

# Logs and Stumps in Clearcuts Support Similar Saproxyllic Beetle Diversity: Implications for Bioenergy Harvest

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Stumps from clear cuts are increasingly used for bioenergy. Extracting this wood will reduce the habitat available for saproxyllic (wood-living) organisms. As little is known about the species assemblages that will be affected, we investigated the diversity of saproxyllic beetles in stumps on clear-felled sites and as a reference, we compared it with the diversity in downed logs. Stumps and logs of aspen (*Populus tremula* L.), birch (*Betula pubescens* Ehrh. and *B. verrucosa* Ehrh.[syn. *B. pendula* Roth]), spruce (*Picea abies* (L.) Karst.) and pine (*Pinus sylvestris* L.) were examined in clear cuts of two different ages: one summer old and 4–5 years old. The beetles were sampled by sieving bark (0.25 m<sup>2</sup>) peeled from the wood. The samples were taken in pairs of one log and one stump situated close together and of the same tree species, age since death and diameter. In total 3348 saproxyllic beetles belonging to 124 species were found in 176 samples. The stumps had a similar number of species to the logs both as measured per sample and as an accumulated number. Exceptions were 4–5 years old wood of birch and pine where the number was significantly higher in the stumps. The number of red-listed species was also similar between stumps and logs. Species composition was more different between the stumps and logs of conifers than of deciduous trees. We conclude that clear-felled stumps have a diverse saproxyllic insect fauna. This has to be taken into account if large scale extraction of logging stumps is implemented.

**Keywords** beetles, biodiversity, bioenergy, Coleoptera, logs, insects, stumps

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## 1 Introduction

The wood from clear-felled stumps has recently received attention as a currently unexploited source of renewable energy. The largest benefit is the replacement of fossil fuels and thus lower net emissions of CO<sub>2</sub>. However, for saproxylic species (i.e. species dependant on dead wood), stump removal reduces the amounts of available substrate (Walmsley and Godbold 2010) and if done on large scale it will impact on this species assemblage. Saproxylic species, especially those dependent on coarse dead wood, have been identified as one of the major losers in modern forestry (Grove 2002). The main reason is the small amounts of dead wood; in the managed forests of Scandinavia this amounts to only 2–10% of the amount present in natural forests where saproxylic species evolved (Fridman and Walheim 2000, Siitonen 2001).

In contrast to most other dead wood in the landscape, the wood in clear cuts is exposed to the sun. Many saproxylic insect species are favoured by, or even dependent on, sun-exposed wood and, for these, the main source of wood suitable for reproduction is found in clear cuts (Kaila et al. 1997, Kouki et al. 2001, Lindhe and Lindelöw 2004). These insect species evolved to reproduce in the wood from trees killed by large-scale disturbances, such as fires or severe storms. Such fires were much more frequent before humans were able to control them (Zackrisson 1977, Niklasson and Drakenberg 2001). Because the insects dispersed readily, they were able to move around in the landscape to new disturbed sites. As such natural disturbances have become rarer and less extensive, the main way that sun-exposed dead wood is currently created in Scandinavia is through clear-felling operations. The amount of stump-wood on the clear cuts is large, and has been estimated to 23 m<sup>3</sup> above ground/ha (67 m<sup>3</sup>/ha with wood below ground included) on clear cuts in southern Sweden (Hofsten 2006). On more northern (boreal) sites in Finland Eräjää et al. (2010) estimated the amount of stump wood above ground to be 12 m<sup>3</sup>/ha. These values are substantially greater than the 2–6 m<sup>3</sup>/ha, which is the usual amount of coarse dead wood (i.e. logs and standing dead trees) in managed forests of

south Sweden (Fridman and Walheim 2000).

The harvesting of clear-felled stumps is undertaken after timber and pulpwood have been extracted. The present technique is to use a stump removal head mounted on an excavator that first splits the stump into two halves before lifting these out (Hofsten 2006, Walmsley and Godbold 2010). Usually the roots break at a diameter of about 5 cm (Hofsten 2006). Harvesting stumps is most widespread in Finland where it began in 2002 and expanded rapidly (Röser et al. 2008, Walmsley and Godbold 2010). In 2007, 313 000 m<sup>3</sup> of wood chips were produced from stumps and roots (Peltola 2008). In Sweden, stump harvesting began in 2005 but at first it was only conducted at an experimental level, prior to management recommendations from the forestry board, which were released in 2009 (Skogsstyrelsen 2009). In Sweden, stumps were also harvested in the 1970s and 80s for use as pulp wood, but the quality was so poor that this was abandoned. Stumps are also harvested in the UK, US and Canada (Walmsley and Godbold 2010).

Even though much research has been conducted on saproxylic insects during recent years, very little is known about which insects utilise clear-felled stumps (but see Hjäältén et al. 2010). This is largely because this type of wood has been regarded as too trivial and therefore has been overlooked. It has often not even been considered when the amount of available habitat for saproxylic organisms has been estimated (e.g. Ekbohm et al. 2006). The few studies that have been undertaken indicate that the insect fauna of clear-felled stumps is different from the fauna of high stumps (Abrahamsson and Lindblad 2006, Hedgren 2007). More generally, it is known that saproxylic species composition is affected by several properties of the wood, such as tree species, sun-exposure, diameter and fungal flora (Palm 1959, Grove 2002, Jonsell et al. 2005, Lindhe et al. 2005).

This study aimed to see if there is an assemblage of species in clear felling stumps that needs to be accounted for at stump harvest. The overall question is which species occur in clear felling stumps, and if there are species of interest for nature conservation among them. Downed logs on the ground were used as a reference to compare with as they are regarded as a substrate

well known for its diversity of saproxyllic beetles (Jonsell et al. 1998, Tikkanen et al. 2006). As stumps until present has been regarded as too trivial for even being measured as dead wood, we hypothesised that stumps would have a less diverse beetle fauna than the logs.

Two measures of species number were used in the comparisons: 1) the average number of species per sample; and 2) the accumulated number of species from all samples within a wood category. If one category has a more homogenous fauna between samples than another, the accumulated number of species will be relatively lower than the average number per sample. In the analyses, particular attention was paid to red-listed species as they can indicate higher conservation values than unlisted species. We studied stumps of two different ages: one summer after clear-felling and 4–5 years after clear-felling, and four different tree species: aspen (*Populus tremula* L.), birch (*Betula pubescens* Ehrh. and *B. verrucosa* Ehrh. [syn. *B. pendula* Roth]), spruce (*Picea abies* (L.) Karst.) and pine (*Pinus sylvestris* L.). More specifically we addressed the following questions:

- Are clear-felled stumps as species-rich as downed logs per wood-object (=sample)?
- Do clear-felled stumps have a lower accumulated number of species over several wood-objects?
- Do red-listed species occur in clear-felled stumps?
- Do different tree species or ages of wood exhibit the same patterns with respect to the questions above?

## 2 Materials and Methods

### 2.1 Study Sites

Samples of stump wood were collected from clear cuts in Uppland, Sweden. The sites were situated within an area measuring 50 km from north to south and 40 km from east to west, with a mid point at 59°50'N, 18°10'E. The region belongs to the hemiboreal region (Ahti et al. 1968) and about half of the land is covered by forests. Almost all forests are managed for timber production and therefore have a rather even age distribution between 0 and 100 years. Most of the forests,

including our sites, are dominated by conifers: Norway spruce and Scots pine. Deciduous trees are usually mixed into the stands. Birch is the most common genus, while aspen and some other species occur more patchily.

Seven clear cuts were selected on the criteria that sites should contain stump wood of all four tree species (aspen, birch, pine and spruce) and that half of the sites should be one summer old and the other half 4–5 years old. The reason to have two age classes was that they contain very different species assemblages, and both might be affected by stump harvest. We ended up with four one summer old clear cuts and three 4–5-year-old clear cuts.

### 2.2 Sampling Procedure

We sampled the beetle fauna by sieving bark from pairs of stumps and logs. The sampling began with a search for downed logs on the clear cuts. The logs could be windblown trees or pieces of timber that the forestry operatives missed during logging. If a log was judged to have been created at the same time as the stumps on the clear cut, it was paired with the nearest stump on the clear cut that was of the same tree species and of similar diameter. We aimed to have a minimum diameter of 20 cm, but as supply of potential objects for the comparison was limited we even included wood down to 12 cm diameter. From both wood pieces, 0.25 m<sup>2</sup> of the bark was peeled off using a knife or axe, and collected in a sieve; then was broken into smaller pieces and sieved. Bark was taken from one patch on the wood object: from the side of the logs and in any direction where bark was present on the stumps. On smaller stumps all bark was sieved. On each clear cut, we sampled as many such pairs as possible for each of the four tree species, up to a maximum of four per species. For some tree species it was not possible to find a single log that met our criteria on some of the one summer old clear cuts (Table 1). In total 4–14 pairs of samples were collected from each one summer old clear cut and 16 pairs of samples were collected from each 4–5-year-old clear cut (Table 1), making totals of 80 and 96 samples respectively. At the time of sieving, each wood item was described on the basis of six variables:

Type (Stump/Log), Age (One summer old/ 4–5 years old), Tree species (Aspen/ Birch/ Spruce/ Pine = *Populus tremula* / *Betula pubescens* and *B. verrucosa* / *Picea abies* / *Pinus sylvestris*), Diameter (cm, measured at the top of the stumps and where the sieve sample was taken on the logs), Bark cover (% estimated by the eye) and Height of stumps (cm) (Table 2).

The sieves had a mesh size of 5–8 mm. The sieved material was brought to the laboratory where beetles were extracted in a Tullgren funnel (also named Berlese funnel) over a period of at least 24 hours (New 1998). This method catches mainly beetles in and under the bark, and beetles that are in the adult life stage when sampling is done (Jonsell and Hansson 2007). The sampling was conducted during 31 October–1 December 2006 and 22 March–4 April 2007. Sieving during these seasons produces more species-rich samples than during the summer (Wikars et al. 2005).

**Table 1.** The number of pairs of samples per clear cut.

|                     | Aspen | Birch | Spruce | Pine |
|---------------------|-------|-------|--------|------|
| One summer old wood |       |       |        |      |
| Clear cut 1         | 4     | 4     | 4      | 2    |
| Clear cut 2         | 0     | 0     | 4      | 0    |
| Clear cut 3         | 0     | 4     | 4      | 2    |
| Clear cut 4         | 0     | 4     | 4      | 4    |
| Sum                 | 4     | 12    | 16     | 8    |
| 4–5-year-old wood   |       |       |        |      |
| Clear cut 5         | 4     | 4     | 4      | 4    |
| Clear cut 6         | 4     | 4     | 4      | 4    |
| Clear cut 7         | 4     | 4     | 4      | 4    |
| Sum                 | 12    | 12    | 12     | 12   |

All saproxylic beetles were determined to species according to Lundberg and Gustafsson (1995). Whether species were saproxylic or not was based on data from Palm (1959), Hansen (1964) and Koch (1989–1992). Red-list categories followed Gärdenfors (2000, 2005, 2010). All species on any of these versions of the red-list were included as we think they are useful as indicators of high conservation value.

### 2.3 Statistics

Differences in beetle species number between stumps and logs were analysed both as average number of species per sample and as total number of species for all samples in the category under consideration (=species density; Gotelli and Colwell 2001). Statistically significant differences ( $p < 0.05$ ) between averages of species per sample were tested with a pairwise t-test, conducted using Statview 5.0.1 for Mac. Pairwise t-testing is useful when sample pairs are collected under the same environmental conditions (Sokal and Rohlf 1995), here defined by the diameter, position and species. For accumulated species number over all samples within a category, 95% confidence limits were calculated by rarefaction using the software EstimateS (Colwell 2006). As numbers of samples were the same in compared categories, all samples could be used in comparisons of species density. Significant differences between categories were considered to have occurred when no category was included within the other category's 95% confidence limits.

**Table 2.** Description of the sampled wood objects shown as average  $\pm$  standard deviation.

|                | Diameter (cm) | Stumps<br>Bark cover (%) | Height (cm) | Logs          |                |
|----------------|---------------|--------------------------|-------------|---------------|----------------|
|                |               |                          |             | Diameter (cm) | Bark cover (%) |
| One summer old |               |                          |             |               |                |
| Aspen          | 40 $\pm$ 7    | 94 $\pm$ 6               | 46 $\pm$ 11 | 27 $\pm$ 4    | 66 $\pm$ 36    |
| Birch          | 34 $\pm$ 9    | 98 $\pm$ 5               | 39 $\pm$ 10 | 18 $\pm$ 3    | 80 $\pm$ 5     |
| Spruce         | 38 $\pm$ 17   | 95 $\pm$ 9               | 54 $\pm$ 30 | 25 $\pm$ 8    | 88 $\pm$ 20    |
| Pine           | 40 $\pm$ 11   | 99 $\pm$ 4               | 34 $\pm$ 13 | 27 $\pm$ 8    | 89 $\pm$ 9     |
| 4–5 yrs old    |               |                          |             |               |                |
| Aspen          | 33 $\pm$ 11   | 87 $\pm$ 25              | 96 $\pm$ 91 | 33 $\pm$ 15   | 55 $\pm$ 56    |
| Birch          | 29 $\pm$ 6    | 87 $\pm$ 16              | 57 $\pm$ 23 | 19 $\pm$ 5    | 71 $\pm$ 21    |
| Spruce         | 36 $\pm$ 11   | 72 $\pm$ 19              | 52 $\pm$ 23 | 25 $\pm$ 8    | 57 $\pm$ 45    |
| Pine           | 42 $\pm$ 6    | 80 $\pm$ 19              | 54 $\pm$ 25 | 33 $\pm$ 8    | 30 $\pm$ 18    |

Species composition was examined using multivariate ordination. Canonical correspondence analysis (CCA) was used to evaluate how important substrate variables were for species composition. The CCA was run with a model including all the variables listed in Table 2. One ordination was run for each tree species to avoid the total inertia being too large ( $>20$ ). Species data were square root transformed, which is advised for count data (Leps and Smilauer 2003). Whether a substrate variable could significantly ( $p < 0.05$ ) explain the species composition was determined by a Monte Carlo simulation test with 499 permutations. The ordination was conducted using CANOCO for Windows 4.5.

Associations between individual species and substrate variables were analysed using multiple regression models, including all variables listed in Table 2. This was conducted for the 35 species occurring in more than five samples. The number of individuals in each sample was the dependent variable. Poisson regression was used, since it is suitable for analysing count data, especially when there are many zeros (Quinn and Keough 2002). However, some species (especially bark beetles), frequently were present either in large numbers or were totally absent. This does not fit well with the Poisson distribution and causes "overdispersion" in the model, implying that levels of significance are likely to be overestimated. Therefore the deviance was rescaled when assessing significance levels, using the DSCALE command in SAS, so that the deviance/df=1. This was done for all species. A variable was judged to be significantly associated with species occurrence if its effects had a probability  $< 0.05$  when it was added last to a model with all variables (Type 3 tables in the SAS software). Another problem with the models is that the calculations fail if a species is totally absent from one category of any variable. In such cases, these categories were excluded from the model; consequently, a variable was entirely excluded in cases where a species occurred in only one variable-category. Statistical test between these categories was made with presence absence data and a Fisher test. The regressions were conducted using SAS (1989–96).

### 3 Results

In the 176 sieve samples a total of 3613 beetles were caught and, of these, 3348 were classified as saproxyllic (Table 3). The material included 124 saproxyllic species, of which 11 are, or have been, red-listed (Table 4). One non-saproxyllic red-listed species, *Stenichnus poweri* in the 2010 red-list category DD (Data Deficient), was represented by one specimen in a spruce log. One species was threatened (=red-listed in a higher category than NT or DD), namely *Corticeus longulus*, which was represented by four specimens in a pine log.

In the paired sieve samples, the average number of species in the one summer old wood (with all tree species pooled) was 3.1 (Standard Error of mean=0.43) for the stumps and 2.6 (SE=0.30) for the logs, but the difference was not statistically significant (paired t-test; df=39;  $t=1.15$ ;  $p=0.26$ ). For the 4–5-year-old wood the stumps contained on average 5.2 (SE=0.48) species and the logs 3.5 (SE=0.35), and this difference was strongly significant (paired t-test; df=47;  $t=3.1$ ;  $p=0.0035$ ). If the data were analysed per tree species, the stumps had a higher average number of species than logs in five of the eight comparisons (Fig. 1a). For the 4–5-year-old birch and pine wood the differences were significant ( $p < 0.05$ , paired t-test, Fig. 1a), whereas no category had a significantly higher number of species associated with the logs.

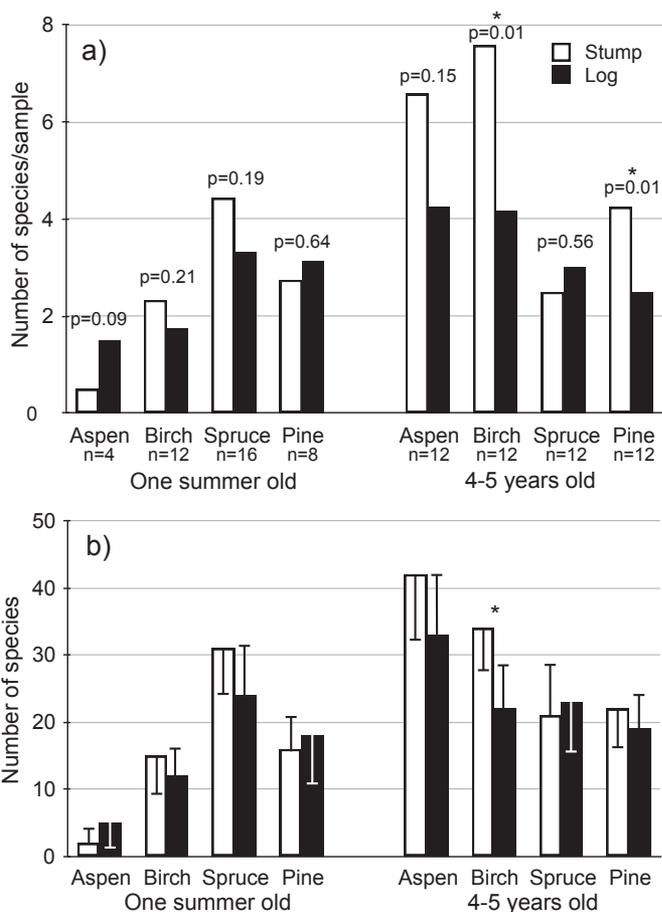
The accumulated species number exhibited a pattern similar to the average number of species per sample: for all comparisons the wood type with highest number of species was the same (Fig. 1b). However, only one comparison produced a significant difference between stumps and

**Table 3.** The total number of beetles collected during the study.

|                                | Stumps | Logs | Total |
|--------------------------------|--------|------|-------|
| No of samples                  | 88     | 88   | 176   |
| No. of beetle individuals      | 1769   | 1844 | 3613  |
| No. of saproxyllic individuals | 1590   | 1758 | 3348  |
| No. of saproxyllic species     | 93     | 87   | 124   |

**Table 4.** Red-listed species (Gärdenfors 2000, 2005 & 2010) of saproxylic beetles encountered in clear cut stumps and logs. Occurr. = Number of samples in which the species occurred; Inds. = Sum of individuals in these samples. Red-list categories: NT = Near Threatened; VU=Vulnerable; EN = Endangered.

| Species                       | Redlist cat.<br>2000, 05, 10 | Stump   |       | Log     |       | No of occurrences in |       |        |      |
|-------------------------------|------------------------------|---------|-------|---------|-------|----------------------|-------|--------|------|
|                               |                              | Occurr. | Inds. | Occurr. | Inds. | Aspen                | Birch | Spruce | Pine |
| <i>Tachyta nana</i>           | -, -, NT                     | 1       | 1     | 5       | 10    | 2                    | 3     | 0      | 1    |
| <i>Plegaderus caesus</i>      | NT, -, -                     | 2       | 2     | 0       | 0     | 1                    | 1     | 0      | 0    |
| <i>Ptinella aptera</i>        | NT, -, -                     | 5       | 23    | 1       | 11    | 2                    | 3     | 0      | 1    |
| <i>Agathidium mandibulare</i> | NT, NT, NT                   | 1       | 2     | 0       | 0     | 1                    | 0     | 0      | 0    |
| <i>Agaricochara latissima</i> | VU, NT, NT                   | 0       | 0     | 1       | 1     | 1                    | 0     | 0      | 0    |
| <i>Cyphea curtula</i>         | NT, NT, NT                   | 0       | 0     | 1       | 1     | 1                    | 0     | 0      | 0    |
| <i>Lacon fasciatus</i>        | -, -, NT                     | 1       | 1     | 1       | 1     | 0                    | 0     | 1      | 1    |
| <i>Ampedus cinnabarinus</i>   | NT, NT, NT                   | 3       | 3     | 0       | 0     | 0                    | 2     | 0      | 1    |
| <i>Cerylon deplanatum</i>     | NT, -, NT                    | 0       | 0     | 2       | 27    | 2                    | 0     | 0      | 0    |
| <i>Ennearthron laricinum</i>  | NT, NT, NT                   | 0       | 0     | 1       | 1     | 0                    | 0     | 1      | 0    |
| <i>Corticеus longulus</i>     | -, NT, EN                    | 0       | 0     | 1       | 4     | 0                    | 0     | 0      | 1    |
| No of species                 | 11                           | 6       |       | 8       |       | 7                    | 4     | 2      | 5    |
| No of occurrences             | -                            | 13      |       | 13      |       | 10                   | 9     | 2      | 5    |



**Fig. 1.** Number of species associated with clear-felled stumps and logs sampled pairwise: a) average number of species per sample; b) the accumulated number of species for all samples within each category. n=number of pairs; p-values are given for each pairwise t-test; “\*” denotes a significant (p<0.05) difference; Error bars indicate half of the 95 % confidence limit. (t-values for comparisons in graph a were: -2.44, 1.34, 1.39, -0.48, 1.52, 2.87, -0.60, 3.09 respectively).

**Table 5.** Results from the CCA-ordinations for different tree-species of the saproxyllic beetle species composition. Values for the different variables are p-values from a Monte Carlo simulation testing whether the variables significantly ( $p < 0.05$ ) explain species composition.

|                       | Aspen | Birch | Spruce | Pine  |
|-----------------------|-------|-------|--------|-------|
| Total inertia         | 10.6  | 12.1  | 16.6   | 12.4  |
| Canonical eigenvalues | 1.6   | 1.1   | 1.7    | 1.6   |
| Variables             |       |       |        |       |
| Type                  | 0.24  | 0.44  | 0.002  | 0.006 |
| Age                   | 0.018 | 0.002 | 0.002  | 0.002 |
| Diameter              | 0.004 | 0.30  | 0.39   | 0.52  |

logs: the 4–5-year-old birch-wood (Fig. 1b). When all tree species were pooled, the one summer old stumps and logs contained the same number of species, 43 (95 % confidence limits =  $\pm 6.92$  for stumps and  $\pm 9.67$  for logs), whereas the 4–5-year-old stumps had 68 ( $\pm 10.85$ ) species and the logs 58 ( $\pm 10.94$ ). The difference, however, was not significant, as both categories laid within the 95 % confidence limits of the other category.

There were six red-listed species associated with the stumps and eight with the logs (Table 4). If only species red-listed in 2010 were counted, the equivalent numbers were four and seven, respectively. The numbers of occurrences (sum of number of species per sample) of red-listed species were same (13) in the stumps and the logs (Table 4). Aspen had the highest number of red-listed species (seven), and spruce the lowest (two) (Table 4).

The species composition was, according to the CCA analysis, significantly different between stumps and logs of both spruce and pine (Table 5). For aspen and birch the difference between stumps and logs was far from significant.

Individual associations with substrate variables were analysed for 35 insect species: 17 of these were significantly associated with stumps, and seven with logs (Table 7). However, *Cis punctulatus* was the only species found in just one category (logs).

Among the beetle species associated with aspen or birch about half had a significant association with one of the substrate types (stump or log) and the other half had no significant association

**Table 6.** Number of beetle species associated with different combinations of wood categories as revealed by the Poisson regression models (Table 7). A beetle species might be associated with more than one tree species, explaining why the total sum of associations exceeds the number of species.

|        | Association with |     |     | Species with no specific association with Stump or Log |
|--------|------------------|-----|-----|--|
|        | Stump            | Log | Sum |  |
| Aspen  | 5                | 1   | 6   | 6  |
| Birch  | 8                | 0   | 8   | 7  |
| Spruce | 7                | 3   | 10  | 1  |
| Pine   | 6                | 1   | 7   | 1  |
| Old    | 10               | 3   | 13  | 6  |
| Young  | 5                | 4   | 9   | 1  |

(Table 6). For species associated with spruce or pine almost all species were significantly associated with either stumps or logs.

## 4 Discussion

Contradictory to our expectations, we found the clear-felled stumps to be at least as species rich as the logs, with respect to both the average number of species per sample and the accumulated species density. Although there were some difference in average diameter between the categories (Table 2), we think our study gives a valid comparison between stumps and logs, because influence of diameter on the beetle fauna has been proven to be small within the range studied here (Sverdrup-Thygeson and Ims 2002, Jonsell et al. 2005, Lindhe et al. 2005). Also our not yet published own data from clear-felling stumps show small, if any, effects. In two of the eight comparisons between wood types the average number of species per sample was actually significantly higher for stumps than for logs; there was no case in which logs were more species rich than stumps. For the accumulated species density, one category had significantly more species in stumps than in logs. Thus, we conclude that stumps harbour a species rich fauna of saproxyllic beetles, a conclusion supported by another recent study in north Sweden (Hjältén et al. 2010).

**Table 7.** Results of Poisson regressions for individual species where numbers report the parameter estimate of which **bold** numbers are categories/variables with significant ( $p < 0.05$ ) associations. For categories estimates are given as compared to the reference category, marked with "0". "N" = All samples used in the model. "n" = the number of samples in which the species occurred. "dev/df" = Deviance/degrees of freedom for the model. "-" denotes no occurrence of the species in the category, which therefore was excluded from the model (as calculations fail). "+" denotes a category including all occurrences of a species. All species occurring in >5 samples are analysed and listed in systematic order (Lundberg and Gustafsson 1995).

| Species                                    | N(n)    | dev/df | Type        |             | Age         |             | Tree species |             |             |             | Diameter     |
|--|---------|--------|-------------|-------------|-------------|-------------|--------------|-------------|-------------|-------------|--------------|
|  |         |        | Stump       | Log         | Young       | Old         | Aspen        | Birch       | Spruce      | Pine        |              |
| <i>Tachyta nana</i>                        | 72(6)   | 0.70   | 0           | <b>2.35</b> | -           | +           | 0.001        | 0.61        | -           | 0           | 0.01         |
| <i>Ptinella aptera</i>                     | 72(6)   |        | 0.55        | 0           | -           | +           | <b>2.91</b>  | <b>3.37</b> | -           | 0           | 0.04         |
| <i>Ptinella tenella</i>                    | 72(9)   | 8.96   | <b>1.72</b> | 0           | -           | +           | 1.45         | <b>2.24</b> | -           | 0           | 0.01         |
| <i>Microscydnum nanus</i>                  | 72(6)   | 2.77   | <b>4.01</b> | 0           | -           | +           | 0.82         | 0.13        | -           | 0           | -0.04        |
| <i>Phosphuga atrata</i>                    | 72(11)  | 0.72   | 0           | <b>1.16</b> | -           | +           | 0.80         | -           | 0           | 0.23        | <b>-0.08</b> |
| <i>Gabrius splendidulus</i>                | 96(22)  | 1.42   | <b>2.25</b> | 0           | -           | +           | <b>1.99</b>  | 1.08        | 0           | <b>1.55</b> | 0.03         |
| <i>Nudobius lentus</i>                     | 175(16) | 0.45   | 0           | <b>0.92</b> | <b>2.59</b> | 0           | 0.94         | 0           | 0.39        | 0.55        | <b>0.03</b>  |
| <i>Euplectus nanus</i>                     | 96(13)  | 1.44   | 0.38        | 0           | -           | +           | <b>3.19</b>  | 1.89        | 0           | 1.21        | 0.04         |
| <i>Tyrus mucronatus</i>                    | 175(24) | 0.84   | <b>1.42</b> | 0           | 0           | <b>2.65</b> | 0            | <b>1.85</b> | <b>0.71</b> | <b>2.52</b> | 0.02         |
| <i>Phloeonomus pusillus</i>                | 71(15)  | 2.67   | <b>1.33</b> | 0           | +           | -           | -            | 0           | <b>3.79</b> | <b>2.55</b> | -0.02        |
| <i>Phloeonomus sjoeborgi</i>               | 48(10)  | 1.23   | <b>1.24</b> | 0           | +           | -           | -            | -           | <b>0.85</b> | <b>0</b>    | -0.03        |
| <i>Phloeocharis subtilissima</i>           | 175(15) | 0.69   | <b>0.79</b> | 0           | 0           | 0.63        | 0            | 0.74        | 1.21        | 1.10        | <b>-0.05</b> |
| <i>Dinaraea aequata</i>                    | 175(7)  | 0.33   | 0           | 0.39        | 0           | 0.23        | 0.11         | 0.23        | 1.15        | 0           | -0.03        |
| <i>Dinaraea linearis</i>                   | 96(8)   | 2.80   | <b>4.17</b> | 0           | -           | +           | <b>4.16</b>  | 0.88        | 0           | 0.59        | 0.02         |
| <i>Leptusa fumida</i>                      | 175(16) | 0.56   | 0           | 0.18        | 0.08        | 0           | 0.003        | 0           | 0.08        | 0.31        | -0.01        |
| <i>Anomagnath. cuspidatus</i>              | 47(6)   | 0.97   | 0.96        | 0           | 0.16        | 0           | -            | +           | -           | -           | -0.05        |
| <i>Homalota plana</i>                      | 175(10) | 1.02   | 0           | <b>2.73</b> | <b>4.09</b> | 0           | <b>1.47</b>  | 0           | 0.25        | <b>3.42</b> | <b>0.08</b>  |
| <i>Glischr. quadripunctatus</i>            | 135(7)  | 0.42   | <b>1.53</b> | 0           | <b>2.48</b> | 0           | <b>1.61</b>  | 0           | <b>1.89</b> | -           | 0.01         |
| <i>Rhizophagus dispar</i>                  | 175(22) | 1.23   | <b>1.45</b> | 0           | 0           | <b>1.81</b> | 1.98         | <b>3.98</b> | <b>2.41</b> | 0           | 0.03         |
| <i>Rhizoph. bipustulatus</i>               | 175(21) | 0.66   | <b>1.70</b> | 0           | 0.43        | 0           | 1.83         | <b>3.48</b> | 0           | 0.67        | <b>-0.05</b> |
| <i>Cerylon histeroides</i>                 | 135(7)  | 0.36   | <b>2.04</b> | 0           | 0           | <b>2.29</b> | <b>1.12</b>  | <b>1.20</b> | 0           | -           | <b>0.05</b>  |
| <i>Enicmus rugosus</i>                     | 175(26) | 1.19   | <b>2.84</b> | 0           | 0           | <b>0.68</b> | <b>1.82</b>  | <b>2.21</b> | 0           | <b>2.54</b> | -0.003       |
| <i>Corticaria rubripes</i>                 | 143(9)  | 0.61   | <b>3.43</b> | 0           | <b>3.06</b> | 0           | -            | 0.13        | 0.15        | 0           | <b>-0.04</b> |
| <i>Corticaria longicollis</i>              | 175(21) | 0.73   | <b>2.28</b> | 0           | 0           | <b>3.04</b> | 0            | <b>3.07</b> | <b>2.80</b> | <b>1.88</b> | 0.01         |
| <i>Cis comptus</i>                         | 96(11)  | 1.60   | <b>3.00</b> | 0           | -           | +           | 1.49         | <b>3.51</b> | 0           | 0.67        | <b>-0.08</b> |
| <i>Cis hispidus</i>                        | 72(22)  | 3.62   | 0.35        | 0           | -           | +           | <b>2.90</b>  | <b>3.26</b> | 0           | -           | -0.04        |
| <i>Cis boleti</i>                          | 79(8)   | 0.66   | 0.84        | 0           | 0           | <b>1.75</b> | <b>0.42</b>  | <b>0</b>    | -           | -           | <b>-0.07</b> |
| <i>Cis punctulatus</i>                     | 12(6)   | 1.24   | -           | +           | -           | +           | -            | -           | +           | -           | -0.04        |
| <i>Sulcacis affinis</i>                    | 96(26)  | 8.32   | 0.11        | 0           | -           | +           | <b>3.80</b>  | <b>5.47</b> | 0           | 1.55        | -0.02        |
| <i>Bitoma crenata</i>                      | 175(40) | 3.46   | 0           | 0.25        | 0           | <b>1.95</b> | <b>2.43</b>  | <b>3.24</b> | 0           | 1.09        | <b>0.04</b>  |
| <i>Litargus connexus</i>                   | 55(8)   | 0.61   | 0.90        | 0           | +           | -           | -            | <b>0.85</b> | 0           | -           | -0.06        |
| <i>Pityogenes chalcographus</i>            | 48(15)  | 16.0   | 0           | <b>2.51</b> | +           | -           | -            | -           | <b>4.56</b> | 0           | <b>-0.23</b> |
| <i>Ips typographus</i>                     | 32(9)   | 14.0   | 0           | <b>4.07</b> | +           | -           | -            | -           | +           | -           | -0.05        |
| <i>Dryocoetes autographus</i>              | 32(9)   | 19.8   | <b>4.08</b> | 0           | +           | -           | -            | -           | +           | -           | -0.01        |
| <i>Crypturgus</i> spp.                     | 143(12) | 9.8    | 0           | 0.78        | 0.32        | 0           | -            | 0           | <b>5.76</b> | <b>3.49</b> | <b>-0.07</b> |
| No of species with significant association | 35      | -      | 17          | 7           | 10          | 19          | 12           | 15          | 11          | 8           | 12           |

Since the patterns for the average number of species per sample and the accumulated species density over all samples were similar, we conclude that there was no difference between stumps and logs with respect to the homogeneity of the

fauna between samples. (A more homogenous category should have a lower accumulated species number than a more heterogeneous, relative to the difference between the two in species number per sample). A higher homogeneity of the fauna has

been identified for man-made high stumps compared to naturally-created high stumps (Jonsell et al. 2004). It has been suggested that the difference is the result of the homogenous mode and timing of death of man-made high stumps compared to natural ones. Correspondingly, since the clear cut stumps in this study were created by a single technique over a short time period, we hypothesised that they would be more homogenous than the logs, which were created by wind throw and by logging and probably also originated at different times of the year (although their successional stage resembled that of the paired stump). This hypothesis was not, however, supported by our data.

Logs had a somewhat higher number of red-listed species than stumps but they had the same number of occurrences. The only threatened species (= species listed in a category higher than 'Near Threatened') was found in a pine log: *Corticium longulus* (Tenebrionidae) which is classified as Endangered (Gärdenfors 2010). This species is often associated with two bark beetle species present in pine, namely *Ips acuminatus* and *Tomicus minor*. Both these species seem to experiencing a decline in their abundance and a contraction of their range; *Ips acuminatus*, in particular, has been added to the red-list (Lindelöw 2010). These two bark beetles do not occur under the thick bark at the tree base (Lekander et al. 1977), so it is unlikely that *C. longulus* would use stumps as its habitat. Thus, the red-listed species in this study show a tendency towards greater diversity in logs than in stumps. However, the difference was far from statistically significant and the absolute diversity values for the stumps were high.

The results of this study contradict results for saproxyllic fungi, for which Hottola (2009) reported that conservationally interesting species were rarely found on "trivial dead wood", such as clear-felled stumps. Instead, they required logs in areas associated with old-growth stands. The moss flora also seems to consist of widespread and common species on stumps. However, the results for lichens are more similar to our beetle results, as several rare but not red-listed lichen species occur on stumps, but they are associated with later successional stages than those studied here (Caruso and Rudolphi 2009).

The difference in results between organism

groups highlights the need to investigate the ecological consequences of management actions across a wide range of different groups, since they can respond very differently. Correspondingly, it raises the question of how representative the results presented here are for the other two insect groups with a rich saproxyllic fauna, namely Diptera and Hymenoptera (deJong et al. 2004). We think that they are more likely to respond in a similar way to the beetles, than to mosses, lichens or fungi, but we have no data to provide evidence for this contention.

Both the ordination and the analysis of substrate associations showed that there were differences in species composition between stumps and logs. However, there was only one species, *Cis punctulatus*, that was restricted to just one of the substrate categories (i.e. logs). This beetle feeds on the fungus *Trichaptum abietinum* (Reibnitz 1999) and, in reality, is probably not restricted to logs as the fungus often is found on stumps (Vasiliauskas et al. 2002, Vasiliauskas et al. 2005). Thus, all species seem to be able to use both types of wood although several are more associated with one of them than the other. This pattern was to be expected, since the clear felling stumps is a relatively new phenomenon compared to natural systems, and no species has had time to evolve to specialise on it. The original habitat of the species associated with clear-felled stumps was probably the bases of standing dead trees. They have a similar, but not the same, fauna (Abrahamsson and Lindbladh 2006). The differences in population densities on various wood categories implies that different species will be differently affected by the same amount of stump harvest: high densities in a wood type that is extensively harvested will lead to larger drop in population size than other occurrence patterns. To understand the effects on population levels one thus need knowledge on amounts of various types of wood and densities of populations in them for a whole landscape.

The difference in species composition between stumps and logs was much stronger for the coniferous than the deciduous trees, as shown both in the ordination and in the analysis of individual species' associations. Similarly, there were more species that had significant associations in the one summer old wood than in the 4–5-year-old wood. It is a well established fact that several bark-beetle

species in conifers have strong associations with specific parts of the trunk (Lekander et al. 1977), and apparently this is also true for other groups of beetles that utilise conifers, since the bark-beetles can explain only part of the difference found here. The lower specificity of beetle species associated with the 4–5-year-old wood is probably connected to the specificity of fungi growing in the wood, since, some years after tree death, the beetle species composition becomes controlled more by the fungal flora than by the actual tree species (Wallace 1953, Lawrence 1989, Jonsell et al. 2005). However, if this is the case, we also have to assume that the fungi used by the beetles are also indiscriminate in their use of substrate (stumps or logs); this does appear to be the case for the more common and widespread wood-decaying fungi (Allmér et al. 2005, Hottola 2009).

Aspen supported the greatest number of red-listed species, while spruce supported the fewest. Similarly, aspen supports a comparatively rich fauna on its logging residues and high stumps (Lindhe and Lindelöv 2004, Jonsell et al. 2007), confirming that it is particularly valuable for biodiversity in Fennoscandia (Niemelä 1997, Martikainen 2001, Sverdrup-Thygeson and Ims 2002, Kouki et al. 2004). In contrast, spruce has rather different numbers of red-listed species depending on what type of wood is considered. On high stumps, spruce supports similar numbers to species such as birch (Lindhe and Lindelöv 2004) and the pattern is similar on the clear-cut stumps although spruce supported somewhat fewer species than the other tree species. However, logging residues has an even lower species number (Jonsell et al. 2007). The lower biodiversity value of spruce logging residues (Jonsell et al. 2007), therefore, seems not to be valid for coarser spruce wood, including stumps.

In conclusion this study shows that the biodiversity value of stump wood in clear cuts is important to consider. At present, the harvesting of stumps is restricted (except, maybe, in Finland) but an expansion would probably lead to problems analogous to those caused by the large scale and effective harvesting of timber during the last century, risking another set of species being placed on the red-list. Some harvesting has to be tolerated despite its biodiversity value, because of the need for additional sources of biofuels, but it is

difficult to set an appropriate level (Jonsell 2007). As these species may use wood of many different kinds, and in all types of forest stands, studies on the landscape level are important to assess the importance of the stumps for the populations on long term. Based on such studies we could learn how to select stands for stump harvest and make recommendations how to minimise the negative effect per volume of harvested stump wood.

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## 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(1–3): 230–237.
- Ahti, T., Hämet-Ahti, L. & Jalas, J. 1968. Vegetation zones and their sections in north-western Europe. *Annales Botanici Fennici* 5: 169–211.
- Allmér, J., Stenlid, J. & Dahlberg, A. 2005. Fungal communities on fine woody debris of Norway spruce (*Picea abies* [L.] Karst.) in clear-cuts, thinned and old-growth forests in east-central Sweden. In: Allmér, J. (ed.). *Fungal communities in branch litter of Norway spruce: dead wood dynamics, species detection and substrate preferences*. Doctoral thesis no 2005:125, Faculty of natural resources and agricultural sciences, SLU, Uppsala, paper III. 21 p.
- Caruso, A. & Rudolphi, J. 2009. Influence of substrate age and quality on species diversity of lichens and bryophytes on stumps. *The Bryologist* 112(3): 520–531.
- Colwell, R.K. 2006. EstimateS: Statistical estimation of species richness and shared species from samples.

- Version 8.0. <http://purl.oclc.org/estimates>.
- deJong, J., Dahlberg, A. & Stokland, J.N. 2004. Död ved i skogen. Hur mycket behövs för att bevara den biologiska mångfalden? *Svensk Botanisk Tidskrift* 98(5): 278–297. (In Swedish.)
- Ekbom, B., Schroeder, M. & Larsson, S. 2006. Stand specific occurrence of coarse woody debris in a managed boreal forest landscape in central Sweden. *Forest Ecology and Management* 221(1–3): 2–12.
- Eräjää, S., Halme, P., Kotiaho, J.S., Markkanen, A. & Toivainen, T. 2010. The volume and composition of dead wood on traditional and forest fuel harvested clear-cuts. *Silva Fennica* 44(2): 203–211.
- Fridman, J. & Walheim, M. 2000. Amount, structure, and dynamics of dead wood on managed forestland in Sweden. *Forest Ecology and Management* 131(1–3): 23–36.
- Gårdenfors, U. 2000. Rödlistade arter i Sverige 2000 – The 2000 red list of Swedish species. ArtData-banken, SLU, Uppsala. 397 p.
- 2005. Rödlistade arter i Sverige 2005. ArtData-banken, SLU, Uppsala. 496 p. (In Swedish.)
- 2010. The 2010 red list of Swedish species. ArtData-banken, SLU, Uppsala. 590 p.
- Gotelli, N.J. & Colwell, R.K. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters* 4(4): 379–391.
- Grove, S.J. 2002. Saproxyllic insect ecology and the sustainable management of forests. *Annual Review of Ecology and Systematics* 33: 1–23.
- Hansen, V. 1964. Fortegnelse over Danmarks biller 1. og 2. del. (Catalogue of the Coleoptera of Denmark 1 and 2nd part). *Entomologiske Meddelelser* 33(1–2): 1–507.
- Hedgren, P.O. 2007. Early arriving saproxyllic beetles (Coleoptera) and parasitoids (Hymenoptera) in low and high stumps of Norway spruce. *Forest Ecology and Management* 241(1–3): 155–161.
- Hjältén, J., Stenbacka, F. & Andersson, J. 2010. Saproxyllic beetle assemblages on low stumps, high stumps and logs: Implications for environmental effects of stump harvesting. *Forest Ecology and Management* 260: 1149–1155.
- Hofsten, H.v. 2006. Maskinell upptagning av stubbar – möjligheter och problem. Arbetsrapport från Skogforsk 621, Uppsala. 11 p. (In Swedish.)
- Hottola, J. 2009. Communities of wood-inhabiting fungi: ecological requirements and responses to forest management and fragmentation. PhD thesis, University of Helsinki.
- Jonsell, M. 2007. Effects on biodiversity at forest fuel extraction, governed by processes working on large scale. *Biomass and Bioenergy* 31(10): 726–732.
- & Hansson, J. 2007. Comparison of methods for sampling saproxyllic beetles in fine wood. *Entomologica Fennica* 18: 232–241.
- , Weslien, J. & Ehnström, B. 1998. Substrate requirements of red-listed saproxyllic invertebrates in Sweden. *Biodiversity and Conservation* 7(6): 749–764.
- , Nittérus, K. & Stighäll, K. 2004. Saproxyllic beetles in natural and man-made deciduous high stumps retained for conservation. *Biological Conservation* 118(2): 163–173.
- , Schroeder, M. & Weslien, J. 2005. Saproxyllic beetles in high stumps of spruce – fungal flora important for determining the species composition. *Scandinavian Journal of Forest Research* 20(1): 54–62.
- , Hansson, J. & Wedmo, L. 2007. Diversity of saproxyllic beetle species in logging residues in Sweden – comparisons between tree species and diameters. *Biological Conservation* 138(1–2): 89–99.
- Kaila, L., Martikainen, P. & Punttila, P. 1997. Dead trees left in clearcuts benefit saproxyllic Coleoptera adapted to natural disturbances in boreal forests. *Biodiversity and Conservation* 6(1): 1–18.
- Koch, K. 1989–1992. Die Käfer Mitteleuropas. Ökologie. Band 1–3. Goecke & Evers, Krefeld. 382 p.
- Kouki, J., Löfman, S., Martikainen, P., Rouvinen, S. & Uotila, A. 2001. Forest fragmentation in Fennoscandia: Linking habitat requirements of wood-associated threatened species to landscape and habitat changes. *Scandinavian Journal of Forest Research Supplement* 7 3: 27–37.
- , Arnold, K. & Martikainen, P. 2004. Long-term persistence of aspen – a key host for many threatened species – is endangered in old-growth conservation areas in Finland. *Journal for Nature Conservation* 12(1): 41–52.
- Lawrence, J.F. 1989. Mycophagy in the Coleoptera: Feeding strategies and morphological adaptations. In: Wilding, N., Collins, N.M., Hammond, P.M. & Webber, J.F. (eds.). *Insect-fungus interactions*. 14th Symp. of R. Entomol. Soc. London. Academic Press, London. p. 1–23.
- Lekander, B., Bejer-Petersen, B., Kangas, E. & Bakke,

- A. 1977. The distribution of bark beetles in the Nordic countries. *Acta Entomologica Fennica* 32: 1–37.
- Leps, J. & Smilauer, P. 2003. *Multivariate analysis of ecological data using CANOCO*. Cambridge University Press.
- Lindelöw, Å. 2010. Aktuellt om svenska barkborrar (Coleoptera: Curculionidae, Scolytinae). *Entomologisk Tidskrift* 131(2): 97–104. (In Swedish.)
- Lindhe, A. & Lindelöw, Å. 2004. Cut high stumps of spruce, birch, aspen and oak as breeding substrates for saproxylic beetles. *Forest Ecology and Management* 203(1–3): 1–20.
- , Lindelöw, Å. & Åsenblad, N. 2005. Saproxylic beetles in standing dead wood – density in relation to substrate sun-exposure and diameter. *Biodiversity and Conservation* 14(12): 3033–3053.
- Lundberg, S. & Gustafsson, B. 1995. *Catalogus Coleopterorum Sueciae*. Naturhistoriska Riksmuseet, Stockholm. 215 p.
- Martikainen, P. 2001. Conservation of threatened saproxylic beetles: significance of retained aspen *Populus tremula* on clearcut areas. *Ecological Bulletin* 49: 205–218.
- New, T.R. 1998. *Invertebrate surveys for conservation*. Oxford University Press, Oxford. 240 p.
- Niemelä, J. 1997. Invertebrates and boreal forest management. *Conservation Biology* 11(3): 601–610.
- Niklasson, M. & Drakenberg, B. 2001. A 600-year tree-ring fire history from Norra Kvills National Park, southern Sweden: implications for conservation strategies in the hemiboreal zone. *Biological Conservation* 101(1): 63–71.
- Palm, T. 1959. Die Holz- und Rindenkäfer der süd- und mittelschwedischen Laubbäume. *Opuscula Entomologica Supplementum* 16: 1–374.
- Peltola, A. 2008. *Statistical yearbook of forestry*. Finnish Forest Research Institute.
- Quinn, G.P. & Keough, M.J. 2002. *Experimental design and data analysis for biologists*. Cambridge University Press, Cambridge. 537 p.
- Reibnitz, J. 1999. Verbreitung und Lebensräume der Baumschwammfresser Südwestdeutschlands (Coleoptera: Cisidae). *Mitteilungen Entomologischer Verein Stuttgart* 1869 e.V. 34: 2–75.
- Röser, D., Asikainen, A., Stupak, I. & Pasanen, K. 2008. Forest energy resources and potentials. In: Röser, D., Asikainen, A., Raulund-Rasmussen, K. & Møller, I.S. (eds.). *Sustainable use of wood for energy – a synthesis with focus on the Nordic-Baltic region*. Springer. p. 9–28.
- SAS. 1989–96. version 6.12 for Mac. SAS Institute Inc, Cary, NC.
- Siitonen, J. 2001. Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. *Ecological Bulletin* 49: 11–41.
- Skogsstyrelsen. 2009. *Stubbskörd – kunskapssammanställning och Skogsstyrelsens kommentarer*. Meddelande 4/2009, Skogsstyrelsen, Jönköping. (In Swedish.)
- Sokal, R.R. & Rohlf, F.J. 1995. *Biometry: the principles and practice of statistics in biological research*. Third edition. W. H. Freeman and company, New York. 887 p.
- 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(3): 347–357.
- Tikkanen, O.-P., Martikainen, P., Hyvärinen, E., Junninen, K. & Kouki, J. 2006. Red-listed boreal forest species of Finland: associations with forest structure, tree species, and decaying wood. *Annales Zoologici Fennici* 43(4): 373–383.
- 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(5): 398–407.
- , Larsson, E., Larsson, K.-H. & Stenlid, J. 2005. Persistence and long-term impact of Rotstop biological control agent on mycodiversity in *Picea abies* stumps. *Biological Control* 32(2): 295–304.
- Wallace, H.R. 1953. The ecology of the insect fauna of pine stumps. *Journal of Animal Ecology* 22(1): 154–171.
- Walmsley, J.D. & Godbold, D.L. 2010. Stump harvesting for bioenergy – a review of the environmental impacts. *Forestry* 83(1): 17–38.
- Wikars, L.-O., Sahlin, E. & Ranius, T. 2005. A comparison of three methods to estimate species richness of saproxylic beetles (Coleoptera) in logs and high stumps of Norway spruce. *The Canadian Entomologist* 137(3): 304–324.
- Zackrisson, O. 1977. Influence of forest fires on the North Swedish boreal forest. *Oikos* 29(1): 22–32.

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