Habitat Requirements of Saproxylic Beetles on Aspen

Implications for Preservation

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Habitat Requirements of Saproxylic Beetles on Aspen – Implications for Preservation

Abstract

In Fennoscandia, most of the forests have been under production management since the 19th or 20th century, which has resulted in decreasing amounts of dead wood (Coarse Woody Debris, CWD). Populations of many saproxylic (wood–dependent) species have declined because of the reduction of CWD. Forestry is currently trying to increase CWD amounts on clearcuts by green–tree retention. As a result of increased mortality of retained trees this can be expected to enhance CWD amounts on clearcuts. This thesis evaluates whether this practice increases diversity of saproxylic beetles inhabiting aspen. One study compares the habitat availability of aspen–associated beetles (beetles preferring aspen CWD over CWD from other tree species) in clearcuts and forests. A second study focuses on how occupancy (proportion of occupied habitat patches) and density of aspen–associated beetles is influenced by habitat patch size and habitat connectivity. A third study evaluates the contribution aspen CWD on clearcuts makes to total beetle diversity. The results demonstrate that retention of living aspen at clearcutting favours aspen–associated species. Increased tree mortality of retained trees generates more CWD on clearcuts compared with in forests. Thus, a significant part of the beetle populations can be expected to occur on clearcuts. The spatial distribution of the CWD influenced beetle occurrence. Both occupancy and density of aspen–associated beetles was generally higher in larger than in smaller habitat patches. Thus, priority should be given to retain large patches of living and dead aspen. A majority (93 %) of the saproxylic beetle species recorded from aspen CWD in this study was not aspen–associated, i.e. they prefer other tree species than aspen. Also when considering all of these species, clearcuts provide a valuable contribution for maintaining the biodiversity in managed forest landscapes. Species richness was as high in clearcut as in forest sites. In addition, species composition differed between the two stand types which mean that they to some extent are complimentary. The thesis also includes two methodological studies. In one study the efficiency of three different beetle sampling methods (bark sieving, emergence trapping and window trapping) were compared. In another study the aim was to find an efficient odour bait for sampling of flying saproxylic aspen–associated beetles.

Keywords: CWD, aspen, beetles, coleoptera, conservation, methods, habitat availability, patch size, exposure

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For all those who believed in me.

Jag kom, jag såg, jag sållade.

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 Lars–Ove Wikars, Erik Sahlin, Thomas Ranius (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.

II Erik Sahlin, Thomas Ranius (2009). Habitat availability in forests and clearcuts for saproxylic beetles associated with aspen. *Biodiversity and Conservation* 18(3), 621–638.

III Erik Sahlin, Leif Martin Schroeder. Importance of habitat patch size for occupancy and density of aspen–associated saproxylic beetles (submitted manuscript).

IV Erik Sahlin, Leif Martin Schroeder. Importance of stand type for saproxylic beetles on aspen – a comparison between clearcuts and forest stands (manuscript).

Papers I–II are reproduced with the permission of the publishers; Entomological Society of Canada (I) and Springer Verlag (II).

The contribution of Erik Sahlin to the papers included in the thesis was as follows:

Ideas: Together with supervisors for papers II, III and IV.

Field work: Main worker papers I, II, III and IV.

Identification of beetles: 80 % of the beetles in papers II, III and IV.

Analyses: Main analyser in paper IV, co–analyser in papers II and III.

Writing: Main author in papers II and IV, co–author in papers I and III.

Abbreviations

CWD Coarse Woody Debris, dead wood with a diameter over 10 cm

1 Introduction

1.1 Forest landscape in change

Boreal forest, the predominant forest type in Sweden, forms a belt across large parts of the northern hemisphere. In Fennoscandia, the forests are dominated by Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*). The most common deciduous trees are birch (*Betula* spp.), aspen (*Populus tremula*), goat willow (*Salix caprea*), and rowan (*Sorbus aucuparia*). Most of the boreal forest land in Sweden is owned by forest companies (Angelstam & Pettersson 1997).

Human activities, especially forest management and fire suppression, dramatically change the structure and dynamics of forests (Östlund 1993). In Fennoscandia, most of the forests have been under production management since the 19th or 20th century (Östlund *et al.* 1997; Kouki *et al.* 2001), which has resulted in decreasing amounts of coarse woody debris (CWD) (Linder & Östlund 1998). CWD is a key element for conservation of biodiversity and plays an important role in determining the structure and function of forests (Harmon *et al.* 1986). Surveys in Fennoscandian forests suggest that the volume of CWD has been reduced by 90–98 % owing to modern forestry practices (Siitonen 2001).

Populations of many saproxylic (wood–dependent) species have declined because of the reduction of CWD caused by forest management (Ehnström & Waldén 1986, Esseen *et al.* 1997, Gärdenfors 2000, Gärdenfors 2005, Jonsson *et al.* 2005). This has been suggested to lead to a regional extinction of more than 50 % of the original saproxylic species in managed forests in Fennoscandia (Siitonen 2001). CWD may be valuable for the saproxylic fauna at both clearcuts and forests, but there is a difference in species composition between these habitats (e.g. Sverdrup–Thygeson & Ims 2002). This could be due to differences between species in requirements regarding the sun exposure of the substrate (e.g. Martikainen 2001).

A large number of studies have assessed the CWD volumes in different forest types, or analysed the habitat requirements of saproxylic species (see Jonsson *et al.* 2005 for a review). Most of these are snapshot studies, revealing CWD volumes or species' occurrence patterns at a certain moment. With such an approach, it is easy to overlook the fact that CWD is a dynamic habitat that is created when trees die and deteriorated by decomposition or destroyed during forestry operations. For that reason there is a need for studies including CWD dynamics.

1.2 Biodiversity and aspen

In Fennoscandian boreal forest, aspen is one of the most important tree species for biodiversity; for instance, in Finland it harbours a higher proportion of critically endangered species than any other tree species (Tikkanen *et al.* 2006). A comparison between the Finnish and Russian Karelia showed that the beetle fauna associated with aspen was richer in Russia (Siitonen & Martikainen 1994). It was suggested that this was because in Russia, non–marketable trees have been left during logging, thus sustaining the continuity of large, dead aspen (Siitonen & Martikainen 1994).

Since aspen is the intermediate host for the pine rust fungus (*Melampsora pinitorqua*) (Mattila 2005), the species has been systematically eliminated from the managed forests in large parts of Fennoscandia (Kouki *et al.* 2004. In Sweden, aspen was killed with herbicides until prohibited around 1980.

During the last 20 years, forest companies have adopted new management methods in order to reduce the negative impact of forestry on biodiversity (Larsson & Danell 2001). One of these measures is green–tree retention at clearcutting. Aspen trees are often retained, which may be because wood from aspen is commercially less valuable than wood from Scots pine or Norway spruce (Jonsson *et al.*, subm. ms.) and because of its high value for biodiversity (Esseen *et al.*, 1997). Mortality of living trees retained after clearcutting is enhanced, mainly as a result of an increased risk for wind damages, resulting in a temporary increase in the amount of CWD the first years after clearcutting (Esseen 1994, Jönsson *et al.* 2007, Sahlin & Ranius 2009). It is important to evaluate the effect on biodiversity of these measures.

Aspen has an aggregated growth pattern because of its ability to generate asexually by suckering and as a consequence aspen CWD is spatially clustered in patches differing in size from single dead trees to large amounts of dead trees. This might influence the occurrence of aspen–associated species. A positive relationship between habitat patch size and occupancy may be caused by smaller and more isolated patches having higher local extinction rates and lower dispersal rates among patches (Hanski 1999). But it could also be an effect of pure habitat loss, i.e. that small habitat patches are in fact fragments of larger ones (the random sample hypothesis, Andrén 1996). In this case the density of individuals within patches will be, on average, the same in small and large patches. Consequently, species occurring at low densities may be absent from many smaller patches. Not only species occupancy, but also the density of individuals within patches may be positively related to patch size, i.e. there are true fragmentation effects (cf. Andrén 1996).

Three processes that may contribute to density – area relationships are: (1) The population density in small habitat patches might be lower than in big patches because the population in small patches may not reach carrying capacity as a result of high extinction risk. (2) Patch size *per se* may influence immigration and emigration rates. (3) The density of generalist matrix species may increase in smaller patches which may negatively affect habitat specialists.

1.3 Saproxylic beetles

Beetles (Coleoptera) are among the largest saproxylic taxa in Fennoscandia (Berg *et al.* 1994, Jonsell *et al.* 1998, Siitonen 2001). In Sweden, more than 1 250 beetle species are classified as saproxylic (Dahlberg & Stokland 2004), i.e., they depend on dead or decaying wood during some part of their life cycle (Speight, 1989). Of these, more than 300 species are redlisted (Gärdenfors 2005). Among the saproxylic beetles in Sweden, almost 500 species are solely dependent on deciduous trees (Dahlberg & Stokland 2004). Over 400 saproxylic beetles can be found on aspen CWD in Sweden, with 35 beetle species classified as dependent on aspen CWD (Dahlberg & Stokland 2004).

1.4 Methods for surveying saproxylic beetles

Several methods can be used to survey saproxylic beetles. Adult beetles and larvae can be collected under bark, either directly in the field (e.g. Väisänen *et al.* 1993, Siitonen & Saaristo 2000) or by bark sieving and subsequent extraction of the beetles in Tullgren funnels in the laboratory (e.g. Jonsell & Weslien 2003). When sieving and collecting insects under bark, larvae and adults inside wood may be overlooked. Emergence trapping is another method, which is done either by enclosing dead wood in situ (Owen 1989, Økland 1996, Lindhe & Lindelöw 2004) or by enclosing cut pieces of dead wood (Weslien 1992, Hammond 1997, Wikars 2002). This method can potentially sample everything anywhere in the wood or bark. Different kinds of window traps have been used to collect flying saproxylic beetles (e.g. Kaila 1993, Jonsell & Nordlander 1995, Økland 1996, Hammond 1997, Martikainen *et al.* 2000, Ranius & Jansson 2002). Window traps can collect large amounts of beetles but they do not only collect insects from specific dead wood objects, but they also collect flying insects associated with other substrates (e.g. Økland 1996, Ranius & Jansson 2002).

2 Aims of the thesis

The first aim concerns the suitability and efficiency of three different sampling methods for saproxylic beetles. The three compared methods were bark sieving, emergence trapping and window trapping. The methods were compared for different kinds of CWD substrates: sun–exposed logs, shaded logs and high stumps of Norway spruce. The methods were compared throughout the season.

The second aim was to find an efficient odour–bait for sampling of flying saproxylic aspen–associated beetles. Aspen–associated beetles are defined as species preferring CWD of aspen over CWD from other tree species. Such a bait would be an efficient tool for studies about relationships between habitat amount and beetle occurrence. The idea was to spread out baited traps in the study landscape randomly or in a grid and then analyse correlations between beetle catches and aspen occurrence on a large scale using aerial photographs (assuming that there is a spatial correlation between living aspen and aspen CWD). This was to circumvent the problems of finding suitable study sites and to be able to set up experiments also in areas without or with very little aspen.

The third aim was to compare the habitat availability for aspen–associated beetles in forests and clearcuts. The current practice of retention of living aspen at clearcutting can be expected to result in enhanced amounts of aspen CWD on clearcuts. It is important to evaluate the effect of this measure on biodiversity. By combining information about the beetles substrate preferences with a model of CWD dynamics, changes in habitat availability over time can be predicted.

The fourth aim was to study how occupancy and density of aspen–associated saproxylic beetles is influenced by habitat patch characteristics and habitat connectivity. Aspen has an aggregated growth pattern which results in patches of aspen CWD. Knowledge about the response of the beetle fauna to fragmentation would be useful as a base for decisions about which kind of aspen stands that are most valuable for preservation of biodiversity.

The fifth aim was to evaluate the contribution that aspen CWD on clearcuts makes to total richness of beetles. Most saproxylic species utilize CWD from more than one tree species. Thus, efforts to increase the amount of aspen CWD on clearcuts (e.g. retention of living aspen) will not only affect species confined to or preferring aspen but also a large number of other species.

2.1 Specific aims of the different studies.

Compare three different methods (bark sieving, emergence trapping and window trapping) used in surveying saproxylic beetles in terms of number of recorded species and species composition. (I)

Develop an attractive odour–bait for saproxylic aspen–associated beetles.

Predict the habitat availability for aspen–associated saproxylic beetles in forests and on clearcuts using a model of CWD dynamics and data on the species substrate preferences. (II)

Study the importance of habitat patch characteristics and habitat connectivity for aspen–associated saproxylic beetles. (III)

Evaluate the importance of aspen CWD on clearcuts for species richness of saproxylic beetles in managed forest landscapes. (IV)

3 Methods

3.1 Study landscape

All of the studies were carried out in a managed forest landscape north–west of Delsbo in the province of Hälsingland, central Sweden (62°N, 13° E), which is situated in the mid–boreal vegetation zone (Ahti *et al.* 1968). The forest is dominated by Norway spruce (*Picea abies* Karst.) and Scots pine (*Pinus silvestris* L.). The study landscape covers 42 000 hectares, of which 36 500 hectares are productive forest land and 751 hectares are protected forest in four reserves. One forest company (Holmen Skog AB) owns almost all the land and therefore the management regime is similar across the entire landscape. Since 1998, the FSC–standard (Anonymous 2000) is followed. During 1995–2000, all living aspen trees were retained when possible at clearcutting. After 2000, this green–tree retention was mainly limited to retaining groups of living trees.

In May 2002, 27 500 hectares were photographed using infrared aerial photography. The photographs were taken just after leaf–flush, to enable clear identification of aspen.

3.2 Study sites

The thesis is based on three different field studies: (1) one for paper I, (2) one for the study of beetle attraction to aspen CWD volatiles (not included in papers) and (3) one for the papers II, III and IV.

In 2001, two study sites situated 14 km from each other (62°02'25"N, 16°31'53"E, and 62°06'47"N, 16°08'11"E) were selected for the method study (I). The study included both closed canopy forest and clearcuts at each site.

The attraction study was done in 2002 on a five–year–old clearcut situated in the central part of the study landscape.

The field study, on which papers II, III and IV are based, included 36 clearcut sites (Fig. 1) and 26 forest sites (Fig. 2) with aspen CWD.

Figure 1. Clearcut with green–tree retention patch of aspen.

Figure 2. Aspen forest with CWD.

These sites were selected in two different ways. In 2002 we selected 17 clearcuts randomly from a pool of clearcut sites supplied by the forest company. In 2003 and 2004 we randomly selected 19 clearcut sites and 26 forest sites containing mature (height > 20 m) aspen trees based on the interpretation from the photographed area (Fig. 3). All clearcut sites had been cut during the last 15 years. The size of studied clearcut sites was defined as that of the forest stand cut during final felling. The minimum size of a clearcut site was 2.7 ha, and the maximum 46.8 ha (mean: 18.7 ha). Forest sites were patches in the forest landscape with occurrence of aspen, identified and delimited from the aerial photographs. According to data from the forest company, the youngest studied forest site was 57 years and the oldest 156 years (mean: 104 years). Among forest sites, the crown cover of aspen varied between 2 % and 85 % (mean: 37 %). The minimum size of a forest site was 0.2 ha, and the maximum 15.2 ha (mean: 3.2 ha). We did not use sites of the same type (forests / clearcuts) that were closer than 500 m from each other.

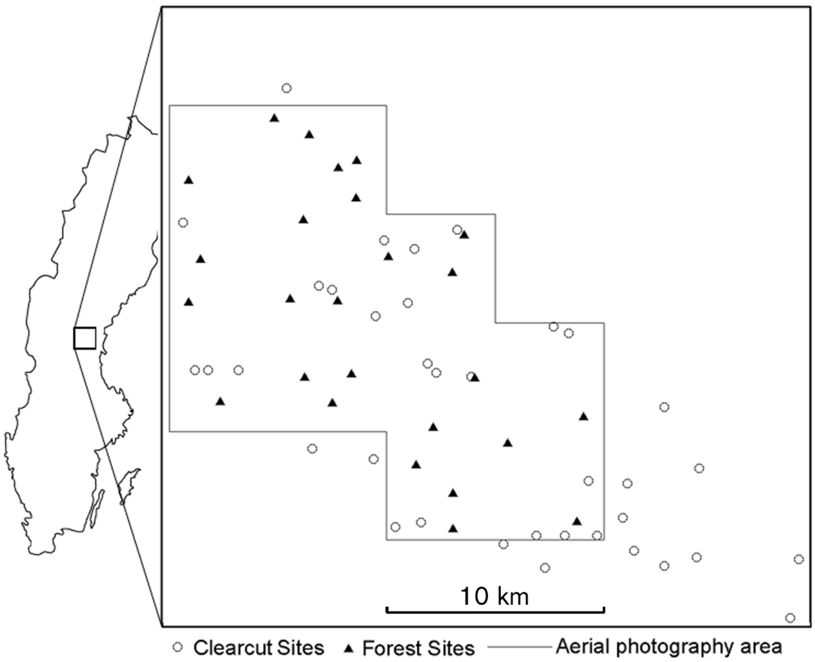

Figure 3. Locations of study sites for paper II, III and IV in the province of Hälsingland in Sweden.

3.3 Measurements and sampling

3.3.1 The method study (I)

Three sampling methods were used on the same substrates; emergence trapping, sieving and window trapping.

We sampled five high–stumps, five shaded logs, and five sun–exposed logs in each one of the two separate study sites. All sampled trees had been dead between three and ten years. The primary successional bark beetles had left the trees but the bark was still intact.

In the emergence trapping we enclosed cut stem sections in insect–impenetrable cloth. In sieving, each sample consisted of 0.5 m^2 bark that was carefully peeled off, fragmented and placed in a sieve with 8 mm mesh size together with all loose material between the bark and wood, and shaken for at least five minutes. Sieved samples were extracted in Tullgren funnels (30 cm wide, 8 mm mesh size). The trunk window traps consisted of a 15 x 20 cm transparent plastic sheet nailed perpendicular to the wood, and a 12 x 9 cm wide and 6 cm deep aluminum container fastened tightly to the substrate under the sheet.

The sampling started on May 15th and lasted until October 1st. Samples were repeatedly taken from the same trees with two to four week intervals using all three methods. We determined most adult beetles to species and beetle larvae at least to family. Taxa not determined to species were excluded from analyses of species richness and similarity.

3.3.2 The attraction study (not included in the papers)

The field experiment was done from May to October 2002. Five treatments were included: 1) ethanol (70 %) with a simulated log; 2) ethanol (70 %) mixed with finely ground, fermented aspen bark with a simulated log; 3) simulated log (control); 4) ethanol (70 %) with a freshly cut aspen (*Populus tremula*) log; and 5) freshly cut aspen log. The simulated logs were constructed from 15 cm ø black plastic drainage pipes that were cut to a length of 1.6 m. Aspen logs were cut to similar length as the simulated logs. The simulated logs and aspen logs were positioned standing vertically. Beetles were caught with trunk–window traps, using propylene glycol and water in a 50:50 % mixture as preserving media. The trunk–window traps, constructed from a 15 x 20 cm plastic window with a 18 x 18 x 10 cm plastic container fastened underneath, was then nailed to the log (simulated or real) at 1.3 m above ground (Fig. 4). Attractant dispensers were attached to the right side of the plastic window. The dispensers had four 3 mm diameter holes drilled in the lid to allow a limited evaporation of volatiles, and they were all refilled three times during the season (the first three emptyings). The different treatments were deployed in a block experiment design with 30 m spacing between treatments. The experiment included 10 blocks. The traps were emptied four times throughout the season. All caught beetles were identified.

Figure 4. Two of the different treatments used in the attraction study; a raised, freshly cut aspen log with ethanol (treatment 4) and a simulated log with ethanol (treatment 1).

3.3.3 Studies II, III and IV,

During 2002–2004, we surveyed CWD of aspen and living aspen trees at our 62 study sites. Each site was surveyed once. All aspen CWD with a diameter ≥ 10 cm was recorded. For standing CWD, the minimum height was 0.5 m.

For each CWD object we measured diameter, length (height for snags), decay stage and percentage of surface area covered by bark (in 10 % classes). Diameter was measured at breast height (1.3 m), or for fallen trees at 1.3 m from the basal end. If the length of the CWD object was less than 3 m, the diameter was measured in the middle. The decay stage of CWD was measured using the same method as Siitonen & Saaristo (2000). If more than one decay class was present on a single object, we estimated the average for the object.

Beetles were sampled on up to ten CWD objects per site by sieving (see the section on beetle sampling below). The sampled bark (0.5 m^2) was classified into one or several of ten bark types according to a system developed during the first year of study. We based this classification on colour, moisture, odour and structure of the bark

To estimate aspen mortality, the number of living aspen trees was counted on the clearcut sites and the amount of living bark area was estimated by multiplying the number of trees with the average bark area per tree. Diameter and height of ten randomly selected, living aspen trees was measured at each clearcut site. The bark area of each tree was calculated by assuming the shape of a cone. For a more detailed description of the CWD estimates see Sahlin & Ranius (2009). Since no living trees were measured in forest sites, we used data from the Swedish National Forest Inventory. According to that, tree mortality of all deciduous trees in forest (thus mainly birch and aspen) was 0.58 % / year (Jonsson *et al.* subm. ms.). This is within the range of the average annual growth–independent mortality rate of aspen in Lithuania, which has been estimated to 0.5 % and 0.9 % (in permanent experimental plots, and forest monitoring plots, respectively; Ozolincius *et al.* 2005). We assumed mortality in young forests (15–30 years) to be an average of the mortality on old clearcuts and in mature forests.

At the 62 study sites where CWD was surveyed, we also assessed the beetle fauna (Fig. 5).

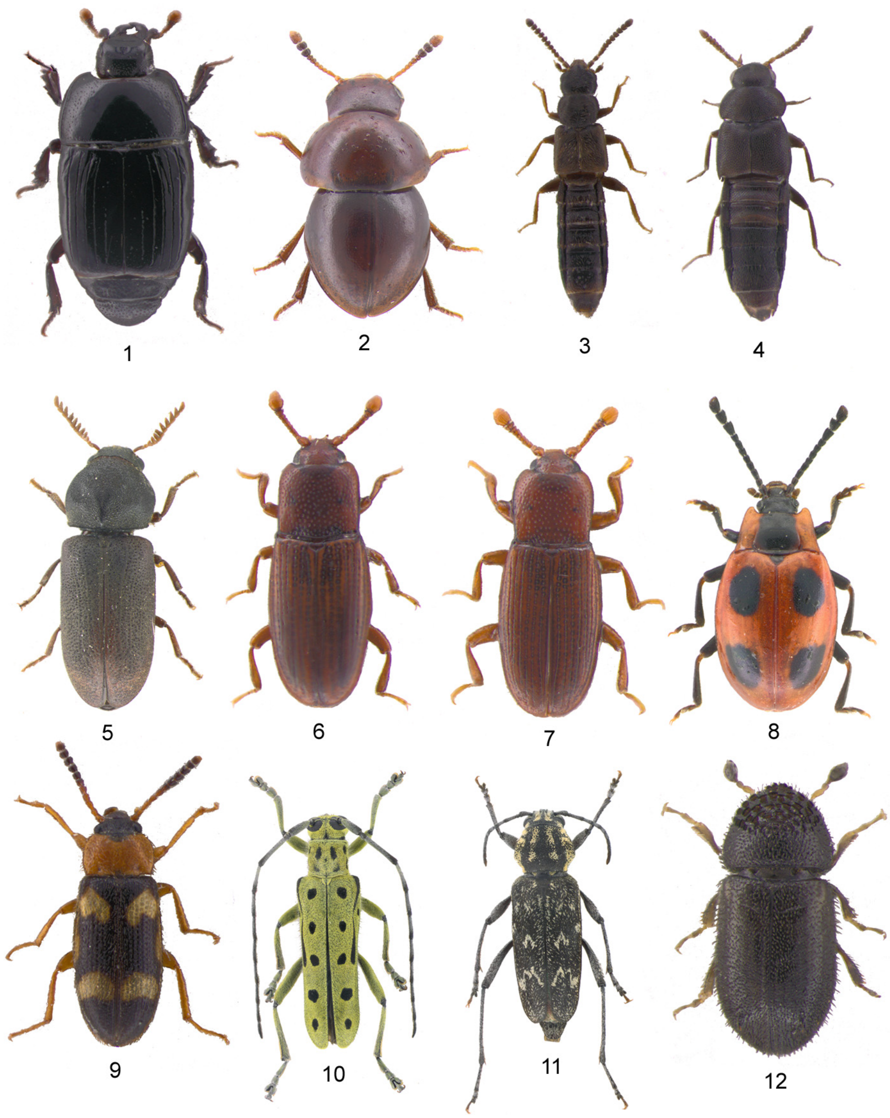

Figure 5. Selection of aspen–associated beetles caught in the studies.
1. *Platysoma deplanata* (3.5 mm), 2. *Agathidium pisanum* (3 mm), 3. *Homalota plana* (2.7 mm), 4. *Cyphaea curtula* (1.7 mm), 5. *Ptilinus fuscus* (4.5 mm), 6. *Cerylon ferrugineum* (2 mm), 7. *Cerylon deplanatum* (1.8 mm), 8. *Endomychus coccineus* (5 mm), 9. *Mycetophagus fulvicollis* (4.5 mm), 10. *Saperda perforata* (16 mm), 11. *Xylotrechus rusticus* (16 mm), 12. *Trypophloeus bispinulus* (1.5 mm)

We used direct sampling of aspen CWD to ensure that the recorded beetles were actually residents of the site, and to be able to record the substrate requirements of the species. Two methods were used: 1) Recording presence of emergence holes and larval galleries of *Ptilinus fuscus*, *Saperda perforata* and *Xylotrechus rusticus* on all aspen CWD objects at every site. A total of 1542 CWD objects were inspected (935 on clearcuts, 607 in forests). These species were chosen because their galleries are readily identifiable in the field (Fig. 6). 2) Sieving of 0.5 m² bark on ten randomly selected aspen CWD objects per site for all species except *P. fuscus, S. perforata* and *X. rusticus*. A total of 351 CWD objects (203 on clearcuts, 148 in forests) were sieved (Fig. 7).

Figure 6. Larval galleries of *X. rusticus* (left) and *S. perforata* and *P. fuscus* (right). *X. rusticus* makes winding galleries that carves the outermost parts of the wood, *S. perforata* makes the large, oval pupal chambers in the wood, *P. fuscus* makes the smaller drill–like holes.

Figure 7. Sieving of a lying, dead aspen. The white sheet is used when gathering bark fragments and for transferring them into the sieve

These CWD objects were also used for description of the bark types (see above). Whenever possible, we took five samples from standing and five from lying CWD. Samples were taken at 1.3 m, or in the case of lying CWD, 1.3 m from the basal end. At sites with less than ten suitable aspen objects, we sampled all available CWD objects. Sieving was done in late September to early October in 2002, 2003 and 2004. The number of beetle species under the bark reaches its maximum in spring and autumn (Wikars *et al.* 2005). Sieved samples were extracted using Tullgren funnels (30 cm wide, 8 mm mesh size) (New 1998). 60 W light bulbs were used as heat and light sources, and extraction lasted for at least 24 hours. Large or very wet samples were divided into two or three funnels.

4 Results and discussion

4.1 A comparison of three methods to estimate species richness of saproxylic beetles (Coleoptera) in logs and high stumps of Norway spruce (I)

We found that the relationship between the type of dead wood and species richness was statistically significant when we used bark sieving and emergence traps, but not when we used window traps. It is impossible to ascertain whether beetles collected with window traps are related to the type of dead wood on which they are found and, therefore, such traps are less useful in studies of specific substrates. The yield from sieving was highest in spring and autumn, whereas species richness in window trap samples peaked in June and July and that in emergence traps peaked from May to July. With emergence traps we collected, on average, about twice the number of species over the whole season as we did by sieving on a single occasion in the spring. Both emergence trapping and sieving reveal what is present in individual pieces of dead wood, but these methods sample partly different faunas.

All methods have their advantages and disadvantages, and the preferred method depends on the resources available and the aim of the study. The aim of the sampling should always determine the method used. If the aim is to yield a species list as complete as possible from an area, window traps are useful, especially in combination with other methods. If the goal is to evaluate how useful different substrates are, it is better to use emergence traps or sieving.

4.2 Attraction of aspen–associated insects to aspen volatiles.

Many earlier studies have shown that saproxylic insects are attracted to volatiles released from their breeding material (e.g. Dunn et al. 1986, Schroeder 1987, Schroeder & Lindelöw 1989, Dunn & Potter 1991, Allison et al., 2004). Most of these studies concern species breeding in early decay stages of conifers. Less is known about the chemical ecology of species utilizing more decayed CWD and species breeding in CWD from deciduous tree species. The aim of this experiment was to test if aspen–associated beetles (species preferring aspen) could be attracted to volatiles from aspen CWD. We also included ethanol in the experiment because it has been demonstrated to attract many species, either alone or in combination with more host–specific volatiles (e.g. Schroeder & Lindelöw 1989, Allison et al. 2004). Ethanol is a natural byproduct of anaerobic respiration and is released from stressed, dying and dead trees.

Only a few individuals of aspen–associated beetle species were caught in the experiment (Table 1). Thus, for most species it was not possible to evaluate if they are attracted or not. For only one of the species (*X. rusticus*) a significant effect of treatment could be demonstrated. Almost all individuals were caught on aspenlog + ethanol. As a result of low catch rates, we decided to abandon the approach with baited traps in favour of more direct sampling methods.

Table 1. *Total number of individuals caught in the five treatments (10 replicates per treatment) of aspen–associated saproxylic beetles. P–values are given for treatment effect for species caught in more than 10 individuals (Friedman test). Multiple comparisons were conducted for species with a P–value < 0.05. Treatments with the same letter are not significantly different at the P = 0.05 level. EtOH = Ethanol.*

	Treatment					
Species	Pipe	Pipe + EtOH	Pipe + Aspen Extract	Aspenlog	Aspenlog + EtOH	P
Rhizophagus cribratus	0	1	0	0	0	–
Trypophloeus bispinulus	0	0	0	0	1	–
Cyphaea curtula	0	1	0	0	1	–
Cerylon deplanatum	0	0	0	1	1	–
Platysoma deplanatum	0	1	1	1	2	–
Homalota plana	0	0	0	3	4	–
Endomychus coccineus	4	4	0	0	0	–
Cerylon ferrugineum	3	0	5	2	5	0.227
Mycetophagus fulvicollis	1	6	3	4	4	0.481
Xylotrechus rusticus	0^{A}	1^{A}	1^{A}	2^{A}	13^{A}	0.007

4.3 Habitat availability in forests and clearcuts for saproxylic beetles associated with aspen (II)

In this study, the habitat availability for beetles associated with aspen CWD was predicted for forests and clearcuts with a model of CWD dynamics. Habitat requirements of eight beetle species (*Agathidium pisanum*, *Cerylon ferrugineum*, *Cyphaea curtula*, *Endomychus coccineus*, *Homalota plana*, *Mycetophagus fulvicollis*, *Ptilinus fuscus* and *Xylotrechus rusticus*) were obtained from their occurrence patterns in different types of CWD objects in forest and on clearcuts. Three species were more frequent in forest and three at clearcuts. The frequency of five species increased with increasing girth of the CWD. Three were more frequent on standing CWD, and two on lying CWD. From the same study area, we also obtained field data on the recruitment of aspen CWD (i.e. tree mortality) and amounts of different types of CWD. Annual tree mortality of aspen was higher for retained aspen trees on recent clearcuts (6.3 %) compared with older clearcuts (1.1 %). For all species, the habitat availability was higher on clearcuts, because enhanced tree mortality increased the amount of recently dead CWD. As a conclusion, green–tree retention of aspen is a conservation effort that is beneficial for species associated with aspen CWD.

4.4 Importance of habitat patch size for occupancy and density of aspen–associated saproxylic beetles (III)

In this study we analyse the importance of habitat patch size and other patch characteristics, and habitat connectivity for the occurrence of saproxylic beetles associated with aspen. First, we demonstrate a significant positive relationship between habitat patch size, estimated as area bark on aspen CWD, and occupancy of aspen–associated beetle species. In contrast, there was no significant relationship between habitat connectivity and occupancy. Second, we test if the relationship between patch size and occupancy can be explained by the random sample hypothesis, i.e. that the beetle density is the same in large as in small habitat patches, or if the alternative hypothesis, i.e. that true fragmentation effects explain the positive relationship between patch size and occupancy, is valid. This is done by analysing the relationship between habitat patch size and proportion of colonised aspen CWD objects or beetle densities (individuals per m^2 bark). Third, we test if the densities of aspen–associated species and matrix species are related to habitat patch area.

Six of nine aspen–associated species, *Xylotrechus rusticus*, *Ptilinus fuscus*, *Mycetophagus fulvicollis*, *Cyphaea curtula*, *Homalota plana* and *Endomychus coccineus*, showed a positive significant relationship between habitat patch size and occupancy. For all these species, except *C. curtula*, there was also a significant positive relationship between patch size and density. Thus, we could reject the random sample hypothesis and demonstrate that the occupancy – patch area relationship was a result of a true fragmentation effect. Also total richness of aspen–associated species was positively related to habitat patch size. Geographic connectivity, measured as crown cover of living aspen in the surrounding landscape, was not significantly related to occupancy. Species not defined as aspen–associated constituted a significantly larger proportion of the total density of saproxylic beetles in smaller habitat patches than in larger patches.

Only a few earlier studies have explored the relationship between habitat patch size and the proportion of objects occupied by saproxylic insect species within patches. In a study by Ranius (2002, see also Ranius & Fahrig 2006) the percentage of occupied hollow oak trees increased with increasing number of hollow oaks per stand for three (*Osmoderma eremita*, *Elater ferrugineus* and *Tenebrio opacus*) of eleven studied species. In a study by Komonen *et al.* (2000) the proportion of fruiting bodies of the fungus *Fomitopsis rosea* colonised by the moth *Agnathosia mendicella* was significantly lower in fragments of old–growth spruce swamp forests than in large continuous stands. In contrast, there was no relationship between storm gap size and percentage of storm–felled spruces per gap colonised by the bark beetle *Ips typographus* in two different studies (Eriksson *et al.* 2005, Schroeder in press).

This study shows that the proportion of occupied objects and density of aspen–associated beetle species increases with habitat patch size. It also indicates that the current habitat amount is too low for long term survival of at least the strictly aspen–associated species. Thus, efforts in the managed forest should be directed towards creating larger patches of living and dead aspen trees and to increase the amount of aspen at the landscape level. Living aspen trees in such patches should be retained during thinning and clearcutting operations and care should be taken not to destroy already existing aspen CWD.

4.5 Moose browsing on aspen CWD (not included in papers)

In the course of the CWD inventories, it was discovered that moose (*Alces alces*) had stripped the bark from some CWD objects and therefore we decided to quantify the amount of bark removed by moose. The amount of bark removed was estimated in 10 % classes. This was done simultaneously with the rest of the CWD measurements. Bark stripping by moose was only detected on CWD objects belonging to decay stages 1 and 2 and almost exclusively on lying CWD objects on clearcuts. Of 72 lying CWD objects on clearcuts belonging to decay stage 1, 32 (44 %) were stripped by moose (resulting in a 17 % reduction in total bark cover), while of 18 standing objects none were browsed by moose. Of 494 lying CWD objects belonging to decay stage 2 on clearcuts, 57 (12 %) were stripped (resulting in 8 % reduction in total bark cover), while of 147 standing objects only one (0.7 %) was stripped. There was no significant relationship between within–patch total mantle area on lying CWD objects and percentage of total mantle area that had been stripped by moose for neither decay stage 1 or 2. In forest stands no bark stripping was recorded on the 15 CWD objects (two lying, 13 standing) of decay stage 1 while of 174 lying objects of decay stage 2, four (3 %) were stripped and of 187 standing objects one (0.5 %) was stripped.

Bark stripping by moose considerably reduced the habitat amount for the aspen–associated species on clearcuts. Almost 20 % of the bark on lying fresh CWD was removed by moose. All the aspen–associated species, except *P. fuscus*, colonise CWD with bark. *P. fuscus*, which colonises CWD without bark, almost exclusively reproduces in standing CWD which was almost unaffected by moose. The lower occurrence of bark stripping on more decayed CWD objects can be partly explained by difficulties to recognise moose stripping after a longer period of time. The much lower number of affected CWD objects in forest can be a result of (i) a higher ratio of trees that die standing (and thus are unsuitable for moose when they fall down), and (ii) a lower moose browsing pressure in forests than on clearcuts.

Moose browsing affects aspen CWD in several ways; feeding on bark on dead aspen which reduces habitat amounts of aspen beetles and browsing on young aspen which threatens the long–term continuity of aspen. Jalkanen (2001) showed that more than 20 % of aspen saplings were damaged by moose browsing. Browsing by moose can effectively delay aspen growth, thereby in the long term reducing or even preventing recruitment of aspen CWD (Ingelög, T. 1987, Angelstam et al. 2000, Kouki et al. 2004). Bark stripping in combination with browsing of saplings indicates that the moose may be a serious threat to aspen–associated insects in Fennoscandia today.

4.6 Importance of stand type for saproxylic beetles on aspen: a comparison between clearcuts and forest stands (IV)

In this study we compared the occurrence of saproxylic beetles on aspen CWD on clearcuts with the occurrence in managed forest. The study was done at the stand level, i.e. each sampled clearcut and forest stand constitutes one replicate.

The questions addressed are: 1) Do qualities of dead aspen wood differ between clearcut and forest sites? 2) Does species richness and assemblage composition of saproxylic beetles on aspen differ between clearcut and forest sites? 3) Does occupancy and density of individual saproxylic beetles on aspen differ between clearcut and forest sites?

There was no significant difference in rarefied species richness between forest and clearcut sites, but species composition differed significantly between the two stand types. This result is in accordance with most earlier similar studies in which species richness and composition of saproxylic beetles has been compared between clearcuts and forest stands for both conifer and deciduous tree species (Table 2).

Table 2. *Overview of the results of nine earlier studies that have compared species richness and species composition of saproxylic beetles between clearcut and forest sites of the same tree species. In the studies clearcuts and forest stands are replicates except for the study by Sverdrup–Thygeson & Ims (2002) in which the sampled locations are spread out over an area of 1 500 ha. All studies were conducted in Fennoscandia except Webb et al. (2008) which was conducted in Canada. The studies using traps have either mounted the traps on CWD objects (denoted window traps on CWD in the table) or used free traps placed in the two stand types. Some of the studies include other stand types than compared in this table (forest stands of other tree species, young forests, burnt sites or different retention levels).*

Study	Method	Habitat/Sieved CWD	Species richness	Species composition
Kaila et al., 1997	Window traps on CWD	White rotted birch	No difference	Different
Sippola et al., 2002	Window traps	Pine	No difference	Different
Sverdrup–Thygeson & Ims, 2002	Window traps on CWD	Aspen	No difference	Different
Hyvärinen et al., 2005	Window traps	Pine	Higher on clearcuts	Different
Gibb et al., 2006	Eclector traps	Spruce	No difference	Different
McGeoch et al., 2007	Sieving	Pine, Spruce Birch	Higher on clearcuts	Different
Djupström et al., 2008	Sieving	Spruce	No difference	Different
Lindbladh et al., 2008	Sieving	High stumps of spruce	No difference or lower on clearcuts	Different
Webb et al., 2008	Funnel traps	Aspen	No difference	Different

Ten of 30 evaluated species showed a significant difference in occupancy between forest and clearcut sites. Six species occupied a higher proportion of forest sites while four species occupied a higher proportion of clearcut sites. For only two species there was a significant difference in density between occupied forest and clearcut sites and for both these the density was higher on clearcuts.

Mean diameter and decay stage of aspen CWD differed between clearcut and forest sites. The larger diameter in clearcut sites could be explained by the fact that prior to clearcutting these stands were mature. The on average somewhat younger decay stage in clearcut sites should mainly be an effect of the increased tree mortality in the first years following cutting.

The results of the present and earlier similar studies demonstrate that CWD on clearcuts provides a valuable contribution for maintaining the biodiversity in managed forest landscapes. In similar earlier studies, species richness of beetles was as high on clearcuts as in forest sites. In addition, species composition differs between the two stand types which mean that they to some extent are complimentary.

4.7 Characteristic scale of response to habitat amount at the landscape scale (not included in papers)

With the computer program FOCUS 2.0 (Holland *et al.* 2004, Colwell 2005) the characteristic scale of response to habitat amount (expressed as percentage of crown cover of living aspen) was calculated for each one of the aspen–associated species. This was done by using circular buffers around the focal patches (47 forest and clearcut sites) from 250 m up to a scale of 3 000 m radius. Only patches with at least 60 % of the buffer within the photographed area were included in the analysis. The Focus program performs multi–scaled species–habitat regressions with a resampling procedure in which only sites with non–overlapping bufferzones are selected. The analyses were set to 100 iterations and the maximum number of plots per iteration was 17 (no duplicate samples). A distance matrix was created using Hawth's Analysis Tools for ESRI's ArcGIS (2.02). The P–values for Pearson correlation coefficients were obtained using Bluman (1997). Percentage habitat was regressed against the mean proportion of colonised CWD objects for the three species sampled by presence of galleries and against mean densities per m^2 bark for the six species sampled by sieving.

Seven of nine aspen–associated species showed a single peak for the model fit between beetle density (species sampled by sieving) or proportion of colonised CWD objects (species sampled by presence of galleries) and habitat amount (crown cover of living aspen) in the surrounding landscape (Fig. 8). Based on the maximum model fit the scale of response was 250 m for *C. ferrugineum*, 500 m for *A. pisanum* and 750 m for *C. curtula*, *E. coccineus*, *P. fuscus*, *X. rusticus* and *S. perforata*. None of the relationships were significant. One species, *C. curtula*, was close to significant (positive correlation coefficient at P = 0.06, 15 d.f.). At their characteristic scale of response all the seven species occurred in habitat patches with less than 0.5 % of habitat in the surrounding landscape.

In an earlier study the strongest response of 12 species of saproxylic cerambycid beetles to forest cover in the surrounding landscape differed from 20 to 2 000 m (Holland *et al.* 2004). Franc *et al.* (2007) demonstrated a positive relationship between species richness of oak–associated saproxylic beetles and area of oak dominated woodland key habitats within 1 000 m.

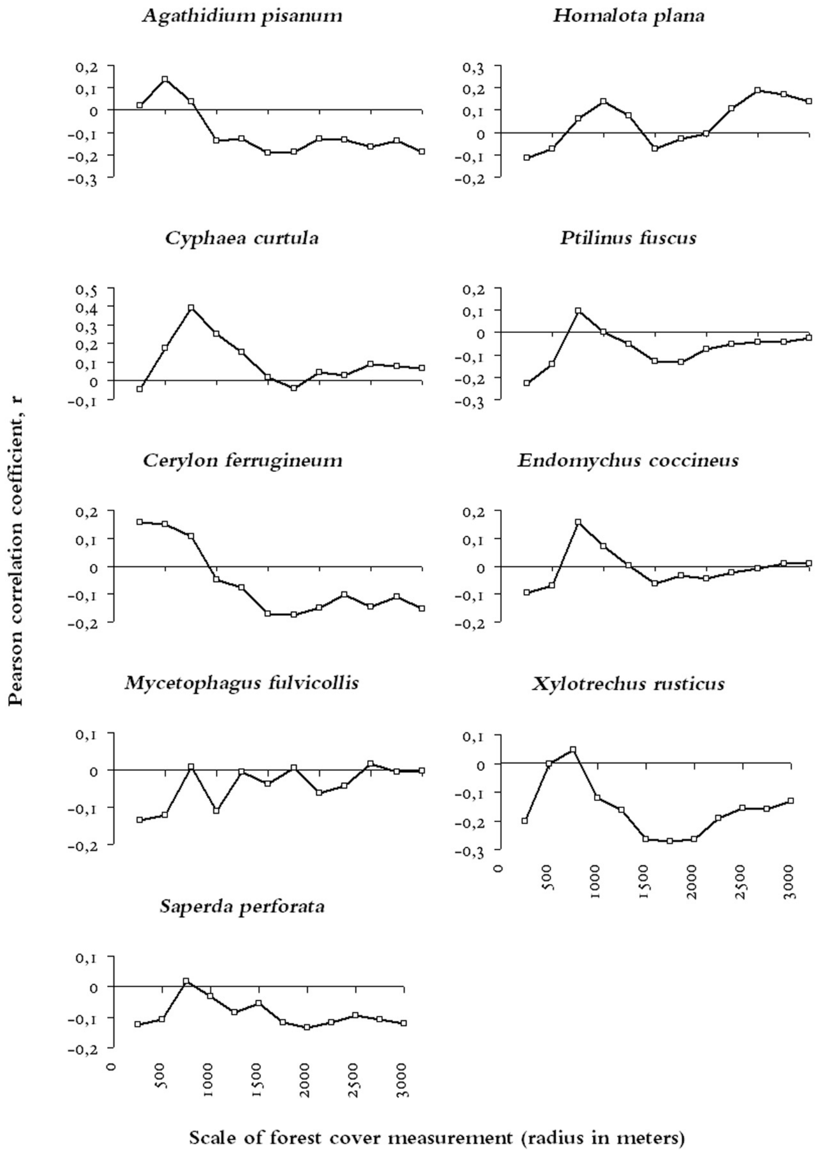

Figure 8. FOCUS program output showing model fit (Pearson correlation coefficient) between aspen crown cover and the mean proportion of colonised CWD objects for the three species sampled by presence of galleries and against mean densities per m^2 bark for the six species sampled by sieving.

5 Main conclusions and future research

This thesis has demonstrated that green–tree retention of aspen on clearcuts favours aspen–associated saproxylic beetles. Increased tree mortality of retained trees generates more CWD on clearcuts compared with in forests. Thus, a significant part of the beetle populations can be expected to occur on clearcuts. Also other ways to increase CWD amounts on clearcuts, like leaving dead aspens at thinning and final cuttings, and by being more careful not to destroy lying CWD during forestry operations, should be encouraged.

The spatial distribution of the CWD influenced beetle occurrence. Both occupancy (proportion of occupied habitat patches) and density of aspen–associated saproxylic beetles was generally higher in larger than in smaller habitat patches. This demonstrates that the species are negatively affected by habitat fragmentation, which means that large patches with aspen CWD produce more aspen–associated beetles per unit CWD than small patches. Thus, priority should be given to retain large patches of living and dead aspen and also to increase patch size of smaller patches if possible. Living aspen trees in such patches should be retained during thinning and clearcutting operations and care should be taken not to destroy already existing aspen CWD, in particular during scarification.

Another factor to consider is the density of moose. Moose negatively affects aspen–associated saproxylic species in two ways: (1) by feeding on bark on newly dead aspen trees and thereby reducing habitat amount and (2) by threatening the long term continuity of mature aspen trees by browsing on young aspens. At high densities of moose, fencing of aspen stands may be one option to decrease these negative effects.

A majority (93 %) of the saproxylic beetle species recorded from aspen CWD in the aspen studies (II, III and IV) was not aspen–associated, i.e. they prefer other tree species than aspen. If considering all of these species, clearcuts provide a valuable contribution for maintaining the biodiversity in managed forest landscapes. In the present and similar earlier studies, species richness of saproxylic beetles has been demonstrated to be as high in clearcut as in forest sites. In addition, species composition differs between the two stand types which mean that they to some extent are complimentary.

The results from this thesis indicate that the current habitat amount in the study landscape is too low for long term survival of at least the strictly aspen–associated species (i.e. species dependent on aspen CWD). Thus, in future studies it would be interesting to contrast the occurrence of such species in a number of landscapes with different amounts of aspen. Such a comparison may provide insight about the habitat amount that is needed at the landscape level for preservation of this fauna.

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