as habitats as long as dead wood is made available, e.g. at thinning operations. This is urgent because these prospective mature forests must make up for the logging of present mature forests, which as shown are important for maintaining biodiversity in managed boreal landscapes.

To fulfil ecological sustainability, forest management must maintain biodiversity for more than one rotation cycle and this may require restoration of many degraded forests (Bawa and Seidler, 1998; Kuuluvainen, 2002), e.g. currently thinned stands. For saproxylic insects this requires increasing the amount and diversity of dead wood. My results along with earlier studies on our experimental substrates show that this must include retention of both logs and snags for sustaining complete and functional saproxylic communities (Paper I; Hilszczański *et al.*, 2005; Gibb *et al.*, 2006a; Johansson *et al.*, 2007). Retention of both living and dead deciduous trees is also necessary as many species, including red-listed beetles (Paper I & III; Martikainen, 2001), are associated with deciduous wood of which there was a deficit in the managed forests studied here (Table 1). Further, in addition to burning of clear-cuts prescribed burning of forested stands is crucial for the survival of some pyrophilus species as the results for several aradids indicate (Paper IV). Specifically, they were only present in burned forest, but not in control areas or on clear-cuts. A likely explanation is that fires are not uniform as fire behaviour and effects varies with the environment (Ryan, 2002), resulting in higher substrate amount and diversity in burned forests than on burned clear-cuts (Hyvärinen *et al.*, 2005).

## 4.2 Sampling saproxylic insects

When studying insect communities, the sampling method must be carefully selected in accordance with the aim of the study as different methods often give different measures (Hyvärinen *et al.*, 2006; Alinvi *et al.*, 2007). This is particularly important for assessing reliable data on species of small populations and irregular distributions, e.g. red-listed saproxylic beetles or saproxylic parasitoids (Paper I & II). In both these studies, the trunk eclector (emergence) and trunk window (flight intercept) traps clearly trapped different subsets of species assemblages. The eclector traps caught more individuals, but they are restrictive in catching only species associated with a certain decay stage, in our case early successional saproxylic insects (see also Gibb *et al.*, 2006b). Thus, eclectors can provide detailed information about substrate associations of saproxylic species (Wikars *et al.*, 2005; Alinvi *et al.*, 2007), which is important for effective conservation of these species. For example, the red-listed *Epuraea longipennis* (categorized as data deficient) emerged from all substrates (Paper I), even from birch logs (Hjältén *et al.*, unpublished data), suggesting that this species is a generalist. Further, detailed data is important for understanding the ecology of dead wood species and in particular learning more about their interactions. For example, eclector traps can provide information about natural hatching periods of saproxylic parasitoids (Paper II) and to a certain degree connect parasitoids to potential hosts (Hilszczański *et al.*, 2005). This could be useful information for controlling forest pest species with natural enemies. However, for even more accurate parasitoid-host relationships more labour-intensive methods like debarking of logs for cambiophagous hosts is recommended. Using debarking, I found a new parasioid-host relationship, i.e. *Bracon obscurator* as parasitoid of *Pissodes gyllenhalii/harzyniae*. Although it is a destructive method and yields relatively small sample sizes (Siitonen, 1994), debarking logs can be a useful species-targeted method for improving our knowledge on individual species, e.g. substrate requirements or species associations of rare or threatened species like parasitoids or red-listed beetles.

Trunk window traps, on the other hand, caught more species than eclectors and are not restricted to a certain decay stage. They should therefore be more suitable for comparing local species pools between stand types. Window traps are in general highly efficient for catching beetles, but one must also be aware of their limitations (Økland, 1996; Martikainen and Kouki, 2003; Sverdrup-Thygeson and Birkemoe, 2009), especially of catching "tourist species" (Saint-Germain *et al.*, 2006). Thus it can be hard to estimate the potential attractiveness of a specific dead wood substrate with trunk window traps. Although, absolute stand type associations may be unreliable for some species when using window traps, the presence of a species in a stand type should not be neglected. For example, finding a threatened old-growth species in a thinned stand might indicate that managed young forests at least can be used as corridors for migration between old-growth forest fragments (see discussion above).

The large free-hanging window traps (IBL2 traps) that were used in Paper III and IV were even more effective. For example, these traps caught a total of 27 196 beetle individuals belonging to 582 species in clear-cuts, mature and old-growth forests pooled (Table 2), compared to 12 606 individuals and 299 species caught in eclectors during the same summer and same sites (unpublished data). Further, the IBL2-traps also proved suitable for sampling rare and threatened beetles, as they in one season caught just slightly less red-listed saproxylics than trunk eclector and trunk window traps did combined in four years (Table 2). However, very few saproxylic parasitoids were captured in the IBL2-traps (unpublished data), probably because these species are good and strong fliers and hold on to the flight intercept instead of falling down into the collecting bottle (Hilszczański pers. comm.) Thus, these traps are unsuitable for sampling of some groups of insects. Still, the IBL2-traps must overall be regarded as highly efficient in assessing broad habitat associations of many beetles and getting a preliminary overview of the local species pool. Further studies are, however, needed on the absolute connection between saproxylics and substrate availability/usage in specific stand types. Combining large free-hanging window traps (instead of trunk window traps) with eclector traps is preferable for assessing saproxylic insect populations, as the former is more efficient than trunk window trap and could also be set-up in the vicinity of a substrate if so desired.

## 4.3 Conclusions

Based on the results from my studies and earlier studies I conclude that:

- The occurrence of rare and threatened saproxylic beetles was highest in old-growth forests, underlining their fundamental value for biodiversity in boreal forests. Mature managed forests did not differ in saproxylic assemblages compared to old-growth forests and must also be included in future conservation planning.
- Despite a sparse supply of dead wood in thinned stands, the occurrence of many old-growth associated saproxylic beetles indicates high dispersal of these species, but also that these forests could serve as habitats if dead wood is made available, e.g. during thinning.
- As shown by the different beetle assemblages on the experimental substrates, retention of dead wood must include both logs and snags. In addition, I found many species associated with deciduous dead wood on clear-cuts, emphasizing that current retention of mainly spruce is not sufficient.
- The input of dead wood in unthinned forests proved to be low, but green tree retention on clear-cuts could secure dead wood continuity in re-growth stands.
- Several flat bugs showed a strong association with burned forest, but were absent from clear-cuts. For preservation of such pyrophilus species in boreal landscapes, prescribed burning of clear-cuts may be insufficient. Instead, prescribed burnings of forests (where dead burned and slowly dying trees are created) might be necessary.
- The different sampling methods provided data on different aspects of insect biology. Window traps caught more species and are more suitable

for habitat comparisons, while eclector traps give detailed information on e.g. substrate associations. Debarking of logs is a suitable method for analyzing parasitoid-host associations.

### 4.3.1 Research and management implications

The research on the impacts of clear-cutting forestry in the boreal biome is extensive and especially a lot of knowledge on saproxylic species has been gathered (Siitonen, 2001). However, more studies are needed on the recovery of saproxylic species in forests regenerating after clear-cutting. Furthermore, for a more ecologically sustainable forestry, present conservation measures must be quantitatively evaluated. Currently, we are working in two ends; protecting old forests and at final harvesting general considerations, green tree and dead wood retention are implemented. My results, however, indicate that restoration of many managed forests is also needed to preserve viable populations on a landscape scale and to keep old-growth reserves functionally connected. This could include dead wood retention during thinning operations in addition to the retention at final harvesting. Confirming studies of beetle reproduction in dead wood in thinned forests are, however, needed (see Lindbladh and Abrahamsson, 2008). Furthermore, changes to current management practices need to be thoroughly evaluated before implemented. For example, short stumps are a substantial part of the dead wood in thinned stands (and on clear-cuts), and might be valuable substrate for some saproxylic species. Thus, before put into common practice, the ecological consequences of new practices like short-stump harvesting need to be evaluated (see however Abrahamsson and Lindbladh, 2006).

In addition, it is surprising how little attention has been given to alternative harvesting methods (to clear-cutting) in boreal Fennoscandia, but should though be considered and evaluated as they have been shown to have positive effects on biodiversity (e.g. Koivula, 2002; Klenner and Sullivan, 2003; Baker *et al*., 2009). My results indicate that selective felling maintains much of the diversity of saproxylic insects and should therefore be considered as an alternative management strategy, at least for some stands.

Last, but not least, more knowledge and quantitative data is needed on rare and threatened species in order to develop effective conservation measures for ensuring new- or re-colonization after larger disturbances and thus sustaining intact saproxylic communities, including species interactions.

*Figure 3. Rhagium mordax* (Lövträdlöpare). (Photo: F. Stenbacka)

# References

Abrahamsson, M. and Lindbladh, M. (2006). A comparison of saproxylic beetle occurrence between man-made high- and low-stumps of spruce (*Picea abies*). *Forest Ecology and Management* 226, 230-237.

Ahti, T., Hämet-Ahti, L. and Jalas, J. (1968). Vegetation zones and their sections in northwestern Europe. *Annales Botanici Fennici* 5, 169-211.

Alinvi, O., Ball, J. P., Danell, K., Hjältén, J. and Pettersson, R. B. (2007). Sampling saproxylic beetle assemblages in dead wood logs: comparing window and eclector traps to traditional bark sieving and a refinement. *Journal of Insect Conservation* 11, 99-112.

Angelstam, P. and Andersson, L. (2001). Estimates of the needs for forest reserves in Sweden. *Scandinavian Journal of Forest Research* Suppl. 3, 38-51.

Anonymous. (1999). *Grönare Skog*. Skogsstyrelsens Förlag, Jönköping. 288 pp. (in Swedish).

Anonymous. (2007a). *The Saproxylic Database - Biodiversity in dead wood*. Available at: http://www.saproxylic.org/

Anonymous. (2007b). *The Swedish Forestry Act*. Swedish Forest Agency, Jönköping. Available at: http://www.svo.se/episerver4/templates/SNormalPage.aspx?id=12677.

Anonymous. (2008). *Swedish FSC Standard for Forest Certification*. Swedish Forest Stewardship Council. Available for download at: http://www.fsc-sweden.org/Documents/tabid/110/Default.aspx.

Anonymous. (2009). *Skogsdata 2008*. Aktuella uppgifter om de svenska skogarna från Riksskogstaxeringen. Tema: Skogens roll för klimatet. Institutionen för skoglig resurshushållning, SLU, Umeå (in Swedish).

Aratrakorn, S., Thunikorn, S. and Donald, P. F. (2006). Changes in bird communities following conversion of lowland forest to oil palm and rubber plantations in southern Thailand. *Bird Conservation International* 16, 71-82.

Askew, R. R. and Shaw, M. R. (1986). Parasitoid communities: their size, structure and development. In: Waage, J. and Greathead, D. (Eds.). *Insect Parasitoids: 13th symposium of the Royal Entomological Society of London*. Academic Press, London, UK. p. 225-264.

Baker, S. C., Grove, S. J., Forster, L., Bonham, K. J. and Bashford, D. (2009). Short-term responses of ground-active beetles to alternative silvicultural systems in the Warra

Silvicultural Systems Trial, Tasmania, Australia. *Forest Ecology and Management* 258, 444-459.

Bawa, K. S. and Seidler, R. (1998). Natural forest management and conservation of biodiversity in tropical forests. *Conservation Biology* 12(1), 46-55.

Bengtsson, J., Angelstam, P., Elmqvist, T., Emanuelsson, U., Folke, C., Ihse, M., Moberg, F. and Nyström, M. (2003). Reserves, resilience and dynamic landscapes. *Ambio* 32(6), 389-396.

Berg, Å., Ehnström, B., Gustafsson, L., Hallingbäck, T., Jonsell, M. and Weslien, J. (1994). Threatened plant, animal, and fungus species in Swedish forests: Distribution and habitat associations. *Conservation Biology* 8, 718-731.

Berg, Å., Ehnström, B., Gustafsson, L., Hallingbäck, T., Jonsell, M. and Weslien, J. (1995). Threat levels and threats to red-listed species in Swedish forests. *Conservation Biology* 9, 1629-1633.

Buddle, C. M., Langor, D. W., Pohl, G. R. and Spence, J. R. (2006). Arthropod responses to harvesting and wildfire: Implications for emulation of natural disturbance in forest management. *Biological Conservation* 128, 346-357.

Callicott, J. B. (2006). Conservation values and ethics. *In*: Groom, M. J., Meffe, G. K. and Carroll, C. R. (Eds.). *Principles of Conservation Biology*. Sinauer Associates, Inc., Sunderland, USA. p. 111-135.

Caruso, A., Rudolphi, J. and Thor, G. (2008). Lichen species diversity and substrate amounts in young planted boreal forests: A comparison between slash and stumps of *Picea abies*. *Biological Conservation* 141, 47-55.

Coulianos, C-C. (1989). Nya landskapsfynd av barkstinkflyn (Hem.-Het., Aradidae) jämte *Aradus truncatus*, ny för Sverige. *Entomologisk Tidskrift* 110, 53-57 (in Swedish).

Dahlberg, A. and Stokland, J. N. (2004). Vedlevande arters krav på substrat - sammanställning och analys av 3600 arter. *Skogsstyrelsen Rapport* 7 (in Swedish with English summary).

Dale, V. H., Pearson, S. M., Offerman, H. L. and O'Neill, R. V. (1994). Relating patterns of land-use change to faunal biodiversity in the Central Amazon. *Conservation Biology* 8(4), 1027-1036.

Dynesius M. and Hylander, K. (2007). Resilience of bryophyte communities to clear-cutting of boreal stream-side forests. *Biological Conservation* 135, 423-434.

Dynesius, M., Hylander, K. and C. Nilsson, C. (2009). High resilience of bryophyte assemblages in stream-side compared to upland forests. *Ecology* 90, 1042-1054.

Ebeling, F. (1978). *Nordsvenska skogstyper*. Sveriges Skogsvårdsförbund, Djursholm (in Swedish).

Ehnström, B. (2002). *Agathidium mandibulare* - Arfaktablad, Artdatabanken, SLU, Sverige At: http://www.artdata.slu.se/rodlista/Faktablad/agat_man.PDF.

Elmqvist, T., Berkes, F., Folke, C., Angelstam, P., Crépin, A-S. and Niemelä, J. (2004). The dynamics of ecosystems, biodiversity management and social institutions at high northern latitudes. *Ambio* 33(6), 350-355.

Esseen, P-A., Ehnström, B., Ericson, L. and Sjöberg, K. (1997). Boreal forests. *Ecological Bulletins* 46, 16-47.

Fitton, M. G., Shaw, M. R. and Gauld, I. D. (1988). Pimpline ichneumon-flies. Hymenoptera, Ichneumonidae (Pimplinae). *Handbooks for the Identification of British Insects* 7(1), 1-110.

Fridman, J. and Walheim, M. (2000). Amount, structure and dynamics of dead wood on managed forestland in Sweden. *Forest Ecology and Management* 131, 23-36.

Gaston, K. J. (1991). The magnitude of global insect species richness. *Conservation Biology* 5, 283-296.

Gibb, H., Ball, J. P., Johansson, T., Atlegrim, O., Hjältén, J. and Danell, K. (2005). Effects of management on coarse woody debris volume and composition in boreal forests in northern Sweden. *Scandinavian Journal of Forest Research* 20, 213-222.

Gibb, H., Pettersson, R. B., Hjältén, J., Hilszczański, J., Ball, J. P., Johansson, T., Atlegrim, O. and Danell, K. (2006a). Conservation-oriented forestry and early successional saproxylic beetles: Responses of functional groups to manipulated dead wood substrates. *Biological Conservation* 129, 437-450.

Gibb, H., Hjältén, J., Ball, J. P., Atlegrim, O., Pettersson, R. B., Hilszczański, J., Johansson, T. and Danell, K. (2006b). Effects of landscape composition and substrate availability on saproxylic beetles in boreal forests: a study using experimental logs for monitoring assemblages. *Ecography* 29, 191-204.

Grove, S. J. (2002a). The influence of forest management history on the integrity of the saproxylic beetle fauna in an Australian lowland tropical rainforest. *Biological Conservation* 104, 149-171.

Grove, S. J. (2002b). Saproxylic insect ecology and the sustainable management of forests. *Annual Review of Ecology and Systematics* 33, 1-23.

Gustafsson, L. (2002). Presence and abundance of red-listed plant species in Swedish forests. *Conservation Biology* 16, 377-388.

Gustafsson, L., Appelgren, L., Jonsson, F., Nordin, U., Persson, A. and Weslien, J-O. (2004). High occurrence of red-listed bryophytes and lichens in mature managed forests in boreal Sweden. *Basic and Applied Ecology* 5, 123-129.

Gärdenfors, U., Hall, R., Hallingbäck, T., Hansson, H. G. and Hedström, L. (2003). Djur, svampar och växter i Sverige 2003. Förteckning över antal arter per familj. *ArtDatabanken Rapporterar* 5. ArtDatabanken, SLU, Uppsala (in Swedish).

Gärdenfors, U. (2005). *Rödlistade arter i Sverige 2005 - The 2005 Red List of Swedish Species*. ArtDatabanken, SLU, Uppsala, Sweden.

Haeselbarth, E. (1979). Zur Parasitierung der Puppen von Forleule (*Panolis Xammea* (SchiV.)), Kieferspanner (*Bupalus piniarius* (L.)) und Heidelbeerspanner (*Boarmia bistortana* (Goeze)) in bayerischen Kiefernwaldern. *Zeitschrift fur Angewande Entomologie* 87 (186–202), 311-332 (in German).

Hammond, H. E. J., Langor, D. W. and Spence, J. R. (2004). Saproxylic beetles (Coleoptera) using *Populus* in boreal aspen stands of western Canada: spatiotemporal variation and conservation of assemblages. *Canadian Journal of Forest Research* 34, 1-19.

Hanski, I., Moilanen, M. and Gyllenbegr, M. (1996). Minimum viable metapopulation size. *American Naturalist* 147(4), 527-541.

Heliövaara, K. and Väisänen, R. (1983). Environmental changes and the flat bugs (Heteroptera, Aradidae and Aneuridae). *Annales Entomologici Fennici* 49, 103-109.

Hilszczański, J., Gibb, H., Hjältén, J., Atlegrim, O., Johansson, T., Pettersson, R., Ball, J. P. and Danell, K. (2005). Parasitoids (Hymenoptera, Ichneumonoidea) of saproxylic beetles are affected by forest successional stage and dead wood characteristics in boreal spruce forest. *Biological Conservation* 126, 456-464.

Hjältén, J., Atlegrim, O., Sandström, F., Pettersson, R. and Rexstad, E. A. (2006). Occurrence of flat bugs (Heteroptera: Aradidae) in burned and unburned forests. *Entomolologica Fennica* 17, 130-135.

Hjältén, J., Johansson, T., Alinvi, O., Danell, K., Ball, J. P., Pettersson, R., Gibb, H. and Hilszczański, J. (2007). The importance of substrate type, shading and scorching for the attractiveness of dead wood to saproxylic beetles. *Basic and Applied Ecology* 8(4), 364-376.

Hurlbert, S. H. (1984). Pseudoreplication and the design of ecological field experiments. *Ecological Monographs* 54, 187-211.

Hyvärinen, E., Kouki, J., Martikainen, P. and Lappalainen, H. (2005). Short-term effects of controlled burning and green-tree retention on beetle (Coleoptera) assemblages in managed boreal forests. *Forest Ecology and Management* 212, 315–332.

Hyvärinen, E., Kouki, J. and Martikainen, P. (2006). A comparison of three trapping methods used to survey forest-dwelling Coleoptera. *European Journal of Entomology* 103, 397-407.

Jacobs J. M., Spence, J. R. and Langor, D. W. (2007a). Influence of boreal forest succession and dead wood qualities on saproxylic beetles. *Agricultural and Forest Entomology* 9, 3-16.

Jacobs J. M., Spence, J. R. and Langor, D. W. (2007b).Variable retention harvest of white spruce stands and saproxylic beetle assemblages. *Canadian Journal of Forest Research* 37, 1631-1642.

Jentsch, A., Beierkuhnlein, C. and White, P. S. (2002). Scale, the dynamic stability of forest ecosystems, and the persistence of biodiversity. *Silva Fennica* 36(1), 393-400.

Johansson, T., Gibb, H., Hilszczanski, J., Pettersson, R. B., Hjältén, J., Atlegrim, O., Ball, J. P. and Danell, K. (2006a). Conservation-oriented manipulations of coarse woody debris affect their value as habitat for spruce-infesting bark and ambrosia beetles (Coleoptera: Scolytinae) in northern Sweden. *Canadian Journal of Forest Research* 36, 174-185.

Johansson, T., Olsson, J., Hjältén, J.. Jonsson, B. G. and Ericson, L. (2006b). Beetle attraction to sporocarps and wood infected with mycelia of decay fungi in old-growth spruce forests of northern Sweden. *Forest Ecology and Management* 237, 335–341.

Johansson, T., Hjältén, J., Gibb, H., Hilszczański, J., Stenlid, J., Ball, J. P., Alinvi, O. and Danell, K. (2007). Variable response of different functional groups of saproxylic beetles to substrate manipulation and forest management: Implications for conservation strategies. *Forest Ecology and Management* 242, 496-510.

Jonsell, M., Weslien, J. and Ehnström, B. (1998). Substrate requirements of red-listed saproxylic invertebrates in Sweden. *Biodiversity and Conservation* 7, 749-764.

Jonsell, M. and Weslien, J. (2003). Felled or standing retained wood - it makes a difference for saproxylic beetles. *Forest Ecology and Management* 175, 425-435.

Jonsson, B. G., Kruys, N. and Ranius, T. (2005). Ecology of species living on dead wood - Lessons for dead wood management. *Silva Fennica* 39(2), 289-309.

Kaila, L., Martikainen, P. and Punttila, P. (1997). Dead trees left in clear-cuts benefit saproxylic Coleoptera adapted to natural disturbances in boreal forest. *Biodiversity and Conservation* 6(1), 1-18.

Kinzig, A. P. and J. Harte, J. (2000). Implications of endemics-area relationships for estimates of species extinctions. *Ecology*, 81(12), 3305-3311.

Klenner, W. and Sullivan, T. P. (2003). Partial and clear-cut harvesting of high-elevation spruce–fir forests: implications for small mammal communities. *Canadian Journal of Forest Research* 33, 2283-2296.

Koch, K. (1989). *Die Käfer Mitteleuropas 1. Ökologie*. Goecke & Evers, Krefeld, Germany. 440 pp.

Koivula, J. (2002). Alternative harvesting methods and boreal carabid beetles (Coleoptera, Carabidae). *Forest Ecology and Management* 167, 103-121.

Komonen, A., Penttilä, R., Lindgren, M. and Hanski, I. (2000). Forest fragmentation truncates a food chain based on an old-growth bracket fungus. *Oikos* 90, 119-126.

Kormilev, N. A. and Froeschner, R. C. (1987). Flat bugs of the World. A synonymic list (Heteroptera: Aradidae). *Entomography* 5, 1-246.

Kouki, J., Löfman, S., Martikainen, P., Rouvinen, S. and Uotila, A. (2001). Forest fragmentation in Fennoscandia: Linking habitat requirements of wood-associated threatened species to landscape and habitat changes. *Scandinavian Journal of Forest Research* Suppl. 3, 27-37.

Kruess, A. and Tscharntke, T. (2000). Species richness and parasitism in a fragmented landscape: experiments and field studies with insects on *Vicia sepium*. *Oecologia* 122, 129–137.

Kuuluvainen, T., Aapala, K., Ahloth, P., Kuusinen, M., Lindholm, T., Sallantus, T., Siitonen, J. and Tukia, H. (2002). Principles of ecological restoration of boreal forested ecosystems: Finland as an example. *Silva Fennica* 36(1), 409-422.

Larsson, S., and Danell, K. (2001). Science and the management of boreal forest biodiversity. *Scandinavian Journal of Forest Research Supplement* 3, 5-9.

La Salle, J. and Gauld, I. D. (1993). *Hymenoptera and Biodiversity*. CAB International, Wallingford, UK.

Lindbladh, M. and Abrahamsson, M. (2008). Beetle diversity in high-stumps from Norway spruce thinnings. *Scandinavian Journal of Forest Research* 23, 339-347.

Lindenmayer, D. B., Franklin, J. F. and Fischer, J. (2006). General management principles and a checklist of strategies to guide forest biodiversity conservation. *Biological Conservation* 131, 433-445.

Linder, P. and Östlund, L. (1998). Structural changes in three mid-boreal Swedish forest landscapes, 1885-1996. *Biological Conservation* 85, 9-19.

Lindhe, A., Lindelöw, Å. and Åsenblad, N. (2005). Saproxylic beetles in standing dead wood - density in relation to substrate sun-exposure and diameter. *Biodiversity and Conservation* 14(12), 3033-3053.

Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J. P., Hector, A., Hooper, D. U., Huston, M. A., Raffaelli, D., Schmid, B., Tilman, D., and Wardle, D. A. (2001).

Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science* 294, 804-808.

Lundberg, S. (1984). Den brända skogens skalbaggsfauna i Sverige. *Entomologisk Tidskrift* 105, 129-141. (in Swedish)

Martikainen, P., Siitonen, J., Punttila, P., Kaila, L.and Rauch, J. (2000). Species richness of Coleoptera in mature managed and old-growth boreal forests in southern Finland. *Biological Conservation* 94, 199-209.

Martikainen, P. (2001). Conservation of threatened saproxylic beetles: significance of retained aspen *Populus tremula* on clear-cut areas. *Ecological Bulletins* 49, 205-218.

Martikainen, P.,and Kouki, J. (2003). Sampling the rarest: threatened beetles in boreal forest biodiversity inventories. *Biological Conservation* 12, 1815-1831.

Meffe, G. K., Carroll, C. R. and Groom, M. J. (2006). What is conservation biology? *In*: Groom, M. J., Meffe, G. K. and Carroll, C. R. (Eds.). *Principles of Conservation Biology*. Sinauer Associates, Inc., Sunderland, USA. p. 3-25.

Millennium Ecosystem Assessment. (2005). *Ecosystems and Human Well-being: Biodiversity Synthesis*. World Resources Institute, Washington D.C., USA.

Mills, N. (2005). Selecting effective parasitoids for biological control introductions: codling moth as a case study. *Biological Control* 34, 274-82.

Neuenschwander, P. (2003). Biological control of cassava and mango mealybugs in Africa. *Biological control in IPM Systems in Africa* (ed. by Neuenschwander et al.), pp. 45-59. CABI Publishing.

Niemelä, J., Langor, D. W. and Spence, J. R. (1993). Effects of clear-cut harvesting on boreal ground beetle assemblages (Coleoptera: Carabidae) in western Canada. *Conservation Biology* 7, 551-561.

Niemelä, J. (1997). Invertebrates and boreal forest management. *Conservation Biology* 11(3), 601-610.

Niemelä, J. (2001). The utility of movement corridors in forested landscapes. *Scandinavian Journal of Forest Research* Suppl. 3, 70-78.

Nilsson, S. G., Hedin, J. and Niklasson, M. (2001). Biodiversity and its assessment in boreal and nemoral forests. *Scandinavian Journal of Forest Research* Suppl. 3, 10-26.

Økland, B. (1996). A comparison of three methods of trapping saproxylic beetles. *European Journal of Entomology* 93, 195-209.

Olsson, J. (2008). Colonization patterns of wood-inhabiting fungi in boreal forest. PhD-thesis, Umeå University.

Palm, T. (1948). *Svensk Insektfauna*. *Kortvingar. Fam. Staphylinidae. Häfte 1.* Entomologiska Föreningen, Stockholm. 133 pp. (in Swedish).

Penttilä, R., Siitonen, J. and Kuusinen, M. (2004). Polypore diversity in managed and old-growth boreal *Picea abies* forests in southern Finland. *Biological Conservation* 117, 271-283.

Ranius, T., Kindvall, O., Kruys, N. and Jonsson, B. G. (2003). Modelling dead wood in Norway spruce stands subject to different management regimes. *Forest Ecology and Management* 182, 13-29.

Richardson, D. M. and Rejmánek, M. (2004). Conifers as invasive aliens: a global survey and predictive framework. *Diversity and Distributions* 10, 321-331.

Ryan, K. C. (2002). Dynamic interactions between structure and fire behavior in boreal ecosystems. *Silva Fennica* 36(1), 13-39.

Saalas, U. (1923). *Die Fichtenkäfer Finlands. II. Spezieller Teil und Larvenbestimmungstabelle*. Ann. Acad. Scient. Fenn. Ser. A 22, Helsinki, Finland. 746 pp.

Saint-Germain, M., Buddle, C. M. and Drapeau, P. (2006). Sampling saproxylic Coleoptera: Scale issues and the importance of behavior. *Environmental Entomology* 35(2), 478-487.

Schiegg, K. (2000). Effects of dead wood volume and connectivity on saproxylic insect species diversity. *Ecoscience* 7(3), 290-298.

Schiegg, K. (2001). Saproxylic insect diversity of beech: limbs are richer than trunks. *Forest Ecology and Management* 149, 295-304.

Shaw, M. R. (1997). *Rearing parasitic Hymenoptera. The Amateur Entomologist Vol. 25*. The Amateur Entomologists' Society, Orpington, UK.

Shaw, M. R. and Hochberg, M. E. (2001). The neglect of parasitic Hymenoptera in insect conservation strategies: The British fauna as a prime example. *Journal of Insect Conservation* 5, 253–263.

Siitonen, J. (1994). Decaying wood and saproxylic Coleoptera in two old spruce forests: a comparison based on two sampling methods. *Annales Zoologici Fennici* 31, 89-95.

Siitonen, J., Martikainen, P., Punttila, P. and Rauh, J. (2000). Coarse woody debris and stand characteristics in mature managed and old-growth boreal mesic forests in southern Finland. *Forest Ecology and Management* 128, 211-225.

Siitonen, J. (2001). Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. *Ecological Bulletins* 49, 11-41.

Similä, M., Kouki, J., Martikainen, P. and Uotila, A. (2002). Conservation of beetles in boreal pine forests: the effects of forest age and naturalness on species assemblages. *Biological Conservation* 106, 19-27.

Similä, M., Kouki, J. and Martikainen, P. (2003). Saproxylic beetles in managed and seminatural Scots pine forests: quality of dead wood matters. *Forest Ecology and Management* 174, 365-381.

Sippola, A-L., Siitonen, J. and Kallio, R. (1998). The amount and quality of coarse woody debris in natural and managed forests near the timberline in Finnish Lapland. *Scandinavian Journal of Forest Research* 13, 204-214.

Southwood, T. and Richard, E. (1978). *Ecological methods with particular reference to the study of insect populations, 2nd edn*. Chapman and Hall, London.

Speight, M .C. D. (1989). *Saproxylic invertebrates and their conservation. Nature and Environment Series 42*. Council of Europe, Strasbourg, France.

Spence, J. R., Langor, D. W., Niemelä, J., Cárcamo, H. A. and Currie, C. R. (1996). Northern forestry and carabids: the case for concern about old-growth species. *Annales Zoologici Fennici* 33, 173-184.

Spence, J. R. (2001). The new boreal forestry: adjusting timber management to accommodate biodiversity. *Trends in Ecology & Evolution* 16(11), 591-593.

Sverdrup-Thygeson, A. and Birkemoe, T. (2009). What window traps can tell us: effect of placement, forest openness and beetle reproduction in retention trees. *Journal of Insect Conservation* 13, 183-191.

Söderström, L. (1988). Sequence of bryophytes and lichens in relation to substrate variables of decaying coniferous wood in Northern Sweden. *Nordic Journal of Botany* 8, 89-97.

Tikkanen, O-P., Martikainen, P., Hyvärinen, E., Junninen, K. and Kouki, J. (2006). Red-listed boreal forest species of Finland: associations with forest structure, tree species and decaying wood. *Annales Zoologici Fennici* 43, 373-383.

Tilman, D., May, R. M., Lehman, C. L., and Nowak, M.A. (1994). Habitat destruction and the extinction debt. *Nature* 371, 65-66.

Tilman, D., Fargione, J., Wolff, B., D'Antonio, C., Dobson, A., Howarth, R., Schindler, D., Schlesinger, W. H., Simberloff, D. and Swackhamer, D. (2001). Forecasting agriculturally driven global environmental change. *Science* 292, 281-284.

Toivanen, T., and Kotiaho, J. S. (2007). Burning of logged sites to protect beetles in managed boreal forests. *Conservation Biology* 21(6), 1562–1572.

Turner, I. M., Tan, H. T. W., Wee, Y. C., Ali Bin Ibrahim, Chew, P. T. and Corlett, R. T. (1994). A study of plant species extinction in Singapore: Lessons for the conservation of tropical biodiversity. *Conservation Biology* 8(3), 705-712.

Turner, E. C. and Foster, W. A. (2009). The impact of forest conversion to oil palm on arthropod abundance and biomass in Sabah, Malaysia. *Journal of Tropical Ecology* 25, 23-30.

Wikars, L-O. (1992). Skogsbränder och insekter. *Entomologisk Tidskrift* 113, 1-11 (in Swedish).

Wikars, L-O. (2002). Dependence on fire in wood-living insects: An experiment with burned and unburned spruce and birch logs. *Journal of Insect Conservation* 6, 1-12.

Wikars, L-O., Sahlin, E. and Ranius, T. (2005). A comparison of three methods to estimate species richness of saproxylic beetles (Coleoptera) in logs and high stumps of Norway spruce. *Canadian Entomologist* 137(3), 304-324.

With, K. A. and Crist, T. O. (1995). Critical tresholds in species' responses to landscape structure. *Ecology* 76(8), 2446-2459.

Östlund, L. (1993). *Exploitation and structural changes in the north Swedish boreal forest 1800-1992*. Dissertations in Forest Vegetation Ecology 4, Swedish University of Agricultural Science, Department of Forest Vegetation Ecology, Umeå.

Östlund, L., Zackrisson, O. and Axelsson, A-L. (1997). The history and transformation of a Scandinavian boreal forest landscape since the 19th century. *Canadian Journal of Forest Research* 27, 1198-1206.

# Acknowledgements

First I would like to show my biggest gratitude to my supervisors Joakim Hjältén, Jacek Hilszczański and Mats Dynesius, who have guided me through the process of becoming a real scientist. We have all worked well together and our student-supervisor relations have been relaxed and comfortable. Special thanks to Joakim, my main supervisor, who has been available up to 99.9% of the time. It has been a tremendous security to know that you've always been at hand if/when I‘ve needed help. I have learned a lot from you and I especially treasure our experiences from the conference-visit "down under" in Tasmania. Jacek, thanks for taking time visiting Umeå and sharing your entomology-specialist skills with me. Thank you Mats for always reading through the manuscripts so carefully, you have a real detective's eye for finding hidden errors.

Many thanks also to the rest of the "Dead wood-team"; John Ball, Roger Pettersson, Therese Johansson, Heloise Gibb and Kjell Danell. It has been an honour and very educational to work with so professional colleagues. Extra thanks to John, my like-minded Rioja-loving and personal gun-dealer friend, and my former master-work supervisor who's had a great deal in my choice of getting into the scientific world. And to always-happy Roger, thanks for all your help with bugs, literature (often from early 1900s), for all the fun teaching at TBE, and for all interesting discussions. We've had some good laughs.

This large-scale field study has required many long days of fieldwork and I want to thank all people that provided invaluable assistance being out there shedding blood, sweat and tears; especially my own two "field-slaves" Nina Stenbacka and Ferry Einarsson, but also Åke Nordström, Eric Andersson, Johan Nilsson, Christer Zackrisson, Claire Godel and Myriam Lamure. With admiration, I send particular thanks to Stig Lundberg, who has spent hours determining thousands of beetles. I am also grateful to Mark R. Shaw for verification and determination of parasitoids, Carl-Cedric Coulianos for valuable information on flat bug biology and to Wojtek Janiszewski for building the water drainage funnels. This study was possible by cooperation with the forest companies Holmen Skog, Sveaskog and SCA, who provided field sites, logs and maps. Special thanks to Kjell Johansson at Holmen in Björna. The study was financed by the Swedish University of Agricultural Sciences (grants to Kjell Danell and Stig Larsson), the Swedish Research Council for Environment, Agricultural Sciences and Spatial Planning (Formas), the Centre of Environmental

Research (Umeå), and the Kempe Foundation (grants to Joakim Hjältén) and Sveaskog (grants to Frauke Ecke).

I have met a lot of new friends at the Department of Wildlife, Fish and Environmental Studies and at SLU. I like the atmosphere at our department and I thank you ALL for wonderful parties and FRÖL-evenings. I also thank those of you who have showed interest in my work, reminded me of “fika” or just asked “how are you today”. It feels good to be among co-workers who look after each other. I especially thank all my PhD-colleagues and I have met some friends for life (hope you feel the same way). Wiebke and Henrik, my sister- and brother-in-arms, we’ve had a great journey with many memories, two ashore one to go. I especially want to thank you Wiebke for your friendship and for keeping us others active with beach volley and arranging nice dinners. Adjan (the “liquorice-monster”), you’re a really funny fellow and I appreciate the opportunities in taking part of your bird studies. With you three, among others, I also share some unforgettable moments from New Zealand. I thank Lars and Carin for arranging that fantastic course and trip. Lars, I’m also grateful for all the expertise help when it comes to birds. Jonas K., I will get two sets from you in badminton and I’m longing for that Vega Sicilia. Nils, you have been a complete breath of fresh air at the department and become a good friend, thanks.

I also want to thank the SLU hunting team, Åmlidens jaktklubb, for all the wonderful days in the wilderness and for your trust in me as hunting leader. My friend Pontus, thanks for dragging me out for fishing. Just being out there, hunting or fishing, recharges my batteries. Similarly, I thank “SLU-Innebandy”.

Finally, to my family, relatives and friends. Thanks for all your love, support and interest in my work. Mom and Dad, thanks for giving me a solid foundation to stand on in life and for our lovely home in Finland, where I’ve spent relaxing vacations with good food & wine, hunting and hot sauna-baths. And thanks for sharing your passion in nature with me. Dad, my best friend, we’ve really had some amazing hunts. I thank my surrogate-family Rosemaj and Bengt for making life in Umeå easier. Juha, it’s always fun chatting with you ; ). Last, but not least, my wife Nina who has put up with many lonely evenings and showed patience with my late working hours. I appreciate all your efforts in keeping our household floating, small things do matter you know. If I hadn’t met you, I probably wouldn’t have taken on this PhD-position. And Glimra, who always cheer me up when I get home. Love you all!!!

# Sammanfattning

I de boreala delarna av Fennoskandien har trakthyggesbruk och intensiv brandbekämpning resulterat i en dramatisk minskning av mängden och diversiteten död ved. Detta har försämrat livsvillkoren för den saproxyliska faunan (d v s arter knutna till död ved) och många av dessa arter är idag hotade. Det är därför ytterst betydelsefullt att vi snarast tar fram mer effektiva bevarande åtgärder för dessa arter, vilket kräver en bättre kunskap om deras krav på livsmiljö och deras överlevnad i det brukade skogslandskapet. I den här avhandlingen har jag studerat både de direkta och mer långsiktiga effekterna av skogsbruk på vedlevande insektssamhällen (skalbaggar, parasitsteklar och barkstinkflyn) genom att jämföra artrikedom, abundans och artsammansättning i hela successionsskalan (ålder) av existerande grandominerade skogar i norra Sverige. Min avhandling bidrar också med data på röd-listade skalbaggars substratkrav, barkstinkflyns respons på skogsbränder och komplementet av att använda olika fångstmetoder för att erhålla data på ovanliga och hotade arter.

Reservaten innehöll de mest intakta samhällena och de högsta tätheterna av vedlevande insekter och är således mycket viktiga som spridningscentra, speciellt för röd-listade arter. Avverkningsmogna brukade skogar var väldigt lika reservaten i avseende på artsammansättning, vilket indikerar höga naturvärden i dessa skogar. Överraskande nog, så återfanns många arter knutna till sena successionsstadier också i medelålders gallrade skogar. Detta visar att även dessa skogar kan utgöra lämpliga habitat för dessa arter om död ved görs tillgänglig i tillräcklig mängd och kvaliteter. I motsats, så visade sig unga ogallrade skogar ha en liknande artsammansättning som kalhyggen, och i dessa två beståndstyper återfanns det få röd-listade skalbaggar. Skogar som växer upp efter slutavverkning innehöll överlag lite död ved jämfört med äldre skogar, speciellt urskogs-reservaten. Mina resultat visar att mängden och diversiteten av död ved måste öka i det brukade skogslandskapet. Slutligen, fann jag att naturvårdsbränningar är nödvändiga för vissa arter, t.ex. pyrophila barkstinkflyn.

Fönster- och eklektorfällor fångade olika artsammansättningar av både röd-listade vedlevande skalbaggar och vedlevande parasitsteklar. Fönsterfällor gav ett bättre mått på den lokala artpoolen, medan eklektorfällorna gav mer detaljerad information om substratkrav, värd-parasit associationer och kläckningsperioder. För än mer precisa parasite-värd förhållanden rekommenderas avbarkning av stockar. M a o bör olika fångstmeoder noggrannt avvägas mot de specifika frågeställningarna i varje enskild studie.