

# Long and short term effects of stump harvesting on saproxylic beetles and ground flora

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## Abstract

Research on the effects from forest management on biodiversity has been going on for decades but still there are many questions unanswered. With every introduction of a new forestry method there is risk for increased pressure on biodiversity.

The harvesting of low stumps left after final harvesting is a relatively new method used in forestry. I therefore investigated the importance of low stumps for saproxylic (wood living) species by comparing the species richness, abundance, and species assemblages of beetles in low stumps with the levels in high stumps and logs. Furthermore, I also investigated the long-term effects from stump harvesting on this group of species. I used window traps to collect beetles in young forests that had been stump harvested 25 years prior to the study and compared these stands with stands of the same age that had not been stump harvested. I also wanted to investigate the short-term effects from stump harvesting on the ground flora. This was done by comparing the plot frequency of all bryophytes and vascular plants found on stump harvested clear-cuts with clear-cuts that had not been stump harvested.

Low stumps on clear-cuts were proved to constitute important habitat for wood living beetles and they produced as many species and individuals of saproxylic beetles as logs and high stumps. Individual species showed preference for certain substrates. For example, the saproxylic fungivore *Enicmus rugosus*, was mostly found on low stumps. The overall impression after comparing the three substrate types was that low stumps might be an underestimated source of habitat for wood living insects. The long-term experiment indicated that effects of stump harvesting may last two and a half decades on certain groups of beetles. However, the effects from the surrounding landscape explained the patterns in beetle occurrence better than stump harvesting did. Results from the study of short-term effects on the ground flora showed that the effects from stump harvesting were limited to common species of bryophytes and vascular plants. The plot frequency of the common dwarf shrub *Vaccinium vitis-idaea* was, nevertheless 80% lower on the stump harvested clear-cuts, indicating that the early response of stump harvesting may be strong on individual species.

*Keywords:* stump harvesting, saproxylic beetles, ground flora, low stumps, boreal forest, substrate types

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# Dedication

My patient wife and my four wonderful daughters

*Lyss till den granens susning, vid vars rot ditt bo är fäst*

Viktor Rydberg

# Contents

<b>List of Publications</b>	<b>7</b>
<b>1 Introduction</b>	<b>9</b>
1.1 Modern forestry, dead wood and threats to biodiversity	9
1.2 Beetle succession and decomposition of dead wood	10
1.3 The forest ground flora and forest management	11
1.4 Management and forest biodiversity	12
1.5 Stump harvesting	13
<b>2 Objectives</b>	<b>15</b>
<b>3 Materials and methods</b>	<b>17</b>
3.1 Geographical placement of the study areas	17
3.2 Experimental design	19
3.2.1 The saproxylic beetle fauna and low stumps (Paper I & II)	19
3.2.2 Long-term effects on beetles (Paper III)	19
3.2.3 Short-term effects on the ground flora (Paper IV)	21
<b>4 Major findings</b>	<b>23</b>
4.1 Paper I & II	23
4.2 Paper III	24
4.3 Paper IV	25
<b>5 Discussion</b>	<b>27</b>
5.1 Paper I & II	27
5.2 Paper III	30
5.3 Paper IV	32
<b>6 Conclusions and implications for forestry</b>	<b>35</b>
6.1 Implications for forestry	36
<b>7 Future research</b>	<b>39</b>
<b>References</b>	<b>41</b>
<b>Acknowledgements</b>	<b>49</b>



## 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. & Andersson, J. (2010). Saproxylic beetle assemblages on low stumps, high stumps and logs: Implications for environmental effects of stump harvesting. *Forest Ecology and Management*, 260: 1149-1155.
- II Andersson, J., Hjältén, J. & Dynesius, M. Wood-inhabiting beetles on 6-9 year old clear-cuts in boreal forest - Substrate associations and inter-annual variation. (manuscript)
- III Andersson, J., Hjältén, J & Dynesius, M. (2012). Long-term effects of stump harvesting and landscape composition on beetle assemblages in the hemiboreal forest of Sweden. *Forest Ecology and Management*, 271: 75-80.
- IV Andersson, J., Dynesius, M. & Hjältén, J. Short-term response to stump harvesting by the ground flora on boreal clear-cuts. (manuscript)

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The contribution of Jon Andersson to the papers included in this thesis was as follows:

- I Andersson contributed to the experimental design, contributed to the interpretation of the results and writing.
- II Andersson main responsible for planning and conduction of the field work, all data analysis and main responsibility for writing.
- III Andersson main responsible for planning and conduction of the field work, main part of all data analysis and significant part of writing.
- IV Andersson full responsibility for planning and conduction of the field work, all data analysis and main responsibility for writing.



# 1 Introduction

## 1.1 Modern forestry, dead wood and threats to biodiversity

Transformation and destruction of habitats is the largest threat to global biodiversity (Vitousek *et al.*, 1997). Extraction activities such as farming, logging and mining together with human development (human settlements, roads and industry) and overexploitation are the most important factors behind this threat (Groom *et al.*, 2006). The result of these negative effects on biodiversity is species extinction rates of one hundred to one thousand times their pre-anthropogenic levels and if all species considered to be “threatened” would perish during this century, the extinction rate might raise another 10 times. (Pimm *et al.*, 1995). In Scandinavia there have been few known recent extinctions. However, the Swedish national red list, with threat categories defined by the International Union for the Conservation for Nature (1988), does include a little over 4,200 threatened species. Out of these species, 232 are currently denoted as “critically endangered” (Gärdenfors, 2010) and there is a risk that species now surviving in small isolated populations already are lost (Hanski, 2000). In Scandinavia, where a large part of the land area is covered in boreal forest, forestry is thought to be one of the main causes of the threats on biodiversity (Berg *et al.*, 1994; Esseen *et al.*, 1997). Negative effects from forest management have been found on several organism groups: bryophytes (Palviainen *et al.*, 2005; Patino *et al.*, 2009), lichens (Johansson, 2008), fungi (Berglund *et al.*, 2011a), insects (Siitonen & Martikainen, 1994), birds (Imbeau *et al.*, 2001) and small mammals (Nixon *et al.*, 1980; Klenner & Sullivan, 2003). The negative impact from forestry is also reflected in the red-list of Swedish species, in which 43% of the listed species are confined to forest habitats (Gärdenfors, 2010).

Dead wood is acknowledged as one of the most important factors for biodiversity in the forest ecosystem (Berg *et al.*, 1994; Berg *et al.*, 1995; Esseen *et al.*, 1997; Siitonen, 2001; Grove, 2002; Jonsson *et al.*, 2005).

Between 6,000 and 7,000 of Sweden's 61,000 species are thought to be associated with dead wood and 1,126 of these are red-listed (Dahlberg and Stokland, 2004). In the old-growth forests of the past, natural disturbances like gap dynamics, insect outbreaks and forest fires continuously produced a variety of dead wood (Zackrisson, 1977; Niklasson & Granström, 2000; Grove, 2002). Intensive forestry with planting, clearing, thinning and finally clear-cutting has transformed large parts of the Scandinavian boreal forest into evenly aged stands with little in common with the natural forest landscape existing before this alteration (Zackrisson, 1977; Siitonen, 2001; Linder & Östlund, 1998). Modern forestry and the effective reduction of forest fires in particular, have dramatically reduced the amount of dead wood in the forest landscape (Linder & Östlund, 1998; Brassard & Chen, 2006). In old-growth forest the volume of dead wood may vary between 60-90 m<sup>3</sup> per hectare, while the dead wood volume in managed forests is around 2-10 m<sup>3</sup> per hectare (Siitonen, 2001). In natural forests the volume of dead wood depends on several factors: the site productivity which is affecting the input rate of dead wood, the decay rate of dead wood and disturbances affecting input rate (Harmon *et al.*, 1986). The quality of dead wood can, however, be as important for saproxylic species as volume alone (Siitonen, 2001; Juutinen *et al.*, 2006) and forest management does also change the spatial distribution and quality of dead wood (e.g. Økland *et al.*, 1996). Another structural change is the redistribution of the forest age. In Sweden for instance, only 4% of the forest is older than 160 years (Anon, 2006). In the pre-exploitation forests landscape, the forests were dominated by stands > 200 years (Linder & Östlund, 1998).

## 1.2 Beetle succession and decomposition of dead wood

When investigating the species composition of saproxylic insects, the successional stage is crucial for the understanding of the assemblage patterns we observe. Species with specific requirements on dead wood quality are likely to occur in different time intervals after tree death, i.e. in a successional pattern. Beetle succession in dead wood can be separated in four partially overlapping phases (Esseen *et al.*, 1992), although pathways may differ depending on tree species (Saint Germain *et al.*, 2007). In phase one, the assemblage is dominated by primary cambium consumers such as species of bark beetles, some long horn beetles and weevils, feeding on the nutrient rich inner bark of the recently dead tree. Predators and parasites associated with these early species also colonize (Ehnström & Axelsson, 2002). Phase two is characterized by secondary cambium feeders utilizing the remaining inner bark and fungivores associated with the newly established fungi growing under the

loose bark (Stokland & Siitonen, 2012). In phase three the cambium has been more or less eaten by insects and the beetle assemblage is dominated by fungivores consuming the mycelia, fruiting bodies and spores of different Polyporaceae. In phase four, the beetle assemblage is mainly composed of species feeding on the fungus ridden wood and detritus feeding species now start to occur (Stokland & Siitonen, 2012). Species succeed each other and the dead wood is slowly decomposing to ultimately become soil. The decomposition of dead wood can follow several alternative pathways depending on the fungal communities developing in the wounded trees. These pathways are dependent on the type of rot caused by different wood fungi; one species of wood fungi may facilitate the colonization of another species of fungi or saproxylic insect species. As decomposition progresses, it is thought that the species assemblages of saproxylic species in different types of dead wood becomes increasingly similar (Stokland & Siitonen, 2012).

### 1.3 The forest ground flora and forest management

A great proportion of biodiversity in forest ecosystems consists of bryophytes, lichens and species of vascular plants (Roberts, 2004) and it is well known that bryophytes and lichens are among the first organisms to colonize in pioneer land habitats (Longton, 1992). Lichens and bryophytes are unlike vascular plants unable to regulate water uptake. This makes them vulnerable and sensitive to dramatic environmental changes such as thinning and clear-cutting. After a drastic disturbance like clear-cutting the ground vegetation faces higher intensities of abiotic factors like solar radiation, temperature and wind which in general are causing the cover of bryophytes to decline and species assemblage to alter (Fenton *et al.*, 2003). The extent of these effects may however vary depending on slope aspect (Åström *et al.*, 2007) or substrate form (Hylander *et al.*, 2005).

The effects of forest management on the ground vegetation have been well studied and several studies have reported negative effects from management (Jalonen & Vanha Majamaa, 2001 (bryophytes); Hannerz & Hånell, 1997 (vascular plants). Other studies have found positive effects from forest management on early successional plant species (Pykälä, 2004; Widenfalk & Weslien 2009). Lately, there have also been studies investigating the possible effects on ground vegetation by intensified harvesting e.g. slash harvesting (Åström *et al.*, 2005; Caruso *et al.*, 2008) but there are still just a few dealing with effects of stump harvesting (but see Saana *et al.*, 2011; Kaye *et al.*, 2008). The cut surface of low stumps may also provide an important substrate for both lichens and bryophytes (Caruso *et al.*, 2008) and the few available studies

made to investigate the effects of stump harvesting on plants, indicate long-term negative effects on the ground vegetation (Kaye *et al.*, 2008) and that exposed mineral soil caused by stump harvesting in the short-term may increase coverage of the ground vegetation (Saana *et al.*, 2011).

## 1.4 Management and forest biodiversity

As a reaction to the accumulating evidence of negative influences of forestry on biodiversity, the sustainability of modern forestry has been questioned. As a result, changes were made to the Swedish forestry act (Anon, 1994) which now states that environmental protection and forestry production should be of equal importance. Other efforts to mitigate negative effects on biodiversity include the introduction of new forest certification schemes like the Forest Stewardship Council (FSC) and the Programme for the Endorsement of Forest Certification (PEFC). According to these schemes the certified partners should make conservation efforts like: leaving high stumps, leaving standing and lying dead trees, green tree retention and buffer strips along lakes and creeks. Mimicking natural disturbance like forest fire should also be done with prescribed fires on clear-cuts and in mature forest (Larsson & Danell, 2001; Mielikäinen & Hynynen, 2003).

Improvements like these may help to dampen the negative trends caused by modern forestry (Johansson *et al.*, 2009; McGeoch *et al.*, 2007; but see Schroeder *et al.*, 2006). Schroeder *et al.* (2006) evaluated the importance of high stumps on landscape level and found that high stumps only made up a minute proportion of the total volume of dead wood on landscape level and for most species high stumps did only constitute less than 1% of the total population. High stumps were however found to be the most important substrate for one species, *Hadreule elongatula*. The red-listed Trogostide, *Peltis grossa* is another species strongly favored by high stumps on clear-cuts (Djupström *et al.*, 2012). Green tree retention has also been shown to decrease the negative effects from clear-cutting on ground flora (Halpern *et al.*, 2005) and saproxylic beetles (Sverdrup-Thygeson & Ims, 2002) and the more trees that are left after clear-cutting, the more does the species composition of beetles resemble the one found before harvesting (Hyvärinen *et al.*, 2005). The long-term conservation value of these measures is still not well understood (Johansson *et al.*, 2009) and the evaluation can be difficult (Davies *et al.*, 2008; Jonsell *et al.*, 2005).

An exception to the lack of knowledge in this field is the quite abundant literature on species assemblages in different kinds of substrates on clear-cuts; logs and high stumps in general. Through these studies it has come clear that

the best conservation efforts are made by creating a variety of substrate types (Jonsell & Weslien, 2003; Lindhe & Lindelöw, 2004; Fossetøl & Sverdrup-Thygeson, 2009; Berglund *et al.*, 2011b; Hjältén *et al.*, 2012). However, in the managed forest landscape, dead wood is un-equally dispersed between different forest age classes with a dip in the middle aged, 30-50 year old stands (Stenbacka *et al.*, 2010). Thus, it is suggested that the conservation measures described above should be used not only at final harvesting but also during thinning (Stenbacka *et al.*, 2010).

## 1.5 Stump harvesting

The threats from increasing atmospheric CO<sub>2</sub> levels with subsequent temperature increase have led to demands on CO<sub>2</sub> neutral substitutes. Such new fuel types may constitute of bio-ethanol, methanol and bio-diesels (Mohan, 2006; Song, 2006) agricultural waste or forest fuels. Forest fuels can be divided into three groups: primary, secondary and tertiary forest residues. The primary residues come from clear-cuttings and thinning and mainly constitute of stumps, branches and tree tops. Bark, sawdust and chips, etc. comes from industry and are categorized as secondary residues. The tertiary residues are mainly wood based bi-products and waste from packing and demolition and construction (Röser *et al.*, 2008). In Sweden, 23% of the total energy input derived from biofuels in 2010 (Anon, 2011). Although the contribution of biomass to the energy consumption is high in Nordic countries (Röser *et al.*, 2008), forest fuels does still contribute with a small fraction of the energy consumption in EU as a whole (Hakkila & Parikka, 2002).

Harvesting of branches, twigs and tree tops (slash) left after final harvesting have been conducted after clear-cutting for approximately 30 years in Sweden and an increased demand is thought to further expand the use of biofuels in the future (Anon, 2007). Harvesting of low stumps for biofuel purposes did not start until 2009 in Sweden although this substrate type is an even larger source of raw material for biofuels than slash (Bouget *et al.*, 2012). Stump harvesting was however done on industrial scale in Sweden for a short period in the late 70s to early 80s, but for other reasons; the stumps were used in paper pulp production (Bouget *et al.*, 2012).

Stump harvesting is conducted after final felling with a specific stump harvester set attached to a caterpillar excavator. After harvesting the stumps are left in piles to dry on the clear-cut (Fig. 1), and later transported to a heating plant for burning. As previously mentioned, the availability of dead wood and particularly coarser fractions of dead wood, is in short supply in managed forests. The introduction of a new method to harvest an abundant dead wood

substrate on clear-cuts (low stumps) may counteract the efforts made by forestry to increase the amount of dead wood. Although low stumps have been overlooked in most studies of dead wood on clear-cuts, there are already some studies conducted to evaluate the importance of low stumps for different organisms; beetles (Jonsell & Hansson, 2011; Hedgren, 2007; Abrahamsson & Lindbladh, 2006) and lichens (Caruso *et al.*, 2008). The effects of stump harvesting on vascular plants have also been investigated, but not to any significant extent (but see Kaye *et al.*, 2008; Saana *et al.*, 2011).



Figure 1. Two clear-cuts made in 2010. The left clear-cut is only slash harvested while the right clear-cut is both slash harvested and later stump harvested. The stumps are stored in piles and two of those piles can be seen in the picture; one to the right and one in the far left. (Photos taken by Jon Andersson).

From several previous studies we know that different substrate types produce different assemblages of wood-living insects (Gibb *et al.*, 2006b; Hjältén *et al.*, 2007; Johansson *et al.*, 2007) and studies made to investigate substrates on clear-cuts, have shown that low stumps may constitute important habitat for many saproxylic beetles (Jonsell & Hansson, 2011; Abrahamsson & Lindbladh, 2006). As mentioned in the introduction, previous studies of substrates on clear-cuts have detected substrate specialists, such as *Peltis grossa* (Djupström *et al.*, 2012) and *Hadreule elongatula* (Schroeder *et al.*, 2006) on high stumps. Beetle species specialized on low stumps have so far not been detected.

Studies of the long-term effects from stump harvesting are extremely scarce (but see Kaye *et al.*, 2008 for an example on flora and soil decomposers), and although we did not expect to find any large effects from stump harvesting, two and a half decades after harvesting, further knowledge is important to acquire.

## 2 Objectives

The effects of stump harvesting on different organisms are still, to a large extent, unknown and the aim of this thesis was to gain new knowledge on the effects of stump harvesting on beetle communities and ground flora.

In this thesis I addressed the following questions:

- 1 Do low stumps produce similar abundance, species richness and species assemblages as other dead wood substrates on clear-cuts? Paper I & II
2. Are the patterns in species richness, abundance and species composition consistent over time? Paper II
3. Are there any low stumps specialists? Paper I and II
4. Are there effects on beetle assemblages from stump harvesting conducted 25 years ago? Paper III
5. How does stump harvesting affect the ground flora in short-term? Paper IV





## 3 Materials and methods

### 3.1 Geographical placement of the study areas

Large parts of the Scandinavian forest landscape is covered in stands managed by forestry with small elements of older protected forest. The study areas I used are not exceptions in this respect and can be best described as “typical” for forests with a history of forest management. Three of the four different studies (Paper I, II and IV) were situated in the administrative counties Västerbotten and Västernorrland within the southern-boreal and central-boreal vegetation zone (Ahti *et al.*, 1968) (Fig. 2). Before final harvesting the stands had been dominated by Norway spruce (*Picea abies*) mixed with Scots pine (*Pinus sylvestris*) and with elements of deciduous trees such as birch (*Betula* sp.) aspen (*Populus tremula*) and willows (*Salix* sp.). The ground was mainly moist to mesic and the vegetation was mostly of *Vaccinium myrtillus* type. Altitudes ranged from 12 m to 550 m a.s.l with an average of 277 m.

The fourth study (Paper III) was located in Uppsala and Dalarna, administrative counties within the hemiboreal vegetation zone in Sweden (Ahti *et al.*, 1968) (Fig. 2). The study was conducted in young forest stands with a mixture of Norway spruce, Scots pine and species of deciduous trees. The soil type was predominantly moraine and the ground moisture varied from mesic to wet although most stands grew on mesic soils. In this area the landscape is rather flat and the altitude ranged from 22 m to 137 m a.s.l. with an average of 48 m.

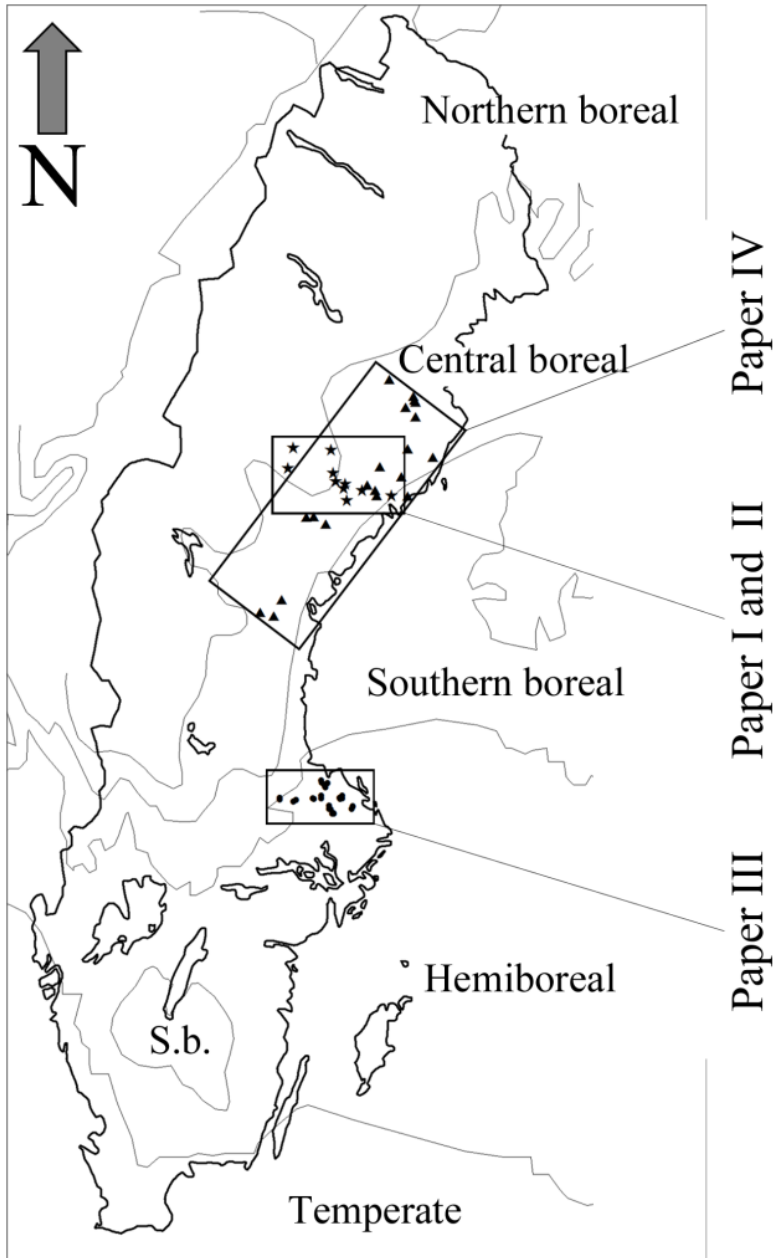


Figure 2. A map showing the vegetation zones (Redrawn from Athi *et al.*, 1968.) in Sweden and the location of the four studies summarized in this thesis. The Papers I and II were conducted at the same sites and in the same study area.

## 3.2 Experimental design

### 3.2.1 The saproxylic beetle fauna and low stumps (Paper I & II)

These two studies were conducted to evaluate the importance of low stumps as a substrate for saproxylic beetles. We used a large scale project ongoing since 2000-2001 where different substrates have been experimentally made to investigate beetle assemblages in coarse woody debris on clear-cuts. We sampled low stumps, logs and high stumps on ten clear-cuts. All substrates were of similar age (approximately six years in Paper I and about six to nine years in Paper II); high stumps and low stumps were created in 2000 and early 2001. The logs were created in 2001.

The high stumps were approx. 3 m high with an average diameter of 22 cm DBH and the logs were 4 m in length with an average diameter of 21 cm (Johansson *et al.*, 2006). The beetles were caught with emergence traps. A defined section of each substrate (three high stumps, three low stumps and three logs per locality) was wrapped inside a black polypropylene weed barrier cloth. In each weed cloth a small hole was made where a white 250 ml plastic bottle was attached to catch the hatching beetles. The diameter of the stumps was in general slightly larger than the diameter on logs and high stumps but in return the enclosed section of these two substrate types were longer which resulted in approximately the same volume and area sampled for all substrate types. The sampling period ran from May to September in 2006, 2007 and 2009.

In Paper I the variation between substrates were analyzed with analysis of variance (ANOVA), but due to the temporal dependence between years in Paper II, we used a linear mixed effects model for the analysis of substrate type and year in this study. The data was  $\log_{10}(x+1)$  transformed before analysis to meet the requirements of normal distribution. For the analysis of species assemblages, permutational multivariate analysis of variance (PERMANOVA) was used and the individual species contributions to the difference in assemblages were analyzed with similarity percentage analysis (SIMPER). The univariate statistics was done in JMP (SAS Institute, 2010) and the multivariate statistics was done in PRIMER-E (V.6.1.12, 2009).

### 3.2.2 Long-term effects on beetles (Paper III)

Stump harvesting is, as mentioned previously, a relatively new method in forestry. Hence, it might be difficult to locate suitable clear-cuts for studies of this kind. However, in the late 70s to early 80s stump harvesting was carried out in the administrative counties Uppsala and Dalarna in Central Sweden as an attempt to use stumps in paper production. We used stump harvested clear-

cuts made in this region to make the first ever effort to evaluate the long-term effects on beetles from stump harvesting.

In this study we used 28 young forest stands. Half were clear-cut and stump harvested 21-28 years prior to the study and half were just clear-cut at the same time, these were used as controls. We trapped beetles with three window traps of the type IBL2<sup>®</sup> (Poland) (Fig. 3) at each stand in June-October 2007. This trap type is made of a thin, semi-transparent plastic sheet tightened between three thin plastic pipes of equal length which makes the trap triangular. On the sides of the trap edges are on each side thicker plastic fabric attached which makes the sides work as a convenient sliding mechanism for insects colliding with the intercept. At the bottom of the intercept there was a two level funnel attached to collect the sliding insects. A 725 ml plastic bottle was attached in the very bottom of the funnel. The bottle was filled up to 1/3 with a 50/50 solution of water and propylene glycol. A small amount of detergent was added to break the surface tension. At each stand, three traps were placed approximately 25 m from each other in a triangular formation.

Apart from investigating the long-term effects from stump harvesting, we also wanted to evaluate the importance of the quality of the surrounding forest landscape. Therefore, data on forest age and the volume of deciduous trees with data from kNN-Sweden were studied. The area of clear-cuts adjacent to the investigated stands was also included as a character of the surrounding landscape. For this we used the web based map database "Skogens källa" (Swedish Forest Agency, 2002). We used the computer software ArcGIS 9.3 (V.9.3.1, ESRI, 1999-2009) to sample the data on the surrounding stand characters in 150 and 300 ha buffers around each trapping site.

The statistical analysis was done in several steps. First we checked for spatial dependence between the different sites with a Mantel test. It showed that there were no such dependences between our study sites. We then examined if stump harvesting which was done 25 years prior to our study had altered the beetle species assemblage. This was done with analysis of similarities (ANOSIM). To analyze the effects of stump harvesting and the relation between the adjacent forest stands and different groups of beetles we used principle component regression (PCR) (Liu *et al.*, 2003). The Mantel test and ANOSIM was done in PRIMER-E (V.6.1.12, 2009) while the regression was done in R (R Development Core Team, 2008).



Figure 3. A photo of the window trap used in Paper III.

### 3.2.3 Short-term effects on the ground flora (Paper IV)

This study was done to evaluate the immediate effects on the ground flora from stump harvesting. We used 20 clear-cuts made between 2008 and 2010. On half of the clear-cuts, stump harvesting was conducted and on all 20 clear-cuts most of the fine dead wood had been harvested (slash harvesting) and the ground had been scarified with machines.

At each of the 20 clear-cuts we sampled all bryophytes and vascular plants. The sampling was done like this: in the computer software ArcGIS 9.3 (V.9.3.1, ESRI, 1999-2009) we created a circle with an area of approximately 7,850 m<sup>2</sup> on each clear-cut. Inside these circles we created 100 evenly dispersed points. From these 100 points we randomly drew a unique set of 40 points. However, in the field it came clear that some of the points had ended up inside compensation patches made during the clear-cutting procedure. Compensation patches are small patches of forest saved during clear-cutting as nature consideration. Some of the points were also located in forest ditches. There was an impendent risk for deviant ground vegetation inside compensation patches as well as in the forest ditches. Hence, such points were

omitted from the survey. Due to the loss of these points we used 775 of the original 800 points; 386 in the stump harvested clear-cuts and 389 in the control clear-cuts. At the 775 GPS points remaining after omitting these points we recorded the plot frequency of bryophytes and vascular plants within a 50x50 cm sampling frame. This plot size and the number of plots resulted in a total area of 10 m<sup>2</sup> sampled on each clear-cut (provided that all 40 sample points were left). Inside the plots we also made a visual assessment of the percentage soil disturbance. Only disturbance to the soil was recorded, thus perturbed boulders and dead wood was not included in this survey. The field survey was conducted between June 28 and July 31 in 2011.

We used three different analysis methods to evaluate the effects of stump harvesting on the flora. To analyze the effects on the overall species assemblage on the ground flora we used analysis of similarities (ANOSIM) which is a non-parametric test for multivariate data. Thereafter we used the Wilcoxon Mann-Whitney test for analyzing the effects from stump harvesting on single species and groups of species. We also wanted to compare the effects from stump harvesting to the factors soil moisture, latitude, solar radiation and a temperature gradient that goes from the coast and land inwards. The factors used are known to influence the occurrence of vascular plants and bryophytes. To gather knowledge about the relative importance of all factors, including stump harvesting, in our models, we used multi-model inference (Andersson, 2008).

## 4 Major findings

### 4.1 Paper I & II

During the years 2006, 2007 and 2009 we trapped 2,670 beetle individuals among which 195 species were classified as either being facultative or obligate saproxylic. Predatory beetles were the nutritional group with highest abundance, 1,132 individuals, followed by the fungivores with a slightly lower abundance, 1,028 individuals. We caught 19 red-listed species and seven of these were found on low stumps. Abundance and species richness of saproxylics did not differ between the three substrate types (high stumps, logs and low stumps) whereas we found a difference in abundance and species richness between these substrates when we divided the saproxylic species into groups of nutritional functionality (Paper II). Fungivores preferred logs to high stumps and the abundance of predatory beetles was higher in the high stumps than in logs and low stumps (see Fig. 4).

The species composition of saproxylic beetles was also examined in both studies. When the data from the first year was analyzed (Paper II) there was a clear difference in species assemblage between all three substrates. This pattern was maintained even when the data from all three years were analyzed (Paper II), but an interaction between substrate and year indicated that the difference between low stumps and high stumps was not consistent. A pair-wise test, examining this interaction revealed that the assemblages no longer differed between high stumps and low stumps the last year of the study. After dividing the saproxylic species into nutritional groups the fungivore saproxylics still showed significant differences in species composition between substrates, while the saproxylic predators composition only differed between logs and the other two substrates.

The analysis of inter-annual effects on saproxylic beetles revealed that when saproxylic beetles were treated as a single group the between year variation had stronger effect on both abundance and species richness than did substrate type. The year 2007 did have higher species richness and abundance than the year 2009. The assemblages of saproxylic fungivores and predators were different in 2009 compared to the two previously investigated years. We also found some interesting substrate preferences on species level. One species, *Enicmus rugosus*, was more common on low stumps and the two species, *Anaspis rufilabris* and *Anaspis marginicollis* were more common on high stumps while *Curtimorda maculosa* was almost exclusively found on logs.

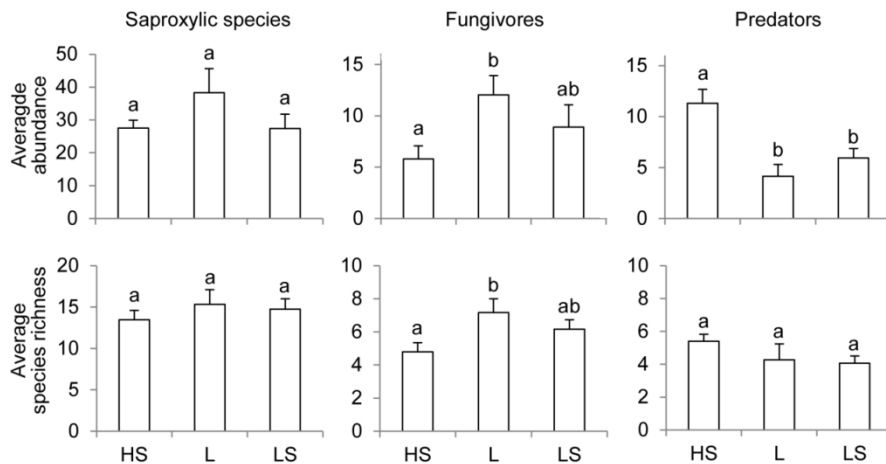


Figure 4. Barplots showing the average abundance and species richness of the two nutritional groups and the saproxylic beetles caught in Paper II. HS, high stumps; L, logs; LS, low stumps. Different letters above the bars indicate significant difference in abundance and/or species richness.

## 4.2 Paper III

During the summer 2007 we trapped 6,429 individuals belonging to 432 beetle species and 55 taxonomic beetle families. Of tall individuals, 46% were caught in the previously stump harvested stands. About 36% of the total abundance belonged to obligate saproxylic beetles. We found 15 red-listed beetle species which were generally occurring in low numbers. The most common nutritional group was the fungivores. The two dominating taxonomic groups were Staphylinidae (1,707 individuals) and Lathridiidae (1,270 individuals) and the most common species was *Enicmus rugosus* (Lathridiidae).



The negative long-term effects from stump harvesting were small and confined to fungivores and the beetle family Lathridiidae and no effect on the overall species composition of beetles could be detected. However, further statistical analysis revealed that the characteristics of the surrounding forest (in the 150-300 ha buffers) had large influence on the occurrence of different groups of beetles. Non-saproxyls and fungivores were positively related to the area of surrounding younger forest stands while the Staphylinidae were positively related to higher volumes of deciduous trees. The Elateridae was positively related to the area of clear-cuts in the vicinity (the 150 ha buffers).

### 4.3 Paper IV

The field survey collected information on 130 different taxa of vascular plants and bryophytes. Forty-two of these were moss taxa, 23 were liverwort taxa and 64 were vascular plants. The immediate effects of stump harvesting on vascular plants and bryophytes were found to be confined to a small number of relatively common species such as the two moss species, *Hylocomium splendens*, *Pleurozium schreberi* and the dwarf shrub *Vaccinium vitis-idaea*. *Vaccinium vitis-idaea* had four times lower plot frequency on stump harvested clear-cuts than on the control clear-cuts (Fig. 5). There were also indications, although the results were not statistically significant, that stump harvesting influenced the occurrence of other species than the previously mentioned. The dwarf shrub *Vaccinium myrtillus* and the moss *Ptilium crista-castrensis* showed a close to significant negative response to clear-cutting (Fig. 5).

Other factors that might be important for the occurrence of different vascular plants and bryophytes on clear-cuts were also investigated. Soil moisture was found to be the most important factor but latitude and radiation were also important factors for some species. Stump harvesting did not have any effect on the overall species composition of the ground flora.

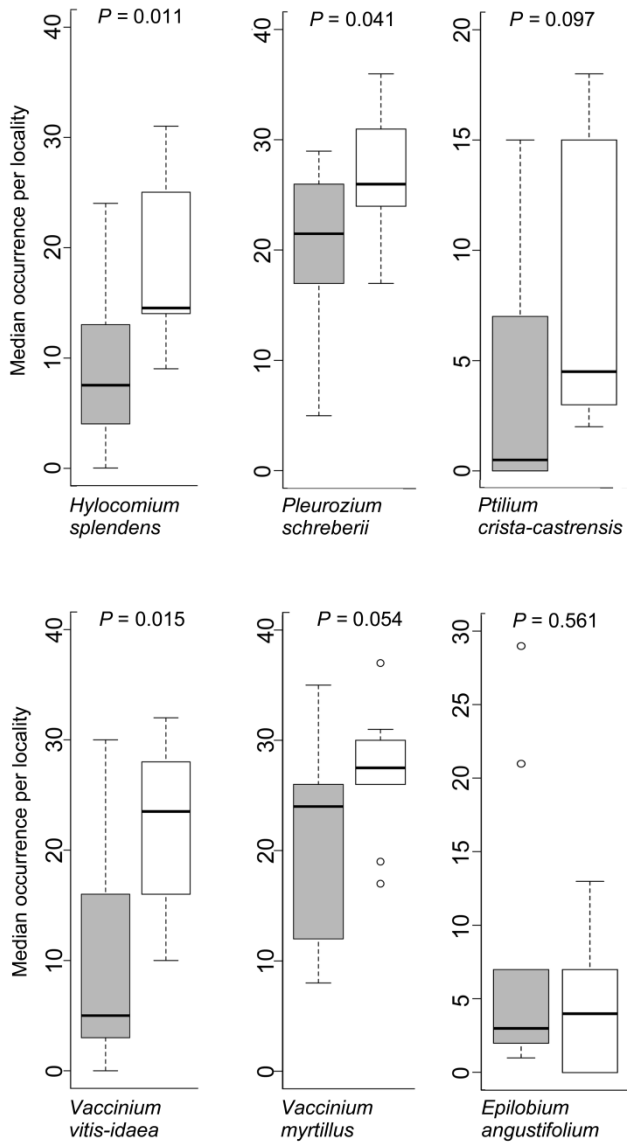


Figure 5. A box plot showing the median occurrence per locality in the stump harvested (white) and the controls (grey) of the three moss species *H. splendens*, *P. schreberii*, *P. crista-castrensis* and the vascular plants *V. vitis-idaea*, *V. myrtillus* and *E. angustifolium*. The *P*-values written above the box plots are the results from the Wilcoxon-Mann-Whitney test.

## 5 Discussion

This thesis was performed to gain new knowledge for the ongoing discussion concerning the effects of biofuel harvesting on species utilizing dead wood in boreal forests. We found that low stumps can support diverse populations of saproxylic beetles and that this substrate produces as high abundance and as many species of saproxylic beetles as high stumps and logs. In a first ever attempt, to investigate the long-term effects from stump harvesting, we found small effects mainly on fungivorous beetle groups. We did also make a study on effects from stump harvesting on the ground flora and found only limited short-term effects.

### 5.1 Paper I & II

The literature on dead wood and saproxylic beetles is extensive, and from these studies we now know that dead wood properties like tree diameter (Jonsell *et al.*, 2007; Lindhe *et al.*, 2005), tree species (Jonsell *et al.*, 1998), degree of sun exposure (Fossestøl & Sverdrup-Thygeson, 2009), decay stage (Esseen *et al.*, 1997; Siitonen, 2001). Forest age (Hjältén *et al.*, 2012) and the features of the saproxylic species inhabiting the dead wood, like dispersal capacity (Jonsell, 2008), are also important factors to consider when studying effects of forest management.

We found that the two nutritional groups studied in Paper II differed in their substrate associations. The fungivores were more common on logs than on high stumps and some of the predators were caught in higher abundance on high stumps than on the other two substrates. Since the substrates used in Papers I and II were of the same species (spruce) and of approximately the same diameter and age, other factors must have contributed to the observed difference. Several studies have proposed that the differences in assemblages between substrate observed could be due to microclimatic differences between (Sverdrup-Thygeson & Ims; 2002; Jonsell & Weslien, 2003; Abrahamsson &

Lindbladh, 2006). The branchless logs in our study were lying close to the ground which most likely made them moister than high stumps. The low stumps are usually sticking up from the ground making them more exposed than logs. Stumps are at the same time firmly attached by their roots to the ground, providing a convenient bridge for vegetative mycelia of fungi (Boddy, 2001, Wallace, 1953). High stumps on the other hand are standing tall above the ground, exposed to wind, which makes them more diverse with a moisture gradient going from the ground to the top which makes them highly diverse (Sverdrup-Thygeson & Ims, 2002; Abrahamsson & Lindbladh, 2006). It is possible that logs, lying close to the ground, constitute better substrate for many species of wood fungi. Consequently, logs would also be a better suited habitat for fungivore beetle species. The higher occurrence of predators in high stumps is however harder to explain.

The difference between saproxylic beetle assemblages in the three substrates types assessed in our study decreased the last year of our second study (Paper II); no difference between high stumps and low stumps in 2009. Stokland & Siitonen (2012) suggested that different substrates, with time, would produce increasingly homogenous species assemblages. Our result supports this suggestion, but the limited time span of the study is not sufficient to adequately confirm this pattern.

Patterns of individual species were recorded in both Paper I and II. Before comparing our studies with others, it is important to mention that the stumps we used were a little older (6-9 years at the time of the studies) than those used in other studies (Abrahamsson & Lindbladh, 2006; Jonsell & Hansson, 2011; Hedgren, 2007). Thus, primary colonizers of cambium were scarce in our material and abundances were instead more or less evenly distributed between fungivores and predators. An exception to this was the comparably high abundance of the cambivore *Crypturgus pusillus* which have been found in large numbers on the same clear-cuts in earlier studies (Gibb *et al.*, 2006a; Johansson *et al.*, 2007).

In Paper I, when we only analyzed the data from 2006, we found five species that were more common on low stumps. Among these were the fungivorous saproxylic *Enicmus rugosus*. This species was more common on low stumps also in 2007 and 2009 (Paper II) and among the species that contributed most to differences in assemblages of saproxylic beetles (Fig. 6). *Enicmus rugosus* have, however, been found on a variety of substrates on clear-cuts (Lindhe *et al.*, 2005; Johansson *et al.*, 2007). Thus, the short-term survival of this species is not “on the ropes” depending on the presence of low stumps. Nevertheless, a strong reduction of stumps caused by stump harvesting can be a problem for other less abundant species. Another clear pattern in

substrate preference was observed for the obligate saproxylic fungivore *Curtimorda maculosa* (Fig. 6); 146 out of 157 (93%) individuals belonging to this species were caught on logs, and it was never caught on high stumps during the entire sampling period (2006, 2007 and 2009).

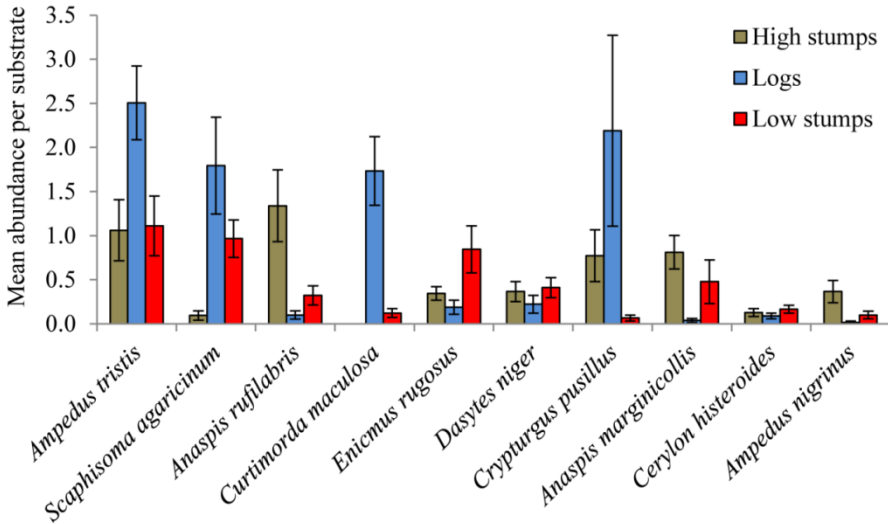


Figure 6. The graph shows the average abundance per sampled substrate ( $\pm$ SE) of the species responsible for the largest average percentage dissimilarity between substrates given by the SIMPER analysis. The species are placed in order of importance from left to right.

*Curtimorda maculosa* is strongly associated with the polypore species *Gloeophyllum sepiarium* (Dahlberg & Stokland, 2004), which prefer logs to high and low stumps (Jonsell & Weslien, 2003; Berglund et al., 2011a; Berglund et al., 2011b). The attraction to *G. sepiarium* by *Curtimorda maculosa* is strongly supported by our study. *Anaspis marginicollis* and *Anaspis rufilabris* are two fungivores that are attracted to the volatiles from the bracket fungi, *Fomitopsis pinicola* (Fäldt et al., 1999). *Fomitopsis pinicola* occurs more frequently on high stumps than on logs (Jonsell & Weslien, 2003) and a different study found that logs were more suitable than low stumps (Berglund et al., 2011b). Both beetle species had significantly lower abundance on logs and higher abundance on high stumps (significant for *A. rufilabris*). Hence, the attraction of these two fungivores by the bracket fungi *F. pinicola* is confirmed by our study.

The results from our two studies (Paper I & II) shows that low stumps left after final harvesting can serve as valuable substrate for wood-living insects. It is also important to remember that low stumps constitute large part of the dead wood on clear-cuts (Egnell et al., 2007; Caruso et al., 2008; Eräjää et al., 2010)

and stumps can last for many years in the newly established stands after clear-cutting (Caruso *et al.*, 2008; Caruso & Rudolphi, 2009).

## 5.2 Paper III

We did not expect to find large effects on beetles this many years after harvesting, although effects from stump harvesting have been found on e.g. the understory vegetation 24-28 years after stump harvesting (Kaye *et al.*, 2008). Nevertheless, the result revealed significant negative effects from stump harvesting on two beetle groups approximately 25 years after harvesting. These two groups were the beetle family Lathridiidae and the nutritional group fungivores. Lathridiidae is a beetle family entirely constituted by fungivores and the other group is also fungivores. We therefore suggest that the reason for the observed pattern could be due to limitations in food supply caused by stump harvesting, as to say less fungi on stump harvested clear-cuts. Other beetle families examined in our study that were also constituted entirely (Ciidae), or mostly (Leiodidae) of fungivores, did not respond significantly to stump harvesting. No study has so far been done to examine the long-term effects from stump harvesting on fungi. Our conclusion considering limitation in food supply as described above can therefore not be confirmed.

In this study we also investigated if the landscape surrounding the 25 year old clear-cuts (now young forest stands) influenced beetle assemblages. Stands with ages between 0-40 years were dominating around our study sites (see Fig. 7) and intensive forest management has been going on in episodes over the last 400 years in this area (Hammarlund *et al.*, 2008; Linder & Östlund, 1998).

The Scarabids caught in our study were mostly belonging to the genus *Aphodius* which in our study showed a positive response to the proportion of clear-cuts in the surrounding landscape. Kuijper *et al.* (2009) found that large ungulates have a preference for open areas like clear-cuts. A large and abundant herbivore species in this area, the moose *Alces alces*, is commonly foraging on clear-cuts. Naturally, species like many of the *Aphodius*, which are mostly found in manure would thrive in such habitats. However, no assessment of moose droppings was made in our study. The beetle family Elateridae was also positively related to clear-cuts. The most commonly species caught in this beetle family; *Melanotus castanipes*, *Athous subfuscus* and *Ampedus balteatus* have been caught on clear-cuts in large numbers before (Lindhe & Lindelöw, 2004; Johansson *et al.*, 2007).

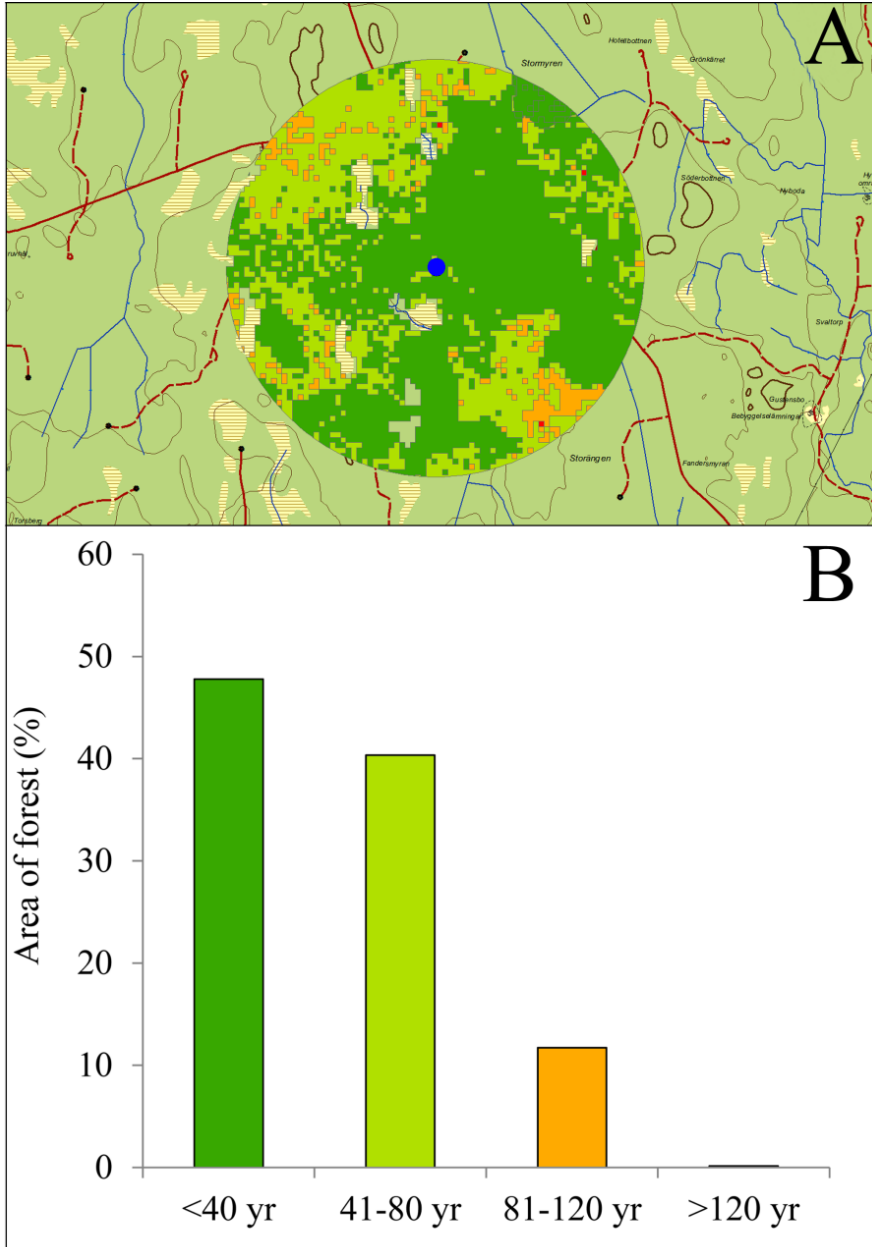


Figure 7. Panels A is showing an example of a map with the circular 300ha (977m radius) buffer zones around the trapping coordinate (blue dot) used in Paper III. Panel B is a graph showing the forest age distribution in the 28 buffer zones. The four age classes are on the horizontal axis and the percentage forest area covered by each age class on the vertical axes. The colors in the two circles (panel A) correspond to the colors on the bar plot (C). Forest > 120 years is colored in red.

Our results conform to other studies in that the patterns in occurrence of many beetle groups can be predicted on basis of the characteristics of the surrounding forest stands (Gibb *et al.*, 2006a; Franc *et al.*, 2007; Abrahamsson *et al.*, 2009; Janssen *et al.*, 2009; Götmark *et al.*, 2011).

We found significant long-term effects of stump harvesting on one taxonomic family (Lathridiidae) and the nutritional group fungivores, and although it is hard to prove from our results, some kind of limitation in food supply seems likely. Thus additional studies are needed to confirm the long-term effects on saproxylic beetles observed on our study and to identify the mechanism behind these potential effects.

### 5.3 Paper IV

Clear-cutting, is usually the most dramatic alteration of the forest stand, which is causing track damages, reduces evapotranspiration and increases solar radiation and wind. Scarification and subsequent slash harvesting, causes additional effects (Bergstedt *et al.*, 2008; Åström *et al.*, 2005) and stump harvesting might cause further damages (Kaye *et al.*, 2008).

In a study similar to ours, by Saana *et al.* (2011) the authors found that the elevated disturbance of the soil layer caused by stump harvesting increased the coverage of ground layer vegetation. We did instead find significant negative effects on some species. These effects were confined to the two moss species *Hylocomium splendens*, *Pleurozium schreberii* and one vascular plant, the dwarf shrub *Vaccinium vitis-idaea*. This result is, however, consistent with studies investigating effects from different harvesting intensities and soil disturbance (Bergstedt *et al.*, 2008; Norberg *et al.*, 1997, but see Bergstedt & Milberg 2001). The response from *Vaccinium vitis-idaea* was strong, with 80% lower plot frequency in the stump harvested clear-cuts, while the close relative *Vaccinium myrtillus* did not significantly respond to stump harvesting. In other studies of different harvesting intensities has *Vaccinium myrtillus* responded negatively (Bergstedt & Milberg, 2001, Jalonen & Vanha-Majamaa, 2001). The reason to why *Vaccinium vitis-idaea* so clearly responded to stump harvesting in our study remains unknown. A relation between *Vaccinium vitis-idaea* and the slightly elevated and more exposed tree bases (which after clear-cutting becomes low stumps) could cause this pattern, but was not tested in this study.

Bergstedt *et al.* (2008) showed that increasing harvesting intensities may have negative impact on abundant forest mosses like *Hylocomium splendens*, *Pleurozium schreberii* and *Ptilium crista-castrensins*. In our study,



*Hylocomium splendens* and *Pleurozium schreberii* responded significantly negatively to the additional effects of stump harvesting, while the negative response from *Ptilium crista-castrensis* was close to significant.

When we compared the effects from stump harvesting to other factors known to have an influence on the ground flora we found that stump harvesting did have as strong impact on the cover of some species as for instance soil moisture and solar radiation. Both soil moisture and light are known to be important factors for plant communities (Tilman, 1985). Some examples of these patterns are: the liverwort *Barbilophozia lycopodioides* that was negatively related to solar radiation in this study is known to favor shadier parts of clear-cuts (Åström *et al.*, 2007). Other species negatively affected by solar radiation were the mosses *Aulacomnium palustre*, *Hylocomium splendens* and *Pleurozium schreberi* and the fern *Gymnocarpium dryopteris*.

Soil moisture was, however, the most influential factor describing the patterns in plot frequency of the species and taxa assessed in our study. In spite of the fact that stump harvesting had a significant effect on the occurrence of some specific species, it did not significantly affect the overall species assemblages of the ground flora or species richness of vascular plants and bryophytes. Neither, could we detect effects on functional groups of bryophytes. Previous studies have found positive effects from clear-cutting on some vascular plant species (Widenfalk & Weslien, 2009) and a species that is known to thrive on clear-cuts is the nitrophilous pioneer plant *Epilobium angustifolium* (Hannerz & Hanell, 1997). Furthermore, Åström *et al.* (2005) showed that *Epilobium angustifolium* may increase slightly after slash harvesting. According to our results this species did not respond significantly to the effects from stump harvest. Slash harvesting is removing residue covering the ground surface. Thus, slash harvesting might benefit fast growing species like *Epilobium angustifolium* because of the increasing availability of new open space. This could be expected after stump harvesting as well, especially because of the increased soil disturbance, but was not detected in our study.

This study showed that the increased soil disturbance caused by stump harvesting can have negative effects on some common species of bryophytes and vascular plants. The rather small sample and plot size in our study might have resulted in low frequencies of the less abundant species. Thus, the detectability of effects on such species might have been low. Our results were in contrast to the previous, similar study by Saana *et al.* (2011). Our study was, however, located much further north than this study and due to this fact climatic factors may have slowed the recovery rate of the ground flora.



## 6 Conclusions and implications for forestry

Biofuel harvesting may have adverse effects on species utilizing dead wood for their survival; both in terms of habitat loss and due to the fact that harvested dead wood residues can become effective traps for saproxylic species (Jonsell, 2008). The two studies in Paper I and II indicate that low stumps left on clear-cuts after final harvesting constitute valuable habitat for many saproxylic beetle species. This conclusion is consistent with other studies (Abrahamsson & Lindbladh, 2006; Jonsell & Hansson, 2011; Hedgren, 2007; Vasiliauskas *et al.*, 2002; Wallace, 1953).

Although a large proportion of the saproxylic beetle fauna is attracted to sun-exposed dead wood (Lindhe *et al.*, 2005; Sverdrup-Thygeson & Ims, 2002) such as the wood found on logging sites, many species are unspecific in their diameter requirements and thereby not confined to CWD such as the wood in most low stumps (Jonsell, 2008). Nevertheless, slash harvesting is already standard procedure following final harvesting; therefore most of the FWD which could provide habitat for the generalist beetle fauna is already removed.

As previously mentioned (see citations in the introduction), in Scandinavia the volume of CWD on in the managed forest is scarce and far below the levels in natural forests (Fridman & Walheim, 2000; Siitonen, 2001; Stenbacka *et al.*, 2010) and further exploitation of this substrate, through stump harvesting, will most certainly not help. Saproxylic beetle species in general are however thought to be good dispersers (Jonsell, 2008) and are probably in most cases not confined to single stands or as in this case single clear-cuts (but see Siitonen & Saaristo; Ranius & Hedin for exceptions). Hence, local removal of suitable substrate done during, for example, stump harvesting might pose a limited threat for most species. If done regularly after final harvesting, stump harvesting may radically reduce the habitat for saproxylic species utilizing the sun-exposed wood available on clear-cuts.

The three different substrate types we studied in the Papers I and II did support a slightly different species assemblage. Others have come to similar conclusions (Abrahamsson & Lindbladh, 2006), and recent studies of substrate types lying outside the scope of our two studies have shown that finer fractions of dead wood also can provide habitat for diverse beetle assemblages (Kruys & Jonsson, 1999; Nordén *et al.*, 2004; Brin *et al.*, 2011). Thus, it is clear that a multitude of substrate types are needed to maintain intact assemblages of saproxylic beetles (e.g. McGeoch *et al.*, 2007; Hjältén *et al.*, 2012).

In addition, the effects of stump harvesting and the increased disturbance to the soil caused negative effects on a few but common vascular plants and bryophytes. Apart from this effect, we can also speculate that the removal of these stumps reduced the available substrate for lichens and bryophytes that colonizes the cut surface of stumps as shown in Carusso *et al.* (2008).

## 6.1 Implications for forestry

As mentioned in the introduction, results from several studies of the impact from forestry and its foot print in forest history have showed that forestry have had large impact on the natural features of the boreal forest, and as a consequence also on biodiversity (Siitonen, 2001; Siitonen & Martikainen, 1994; Linder & Östlund, 1998; Hanski, 2000; Paillet *et al.*, 2010; Esseen *et al.*, 1997; Zackrisson, 1977). There may have been improvements in the form of forest certifications schemes like the FSC and the PEFC (Larsson & Danell, 2001), and maybe we are slowly moving towards a new era with more consideration to forest biodiversity.

Biofuels and the harvesting of such fuels in boreal forests may, according our results, cause effects that might counteract the aims of the forestry certification schemes mentioned above. The result from resent overviews of fuel wood harvesting is pointing in the same direction (Bouget *et al.*, 2012; Walmsley & Godbold, 2010). Furthermore, little is left of the CWD on clear-cuts after stump harvesting (Eräjää *et al.*, 2010), and volumes of dead wood in coarser fractions are, compared to the ones in natural forest, already low in the managed forest landscape. If stump harvesting becomes standard, following final harvesting, the volumes of dead wood on landscape level could be further reduced.

I suggest that stump harvesting is done with caution and that compensation for the reduction of dead wood is made. According to our results and others, a multitude of substrates can facilitate a larger number of species than just one substrate type (e.g. high stumps) (Johansson *et al.*, 2007; Jonsell & Weslien, 2003; McGeoch *et al.*, 2007; Fossetøl & Sverdrup-Thygeson, 2009). Hence,

the compensation should be made by adding a variety of different substrate types. The compensation efforts should also be spatially dependent on areas with reserves or remnants of forests with high biological diversity and made to counteract isolation effects (Hanski, 2000; Jonsson *et al.*, 2005), but temporarily dispersed throughout the whole rotation period to mitigate the dips in dead wood volume observed in thinning stands today (Stenbacka *et al.*, 2010). I also suggest that money is put aside for continuous evaluation of the effects from stump harvesting which have the potential to radically reduce the amount of CWD.



## 7 Future research

I suggest that future studies try to look beyond the effects on stand level and that science try to embrace questions concerning landscape level effects on biodiversity, not only from biofuel harvesting, but from forestry as a whole. This might sound overly ambitious but with joint efforts greater knowledge can be acquired. Forestry has in many regions severely altered the whole forest landscape. There are, however, still areas in the taiga region where forestry has not disrupted natural processes such as gap dynamics, forest fire and insect outbreaks. Thus, there are still natural areas that can be used as “reference” in the evaluation of the effects present on scales larger than on stand level.

In our samples from the substrate investigations in Paper I and II we caught seven red-listed species on low stumps. So far no study has specifically investigated the occurrence of red-listed beetle species in low stumps on clear-cuts and some of these species might reproduce sparsely or even commonly on this substrate. If red-listed species are reproducing in small numbers on clear-cuts, they might be difficult to detect, hence the gathering of knowledge concerning this group of species urgent.

Our result from the study on long-term effects from stumps harvesting (Paper III) suggests that a still unknown effect on fungi caused the effects we found on fungivores. In Paper I and II, concerning substrate preference of beetles on clear-cuts, the patterns we observed on fungivores were also most likely due to patterns in occurrence of fungi. These results imply that future studies should be broadened to include larger parts of the food web when investigating the effects from forestry on a diverse group like insects (for examples see Komonen *et al.*, 2000; Jonsell *et al.*, 2005).

The effects we found on ground flora was confined to a few common species, but effects on other species could still be present although they were not detected in our study. Since other studies have found effects on the same species but from different types of harvesting, future studies of the ground flora

on clear-cuts should be made to investigate the recovery rate of these species. Also, larger study plots than the ones used in our study should be used to detect the effects on less common species.

The management of forests will continue developing and hopefully more of the knowledge acquired through decades of research will be acknowledged in the future design of forest management.



## References

- Abrahamsson, M. & 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.
- Abrahamsson, M., Jonsell, M., Niklasson, M. & Lindbladh, M. (2009). Saproxylic beetle assemblages in artificially created high-stumps of spruce (*Picea abies*) and birch (*Betula pendula/pubescens*) - does the surrounding landscape matter? *Insect conservation and diversity*, 2, 284-294.
- Ahti, T., Hämet-Ahti, L. & Jalas, J. (1968). Vegetation zones and their sections in northwestern Europe. *Annales Botanici Fennici*, 3, 169-211.
- Andersson, D. R. (2008). *Model Based Inference in the Life Sciences: A Primer on Evidence*. Springer, New York.
- Anon (1994). Skogsvårdslagen 1993:553, Handbok, Skogsstyrelsen. [In Swedish]
- Anon (2006). Skogsdata 2006, Tema: Skyddade skogar i Sverige. Institutionen för skoglig resurshushållning och geomatik. SLU, Umeå. [In Swedish]
- Anon (2007). Långsiktsprognos - enligt det nationella systemet för klimatrapportering. Modintryckoffset, Stockholm [In Swedish]
- Anon (2011). Energy in Sweden Facts and figures 2011. [Online]. Available: [www.energimyndigheten.se](http://www.energimyndigheten.se) [Accessed 29.10.12].
- Berg, A., Ehnstrom, B., Gustafsson, L., Hallingbäck, T., Jonsell, M. & Weslien, J. (1994). Threatened plant, animal, and fungus species in Swedish forests - Distribution and habitat associations. *Conservation Biology*, 8, 718-731.
- Berg, A., Ehnström, B., Gustafsson, L., Hallingbäck, T., Jonsell, M. & Weslien, J. (1995). Threat levels and threats to red-listed species in Swedish forests. *Conservation Biology*, 9, 1629-1633.
- Berglund, H., Hottola, J., Penttilä, R. & Siitonen, J. (2011a). Linking substrate and habitat requirements of wood-inhabiting fungi to their regional extinction vulnerability. *Ecography*, 34, 864-875.
- Berglund, H., Jonsson, M., Penttilä, R. & Vanha Majamaa, I. (2011b). The effects of burning and dead-wood creation on the diversity of pioneer wood-inhabiting fungi in managed boreal spruce forests. *Forest Ecology and Management*, 261, 1293-1305.

- Bergstedt, J., Hagner, M. & Milberg, P. (2008). Effects on vegetation composition of a modified forest harvesting and propagation method compared with clear-cutting, scarification and planting. *Applied Vegetation Science*, 11, 159-168.
- Bergstedt, J. & Milberg, P. (2001). The impact of logging intensity on field-layer vegetation in Swedish boreal forests. *Forest Ecology and Management*, 154, 105-115.
- Boddy, L. (2001). Fungal community ecology and wood decomposition processes: from standing tree to complete decay of coarse woody debris. *Ecological Bulletins*, 49, 53-56.
- Bouget, C., Lassauce, A. & Jonsell, M. (2012). Effects of fuelwood harvesting on biodiversity - a review focused on the situation in Europe. *Canadian Journal of Forest Research*, 42, 1421-1432.
- Brassard, B. W. & Chen, H. Y. H. (2006). Stand structural dynamics of North American boreal forests. *Critical reviews in plant sciences*, 25, 115-137.
- Brin, A., Bouget, C., Brustel, H. & Jactel, H. (2011). Diameter of downed woody debris does matter for saproxylic beetle assemblages in temperate oak and pine forests. *Journal of Insect Conservation*, 15, 653-669.
- Caruso, A. & Rudolphi, J. (2009). Influence of substrate age and quality on species diversity of lichens and bryophytes on stumps. *Bryologist*, 112, 520-531.
- Caruso, A., Rudolphi, J. & 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.
- Dahlberg, A. & Stokland, J. (2004). Vedlevande arters krav på substrat. Skogsstyrelsen, Jönköping. [English summary]
- Davies, Z., Tyler, C., Stewart, G. & Pullin, A. (2008). Are current management recommendations for saproxylic invertebrates effective? A systematic review. *Biodiversity and Conservation*, 17, 209-234.
- Djupström, L. B., Weslien, J., Hoopen, J. T., Schroeder, L. M. & ten Hoopen, J. (2012). Restoration of habitats for a threatened saproxylic beetle species in a boreal landscape by retaining dead wood on clear-cuts. *Biological Conservation*, 155, 44-49.
- Egnell, G., Hyvönen, R., Högbom, L., Johansson, T., Lundmark, T., Olsson, B., Ring, E. & Sydow von, F. (2007). Miljökonsekvenser av stubbskörd – en sammanställning av kunskap och kunskapsbehov. Energimyndigheten, Rapport 2007:40. [English summary]
- Ehnström, B. & Axelsson, R. (2002). Insektsgnag i bark och ved. Artdatabanken, SLU, Uppsala. [In Swedish]
- Eräjää, S., Halme, P., Kotiaho, J., Markkanen, A. & Toivanen, T. (2010). The Volume and Composition of Dead Wood on Traditional and Forest Fuel Harvested Clear-Cuts. *Silva fennica*, 44, 203-211.
- Esseen P.A., Ehnström B., Ericson L. & Sjöberg K. (1992). Boreal forests — The focal habitats of Fennoscandia. In: Hansson L. (ed.), *Ecological principles of nature conservation. Applications in temperate and boreal environments*, Elsevier, London.
- Esseen, P.-A., Ehnström, B., Ericson, L. & Sjöberg, K. (1997). Boreal forests. *Ecological Bulletins*, 16-47.
- Fenton, N. J., Frego, K. A. & Sims, M. R. (2003). Changes in forest floor bryophyte (moss and liverwort) communities 4 years after forest harvest. *Canadian Journal of Botany*, 81, 714-731.

- Fossestøl, K. & Sverdrup-Thygeson, A. (2009). Saproxylic beetles in high stumps and residual downed wood on clear-cuts and in forest edges. *Scandinavian Journal of Forest Research*, 24, 403-416.
- Franc, N., Gotmark, F., Okland, B., Norden, B. & Paltto, H. (2007). Factors and scales potentially important for saproxylic beetles in temperate mixed oak forest. *Biological Conservation*, 135, 86-98.
- Fridman, J. & Walheim, M. (2000). Amount, structure, and dynamics of dead wood on managed forestland in Sweden. *Forest Ecology and Management*, 131, 23-36.
- Fäldt, J., Jonsell, M., Nordlander, G. & Borg Karlson, A. K. (1999). Volatiles of bracket fungi *Fomitopsis pinicola* and *Fomes fomentarius* and their functions as insect attractants. *Journal of chemical ecology*, 25, 567-590.
- Gibb, H., Hjältén, J., Ball, J., Atlegrim, O., Pettersson, R. & Hilszczański, J. (2006a). 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.
- Gibb, H., Pettersson, R. B., Hjältén, J., Hilszczański, J., Ball, J. P., Johansson, T., Atlegrim, O. & Danell, K. (2006b). Conservation-oriented forestry and early successional saproxylic beetles: Responses of functional groups to manipulated dead wood substrates. *Biological Conservation*, 129, 437-450.
- Groom, M., Meffe, G. & Carrol, C. (2006). Principles of conservation biology. Sinauer Associates, Inc., Massachusetts.
- Grove, S. J. (2002). Saproxylic insect ecology and the sustainable management of forests. *Annual Review of Ecology and Systematics*, 33, 1-23.
- Gärdenfors, U. (2010). The 2010 red list of Swedish species. Artdatabanken, Uppsala.
- Götmark, F., Åsegård, E. & Franc, N. (2011). How we improved a landscape study of species richness of beetles in woodland key habitats, and how model output can be improved. *Forest Ecology and Management*, 262, 2297-2305.
- Hakkila, P., Parikka, M. (2002). Fuel resources from the forest. (ed.), Bioenergy from Sustainable Forestry. Guiding Principles and Practice. Kluwer Academic Publishers.
- Halpern, C. B., McKenzie, D., Evans, S. A. & Maguire, D. A. (2005). Initial responses of forest understories to varying levels and patterns of green-tree retention. *Ecological Applications*, 15, 175-195.
- Hammarlund, D., Mackay, A., Fallon, D., Pateman, G., Tavio, L. & Leng, M. (2008). A sedimentary record of the rise and fall of the metal industry in Bergslagen, south central Sweden. *Journal of paleolimnology*, 39, 463-475.
- Hannerz, M. & Hånell, B. (1997). Effects on the flora in Norway spruce forests following clearcutting and shelterwood cutting. *Forest Ecology and Management*, 90, 29-49.
- Hanski, I. (2000). Extinction debt and species credit in boreal forests: modelling the consequences of different approaches to biodiversity conservation. *Annales Zoologici Fennici*, 37, 271-280.
- Harmon, M. E., Franklin, J. F., Swanson, F. J., Sollins, P., Gregory, S. V. & MacFadyen, A. (1986). Ecology of coarse woody debris in temperate ecosystems. *Advances in ecological research*, 15, 133-302.
- Hedgren, P. (2007). Early arriving saproxylic beetles (Coleoptera) and parasitoids (Hymenoptera) in low and high stumps of Norway spruce. *Forest Ecology and Management*, 241, 155-161.

- Hjältén, J., Johansson, T., Alinvi, O., Danell, K., Ball, J. & Pettersson, R. (2007). The importance of substrate type, shading and scorching for the attractiveness of dead wood to saproxylic beetles. *Basic and Applied Ecology*, 8, 364-376.
- Hjältén, J., Stenbacka, F., Pettersson, R., Gibb, H., Johansson, T., Danell, K., Ball, J. P. & Hilszczański, J. (2012). Micro and Macro-Habitat Associations in Saproxylic Beetles: Implications for Biodiversity Management. *PLoS ONE*, 7, e41100.
- Hylander, K., Dynesius, M., Jonsson, B. G. & Nilsson, C. (2005). Substrate form determines the fate of bryophytes in riparian buffer strips. *Ecological Applications*, 15, 674-688.
- Hyvärinen, E., Kouki, J., Martikainen, P. & 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.
- Imbeau, L., Mönkkönen, M. & Desrochers, A. (2001). Long-term effects of forestry on birds of the eastern Canadian boreal forests: a comparison with Fennoscandia. *Conservation Biology*, 15, 1151-1162.
- International Union for Conservation of Nature (1988). *IUCN red list of threatened animals*, Gland, Switzerland.
- Jalonen, J. & Vanha-Majamaa, I. (2001). Immediate effects of four different felling methods on mature boreal spruce forest understorey vegetation in southern Finland. *Forest Ecology and Management*, 146, 25-34.
- Janssen, P., Fortin, D. & Hébert, C. (2009). Beetle diversity in a matrix of old-growth boreal forest: influence of habitat heterogeneity at multiple scales. *Ecography*, 32, 423-432.
- Johansson, P. (2008). Consequences of disturbance on epiphytic lichens in boreal and near boreal forests. *Biological Conservation*, 141, 1933-1944.
- Johansson, T., Gibb, H., Hilszczański, J., Pettersson, R., Hjältén, J. & Atlegrim, O. (2006). Conservation-oriented manipulations of coarse woody debris affect its value as habitat for spruce-infesting bark and ambrosia beetles (Coleoptera : Scolytinae) in northern Sweden. *Canadian Journal of Forest Research*, 36, 174-185.
- Johansson, T., Hjältén, J., Hilszczański, J., Stenlid, J., Ball, J. P., Alinvi, O. & 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.
- Johansson, T., Hjältén, J., de Jong, J. & von Stedingk, H. (2009). Generell hänsyn och naturvärdesindikatorer - funktionella metoder för att bevara och bedöma biologisk mångfald i skogslandskapet. WWF, Solna. [In Swedish]
- Jonsell, M., Weslien, J. & Ehnström, B. (1998). Substrate requirements of red-listed saproxylic invertebrates in Sweden. *Biodiversity and Conservation*, 7, 749-764.
- Jonsell, M. & Weslien, J. (2003). Felled or standing retained wood - it makes a difference for saproxylic beetles. *Forest Ecology and Management*, 175, 425-435.
- Jonsell, M., Schroeder, M. & Weslien, J. (2005). Saproxylic beetles in high stumps of spruce: Fungal flora important for determining the species composition. *Scandinavian Journal of Forest Research*, 20, 54-62.

- Jonsell, M., Hansson, J. & Wedmo, L. (2007). Diversity of saproxylic beetle species in logging residues in Sweden - Comparisons between tree species and diameters. *Biological Conservation*, 138, 89-99.
- Jonsell, M. (2008). The effects of forest biomass harvesting on biodiversity. (ed.), Sustainable use of forest biomass for energy – a synthesis with focus on the Baltic and Nordic region. Springer, Dordrecht.
- Jonsell, M. & Hansson, J. (2011). Logs and Stumps in Clearcuts Support Similar Saproxylic Beetle Diversity: Implications for Bioenergy Harvest. *Silva fennica*, 45, 1053-1064.
- Jonsson, B. G., Kruys, N. & Ranius, T. (2005). Ecology of species living on dead wood - Lessons for dead wood management. *Silva fennica*, 39, 289-309.
- Juutinen, A., Mönkkönen, M. & Sippola, A. (2006). Cost-efficiency of decaying wood as a surrogate for overall species richness in boreal forests. *Conservation Biology*, 20, 74-84.
- Kaye, T., Blakeley Smith, M. & Thies, W. (2008). Long-term effects of post-harvest stump removal and N-fertilization on understory vegetation in Western USA forests. *Forest Ecology and Management*, 256, 732-740.
- Klenner, W. & 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.
- Komonen, A., Penttilä, R., Lindgren, M. & Hanski, I. (2000). Forest fragmentation truncates a food chain based on an old-growth forest bracket fungus. *Oikos*, 90, 119-126.
- Kruys, N. & Jonsson, B. G. (1999). Fine woody debris is important for species richness on logs in managed boreal spruce forests of northern Sweden. *Canadian Journal of Forest Research*, 29, 1295-1299.
- Kuijper, D., Cromsigt, J., Churski, M., Adam, B., Jedrzejewska, B. & Jedrzejewski, W. (2009). Do ungulates preferentially feed in forest gaps in European temperate forest? *Forest Ecology and Management*, 258, 1528-1535.
- Larsson, S. & Danell, K. (2001). Science and the management of boreal forest biodiversity. *Scandinavian Journal of Forest Research*, suppl. 3, 5-9.
- Linder, P. & Östlund, L. (1998). Structural changes in three mid-boreal Swedish forest landscapes, 1885-1996. *Biological Conservation*, 85, 9-19.
- Lindhe, A., Lindelöw, A. & Åsenblad, N. (2005). Saproxylic beetles in standing dead wood density in relation to substrate sun-exposure and diameter. *Biodiversity and Conservation*, 14, 3033-3053.
- Lindhe, A. & Lindelöw, A. (2004). Cut high stumps of spruce, birch, aspen and oak as breeding substrates for saproxylic beetles. *Forest Ecology and Management*, 203, 1-20.
- Liu, R. X., Kuang, J., Gong, Q. & Hou, X. L. (2003). Principal component regression analysis with SPSS. *Computer methods and programs in biomedicine*, 71, 141-7.
- Longton, R. E. (1992). The role of bryophytes and lichens in terrestrial vegetation. In: Bryophytes and lichens in a changing environment. Clarendon Press, Oxford.
- McGeoch, M., Schroeder, M., Ekbohm, B. & Larsson, S. (2007). Saproxylic beetle diversity in a managed boreal forest: importance of stand characteristics and forestry conservation measures. *Diversity & distributions*, 13, 418-429.

- Mielikäinen, K. & Hynynen, J. (2003). Silvicultural management in maintaining biodiversity and resistance of forests in Europe-boreal zone: case Finland. *Journal of environmental management*, 67, 47-54.
- Mohan, D. (2006). Pyrolysis of wood/biomass for bio-oil: A critical review. *Energy & fuels*, 20, 848-889.
- Niklasson, M. & Granström, A. (2000). Numbers and sizes of fires: Long-term spatially explicit fire history in a Swedish boreal landscape. *Ecology*, 81, 1484-1499.
- Nixon, C. M., McClain, M. W. & Donohoe, R. W. (1980). Effects of clear-cutting on gray squirrels. *Journal of Wildlife Management*, 44, 403-412.
- Norberg, G., Jäderlund, A., Zackrisson, O., Nordfjell, T. & Wardle, D. A. (1997). Vegetation control by steam treatment in boreal forests: a comparison with burning and soil scarification. *Canadian Journal of Forest Research*, 27, 2026-2033.
- Nordén, B., Ryberg, M., Götmark, F. & Olausson, B. (2004). Relative importance of coarse and fine woody debris for the diversity of wood-inhabiting fungi in temperate broadleaf forests. *Biological Conservation*, 117, 1-10.
- Økland, B., Bakke, A., Hagvar, S. & Kvamme, T. (1996). What factors influence the diversity of saproxylic beetles? A multiscaled study from a spruce forest in southern Norway. *Biodiversity and Conservation*, 5, 75-100.
- Paillet, Y., Berges, L., Hjäältén, J., Ódor, P., Avon, C., Bernhardt-Römermann, M., Bijlsma, R.-J., De Bruyn, L., Fuhr, M., Grandin, U., Kanka, R., Lundin, L., Luque, S., Magura, T., Matesanz, S., Mészáros, I., Sebastia, M.-T., Schmidt, W., Standovár, T., Tóthmérész, B., Uotila, A., Valladares, F., Vellak, K. & Virtanen, R. (2010). Biodiversity differences between managed and unmanaged forests: meta-analysis of species richness in Europe. *Conservation Biology*, 24, 101-12.
- Palviainen, M., Finer, L., Mannerkoski, H., Piirainen, S. & Starr, M. (2005). Responses of ground vegetation species to clear-cutting in a boreal forest: aboveground biomass and nutrient contents during the first 7 years. *Ecological research*, 20, 652-660.
- Patino, J., Gonzalez Mancebo, J., Fernandez Palacios, J., Arevalo, J. & Bermudez, A. (2009). Short-term effects of clear-cutting on the biomass and richness of epiphytic bryophytes in managed subtropical cloud forests. *Annals of forest science*, 66, 609.
- Pimm, S. L., Russell, G. J., Gittleman, J. L. & Brooks, T. M. (1995). The future of biodiversity. *Science*, 269, 347-50.
- Pykälä, J. (2004). Immediate increase in plant species richness after clear-cutting of boreal herb-rich forests. *Applied Vegetation Science*, 7, 29-34.
- R Development Core Team. (2008). R: a language and environment for statistical computing [Online]. Available: [www.cran.r-project.org](http://www.cran.r-project.org) [Accessed 14.11.10].
- Ranius, T. & Hedin, J. (2001). The dispersal rate of a beetle, *Osmoderma eremita*, living in tree hollows. *Oecologia*, 126, 363-370.
- Roberts, M. R. (2004). Response of the herbaceous layer to natural disturbance in North American forests. *Canadian Journal of Botany*, 82, 1273-1283.
- Röser, D., Asikainen, A., Stupak, I & Pasanen, K. (2008). Forest energy resources and potentials. (ed.), Sustainable use of forest biomass for energy – a synthesis with focus on the Baltic and Nordic region. Springer, Dordrecht.

- Saana, K.-a., Hannu, F. & Jari, H. (2011). Short-term responses of soil decomposer and plant communities to stump harvesting in boreal forests. *Forest Ecology and Management*, 262, 379-388.
- Saint Germain, M., Drapeau, P. & Buddle, C. (2007). Host-use patterns of saproxylic phloeophagous and xylophagous Coleoptera adults and larvae along the decay gradient in standing dead black spruce and aspen. *Ecography*, 30, 737-748.
- Schroeder, L., Ranius, T., Ekbohm, B. & Larsson, S. (2006). Recruitment of saproxylic beetles in high stumps created for maintaining biodiversity in a boreal forest landscape. *Canadian Journal of Forest Research*, 36, 2168-2178.
- Siitonen, J. & Saaristo, L. (2000). Habitat requirements and conservation of *Pytho kolwensis*, a beetle species of old-growth boreal forest. *Biological Conservation*, 94, 211-220.
- Siitonen, J. (2001). Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. *Ecological Bulletins*, 49, 11-41.
- Siitonen, J. & Martikainen, P. (1994). Occurrence of rare and threatened insects living on decaying *Populus-tremula* - a comparison between Finnish and Russian Karelia. *Scandinavian Journal of Forest Research*, 9, 185-191.
- Song, C. (2006). Global challenges and strategies for control, conversion and utilization of CO<sub>2</sub> for sustainable development involving energy, catalysis, adsorption and chemical processing. *Catalysis today*, 115, 2-32.
- Stenbacka, F., Hjältén, J., Hilszczański, J. & Dynesius, M. (2010). Saproxylic and non-saproxylic beetle assemblages in boreal spruce forests of different age and forestry intensity. *Ecological Applications*, 20, 2310-2321.
- Stokland, J. N. & Siitonen, J. (2012). Mortality factors and decay succession. (ed.), Biodiversity in dead wood. Cambridge University Press, New York.
- Sverdrup-Thygeson, A. & Ims, R. A. (2002). The effect of forest clearcutting in Norway on the community of saproxylic beetles on aspen. *Biological Conservation*, 106, 347-357.
- Tilman, D. (1985). The resource-ratio hypothesis of plant succession. *American Naturalist*, 125, 827-852.
- Toivanen, T. & Kotiaho, J. S. (2007). Mimicking natural disturbances of boreal forests: the effects of controlled burning and creating dead wood on beetle diversity. *Biodiversity and Conservation*, 16, 3193-3211.
- Wallace, H. R. (1953). The ecology of the insect fauna of pine stumps. *Journal of Animal Ecology*, 22, 154-171.
- Walmsley, J. D. & Godbold, D. L. (2010). Stump Harvesting for Bioenergy - A Review of the Environmental Impacts. *Forestry*, 83, 17-38.
- Vasiliauskas, R., Juska, E., Vasiliauskas, A. & Stenlid, J. (2002). Community of Aphyllophorales and root rot in stumps of *Picea abies* on clear-felled forest sites in Lithuania. *Scandinavian Journal of Forest Research*, 17, 398-407.
- Widenfalk, O. & Weslien, J. (2009). Plant species richness in managed boreal forests-Effects of stand succession and thinning. *Forest Ecology and Management*, 257, 1386-1394.
- Vitousek, P., Mooney, H., Lubchenco, J. & Melillo, J. (1997). Human domination of Earth's ecosystems. *Science*, 277, 494-499.
- Zackrisson, O. (1977). Influence of forest fires on north Swedish boreal forest. *Oikos*, 29, 22-32.

- Åström, M., Dynesius, M., Hylander, K. & Nilsson, C. 2005. Effects of slash harvest on bryophytes and vascular plants in southern boreal forest clear-cuts. *The Journal of applied ecology*, 42, 1194-1202.
- Åström, M., Dynesius, M., Hylander, K. & Nilsson, C. (2007). Slope aspect modifies community responses to clear-cutting in Boreal forests. *Ecology*, 88, 749-758.



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