

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

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**Abstract**—The amount of dead wood in forests has decreased owing to modern forest practices, and many species associated with this habitat are currently threatened. In Sweden during the last decade, naturally downed logs have been retained and, at clearcuts, high stumps have been artificially created to maintain saproxylic (dead wood dependent) insects. We tested how much these types of dead wood are used by sampling saproxylic beetles in dead wood of Norway spruce (*Picea abies* (L.) Karst.; Pinaceae) in managed forests in central Sweden. To analyse how surveys should be conducted in these kinds of studies, we compared three methods over an entire growing season. We found that the relationship between the type of dead wood and species richness was statistically significant when we used bark sieving and emergence traps, but not when we used window traps. It is impossible to ascertain whether beetles collected with window traps are related to the type of dead wood on which they are found and, therefore, such traps are less useful in studies of specific substrates. The yield from sieving was highest in spring and autumn, whereas species richness in window trap samples peaked in June and July and that in emergence traps peaked from May to July. With emergence traps we collected, on average, about twice the number of species over the whole season as we did by sieving on a single occasion in the spring. Both emergence trapping and sieving reveal what is present in individual pieces of dead wood, but these methods sample partly different faunas. We found fewer species on artificially created high stumps (on clearcuts); however, these stumps seem to be useful for some red-listed species.

**Résumé**—La quantité de bois mort dans les forêts a diminué à cause des pratiques forestières modernes et plusieurs espèces associées à cet habitat se trouvent actuellement menacées. En Suède au cours de la dernière décennie, les troncs tombés naturellement sont laissés sur place et de hautes souches sont créées artificiellement lors des coupes à blanc afin de préserver les insectes saproxyliques (dépendants du bois mort). Nous avons évalué dans quelle mesure ces types de bois mort sont utilisés en échantillonnant les coléoptères saproxyliques dans le bois mort de l'épinette de Norvège (*Picea abies* (L.) Karst.; Pinaceae) dans des forêts aménagées du centre de la Suède. La comparaison de trois méthodes d'inventaire sur une saison entière de croissance nous a permis de déterminer comment procéder dans ce genre d'étude. La relation entre le type de bois et la richesse en espèces est statistiquement significative lorsque nous utilisons les méthodes de tamisage des écorces ou du piège à émergence, mais non celle du piège d'interception vitré. Il n'est pas possible de déterminer si les coléoptères capturés dans les pièges d'interception sont reliés au type de bois mort sur lequel ils sont trouvés; ces pièges sont donc moins utiles pour l'étude de substrats spécifiques. Le rendement du tamisage est maximal au printemps et à l'automne, alors que la richesse en espèces dans les échantillons atteint son sommet en juin et en juillet dans les pièges d'interception et en mai à juillet dans les pièges à émergence. Nous récoltons en moyenne dans les pièges à émergence au cours de toute la saison environ le double des espèces récoltées dans une seule séance de tamisage au printemps. Les pièges à émergence et le tamisage révèlent les espèces présentes dans les pièces individuelles de bois mort, mais ils

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échantillonnent des faunes partiellement différentes. Il y a moins d'espèces sur les hautes souches créées artificiellement sur les sites de coupe à blanc, qui semblent, néanmoins, importantes pour quelques espèces de la liste rouge.

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## Introduction

A large proportion of the species in boreal forests are saproxylic (Siitonen 2001), *i.e.*, they either depend directly on dead wood or live on other saproxylic species during some part of their life cycle (Speight 1989). The amount of dead wood in boreal forests has decreased owing to modern forestry practices and, therefore, many of the species associated with this habitat are currently threatened (Jonsson *et al.* 2005). For that reason there is a need for knowledge of how different silvicultural practices affect saproxylic organisms and also how this fauna and flora should be surveyed. Among saproxylic organisms, beetles (Coleoptera) are among the largest taxa (*e.g.*, Berg *et al.* 1994; Jonsell *et al.* 1998; Siitonen 2001).

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

In this study, saproxylic beetles were surveyed in a managed boreal forest landscape with three different methods: bark sieving, emergence trapping, and window trapping. The beetles captured by the different methods were evaluated in terms of number of species and species composition. To study how seasonality affects the outcome of these kinds of surveys,

we sampled throughout an entire growing season. We compared the saproxylic beetle fauna in three different types of dead wood: sun-exposed logs, shaded logs, and high stumps of Norway spruce (*Picea abies* (L.) Karst.; Pinaceae). High stumps are 3–5 m tall and are artificially created during clear-cutting in an attempt to increase the amount of dead wood available for the saproxylic fauna and flora, whereas logs are usually generated by windthrow of living trees within stands or at stand edges. The three methods were applied simultaneously on each dead wood object. Thus, it was possible to analyse how the sampling method may affect any observed differences between the types of dead wood.

## Materials and methods

### Study area and dead wood characteristics

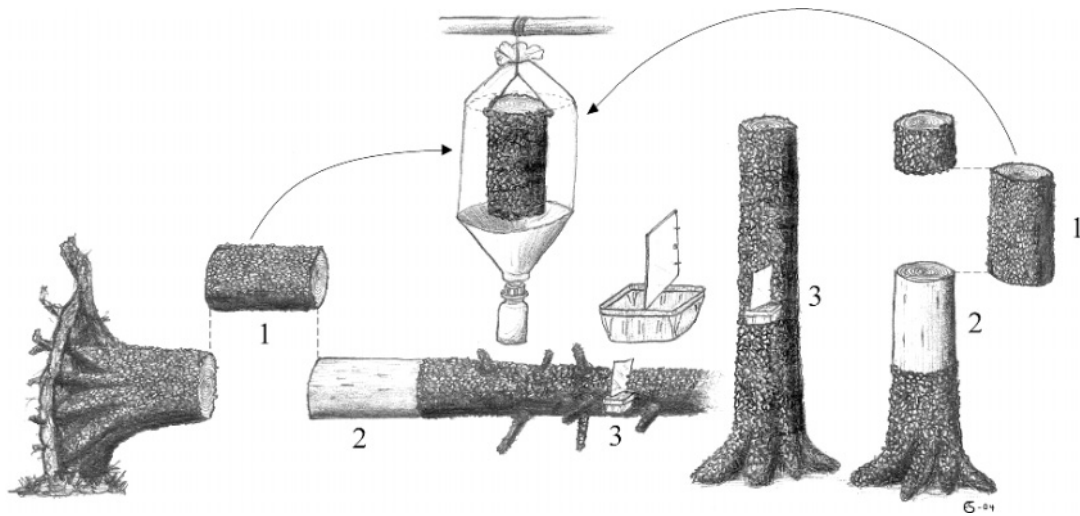
The study was conducted in a managed forest landscape dominated by Norway spruce and Scots pine (*Pinus sylvestris* L.; Pinaceae) in the province of Hälsingland, central Sweden. The landscape is in the mid-boreal vegetation zone (Ahti *et al.* 1968). In managed spruce forests in this region, the amount of dead wood is, on average, 8.5 m<sup>3</sup>/ha (Fridman and Walheim 2000). Two study sites were selected, situated 14 km from each other (62°02'25"N, 16°31'53"E, 325 m a.s.l., and 62°06'47"N, 16°08'11"E, 375 m a.s.l.). At each site, three types of dead Norway spruce were studied: (1) shaded logs situated in mature, closed-canopy forest; (2) sun-exposed logs on stand edges between mature forest and recent clearcuts; and (3) artificially created high stumps on clearcuts. Snags of comparable size and decomposition stage in closed-canopy forest stands were, unfortunately, too rare to be included in the study. The mature forests were about 100 years old, while the clearcuts were 3 or 10 years old. The size of each forest stand was between 10 and 30 ha. Distance between single sampled objects of the same type within a site varied between 5 and 50 m.

Five high stumps, five shaded logs, and five sun-exposed logs were sampled in each of the

**Table 1.** Diameter and decomposition stage of surveyed Norway spruce (*Picea abies*) objects (mean value and range).

Object	Diameter (cm)	Decay stage
Exposed logs	24 (19–35)	2.6 (2–3)
Shaded logs	26 (17–36)	2.7 (2–3.5)
High stump (window trapping)	36 (26–47)	2.0 (2)
High stump (sieving and emergence trapping)	29 (17–42)	2.1 (2–3)

**Fig. 1.** The three sampling methods used on wind-felled logs and cut high stumps of Norway spruce (*Picea abies*): (1) sections used for emergence traps; (2) sections that were bark-peeled and sieved; and (3) window traps.



two study sites. All sampled trees had been dead for between 3 and 10 years. The primary successional bark beetles had left the trees, but the bark was still intact. For each tree, the length (for high stumps, the height), diameter at breast height (1.3 m above ground), and decomposition stage were measured. Decomposition stage classification was based on the hardness of the wood, following the method of Siitonen and Saaristo (2000), which is a modified version of a system described by Renvall (1995). The system includes six decay classes: (1) wood hard, phloem still fresh or currently used by bark beetles, at most 1 year old; (2) wood hard but more than 1 year old; (3–6) a knife can be pushed into the trunk to a depth of 0.5–2.4 cm (3), 2.5–4.4 cm (4), or >4.4 cm (5, 6), with the trunk retaining a cylindrical form (5) or the trunk disintegrating easily and having a flattened form with completely decomposed parts (6). If more than one decay class was present on a single object, we estimated the average. Decomposition stage and diameter

differed somewhat between logs and high stumps, but not between sun-exposed and shaded logs (Table 1). The high stumps used for window trapping, but not the ones used for sieving and emergence trapping, had a significantly larger diameter at breast height than the logs (one-way ANOVA,  $df = 3$ ,  $P < 0.001$ ). Because some of the high stumps were too large to be used in the emergence traps, these stumps were used for window trapping instead, thus generating the biased diameter distribution. However, there was no significant difference in size between high stumps used for window trapping and high stumps used for emergence trapping (one-way ANOVA,  $df = 1$ ,  $P = 0.076$ ). The logs were significantly more decayed than the high stumps (Kruskal–Wallis,  $df = 3$ ,  $P = 0.002$ ).

### Sampling methods

Emergence traps, bark sieving, and window traps were used to sample beetles (Fig. 1). For emergence trapping, cut stem sections were

enclosed in insect-impenetrable cloth. From each dead spruce, one stem section representing 0.5 m<sup>2</sup> of bark was cut out. The length varied between 50 and 110 cm, depending on stem diameter. The cut ends were coated with paraffin to reduce desiccation. The stem sections were then enclosed in cloth and suspended by ropes inside the forest. Beetles were collected in 1-L plastic bottles fastened to the underside of the enclosures. The container was filled with a 50:50 mixture of water and propylene glycol, to preserve samples, plus a few drops of detergent to reduce surface tension. For sieving, each sample consisted of 0.5 m<sup>2</sup> of bark that was carefully peeled off, fragmented, placed in a sieve with 8-mm grid mesh together with all loose material between the bark and wood, and shaken for at least 5 min. The sieved samples were stored in 5-L cotton bags and then extracted in Tullgren funnels (30 cm wide, 8 mm mesh size). As a heat and light source, 60-W light bulbs were used. The extraction lasted for at least 48 h. Large or very wet samples were divided between two or three funnels. Trunk window traps consisted of a 15 cm × 20 cm transparent plastic sheet nailed perpendicularly to the wood and an aluminium container fastened tightly to the substrate under the plastic sheet. The container was 12 cm long × 9 cm wide and 6 cm deep, and was filled with the same collecting fluid as the emergence traps.

### Sampling scheme

Sampling started on 15 May 2001 at one site and on 28 May at the other, and lasted until 1 October 2001 at both sites. Samples were taken repeatedly from the same trees at 2- to 4-week intervals using all three methods (see Results). For emergence traps, the same cut section (one per tree) was repeatedly sampled. High stumps could not be repeatedly sieved because of the limited bark area, so only one sieving sample was taken at the very start of the sampling programme. Because it was impossible to put a window trap on a high stump after a stem section had been cut out for the emergence traps, window traps were put on similar high stumps situated nearby (2–20 m, in a pairwise manner). When logs and cut out stem sections were sieved, we alternately started from the top or base end of the log. At the top, the minimum stem diameter used was 10 cm, and at the base, sampling started 0.5 m from the root. The sieved sample was always adjacent to the preceding sample that had been sieved. Thus,

sampling was done along the length of the log. The bark was left intact for 0.5 m on either side of the window trap. At one of the sites, a few trees could not be sampled by sieving during the last sampling occasion (October) because not enough bark remained. The window traps were positioned at breast height on high stumps, facing southwards, and at the middle of logs on the most southward-facing side (Fig. 1).

### Species determination and classification

Most adult beetles were identified to species and beetle larvae were identified at least to family (Appendix A). Taxa not determined to species were excluded from analyses of species richness and similarity. The nomenclature in Lundberg and Gustafsson (1995) was followed. The beetle species were classified as being non-saproxyllic, facultative saproxyllic, or obligate saproxyllic, according to a Scandinavian database (Dahlberg and Stokland 2004). Obligate saproxyllic species depend upon dead wood or other saproxyllic organisms to fulfil at least one part of their life cycle. Facultative saproxyllic species regularly utilize dead wood in one or more parts of their life cycle, but they also utilize alternative substrates such as litter, soil, and mushrooms in the same part(s) of their life cycle. In other words, dead wood is a significant resource for facultative species, and these species were therefore included among the saproxyllic species in all analyses. Species that can be found occasionally in dead wood but that typically occur in other substrates are not considered facultative saproxyllics (Dahlberg and Stokland 2004).

Species that either develop inside dead wood or are found inside dead wood (and not, for instance, between the dead wood and the bark) during most of the year were identified and tabulated (Saalas 1917; Palm 1946; Koch 1989), as were those that develop exclusively on deciduous tree species (Palm 1951).

### Statistics

In this study all three methods were used over the whole season to determine when sampling is optimal, although this is rarely done in other surveys for practical reasons. To imitate a more realistic sampling scheme when comparing the three methods, we considered specimens from a particular time as a sample. For window traps, we used specimens collected when the traps were emptied in July (they contained specimens trapped between 14 June and

**Table 2.** Number of beetle species collected by the three sampling methods (number of individuals within parentheses).

	Sampling method			Total
	Emergence trap	Sieving	Window trap	
Obligate saproxylic	53 (1401)	63 (4080)	104 (757)	137 (6238)
Facultative saproxylic	14 (49)	24 (149)	42 (448)	56 (646)
Non-saproxylic	13 (33)	19 (69)	81 (1211)	96 (1313)
All species	80 (1483)	106 (4298)	227 (2416)	289 (8197)

**Note:** For each method, 30 Norway spruce dead wood elements were sampled over the whole season.

12 July), when the number of species reaches its maximum. For sieving, we used the sample from May because it was only at that time that high stumps were sieved and also because the number of species reached its maximum then. Emergence traps are most often used over a whole growing season, being emptied only once, and therefore we pooled subsamples from the whole season to yield a sample.

Based on the pooled samples described above, species richness was analysed in relation to both the method and the type of dead wood by analysis of variance with interaction. Pairwise *post hoc* comparisons between methods were done with Tukey's honestly significant difference test (one-way tables) or by comparing least square means (two-way tables). To further compare the three sampling methods, species accumulation curves from sample-based rarefaction were produced using the software EstimateS (Colwell 2000).

Analyses of similarity based on species presence/absence (Sørensen similarity index) were done using the software BIODIV (Baev and Penev 1995) only on samples from logs. To compare the outcome from different methods, we pooled samples from the whole season for each dead wood object. To test whether the species composition differed between spring and autumn, we compared the mean similarity of pairs of logs, both within and between seasons.

## Results

A total of 8197 beetles representing 289 species were collected. Of that total, 1313 belonged to 96 non-saproxylic species (hereafter not included in calculations) (Table 2, Appendix A). The proportion of larvae collected in relation to adults was greater for emergence traps (21%) than for sieving (10%) and was very low in window traps (0.4%). Window traps collected the largest number of beetle species, as

well as the largest number of saproxylic beetle species. Sieving collected the largest number of individuals (Table 2). When counts from different samples were summed, the number of saproxylic species in logs accumulated much faster for window traps than for emergence traps or sieving (Fig. 2). This indicates a larger variability in species composition among window trap samples than among other samples.

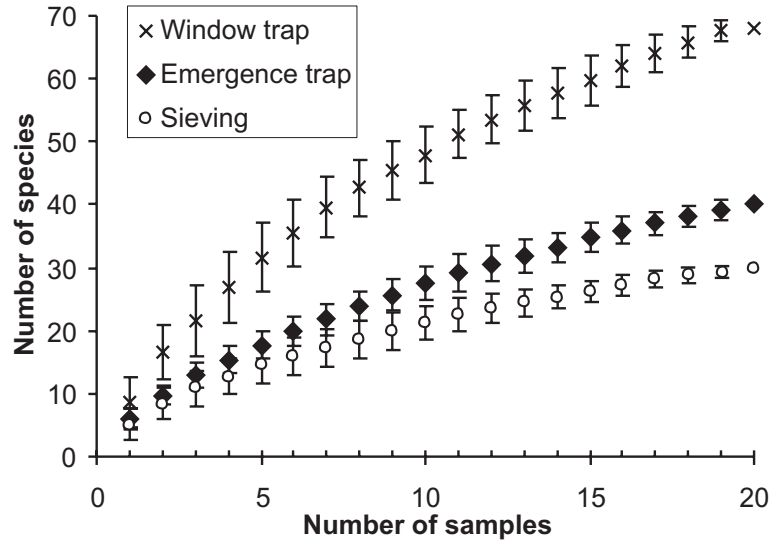
Obligate saproxylic species dominated samples from sieving and emergence traps, whereas they constituted only 31% of all individuals collected by window traps (Table 2). In sieving and emergence trap samples, other species were predominantly facultative saproxylic species, whereas in samples from window traps the great majority of other species were non-saproxylic. Among the obligate saproxylic species there were also species caught that were not associated with the studied dead wood. For instance, window traps caught 10 species that were regarded as mainly being associated with deciduous wood, compared with one for sieving and none for emergence traps (Appendix A).

Comparing emergence traps and sieving, the Sørensen similarity index for saproxylic species collected during the whole season (with samples from each log treated separately) was 0.48, on average. The species composition similarity between window traps and emergence traps and that between window traps and sieving were much lower (0.20 and 0.16, respectively). The similarity was significantly higher between emergence traps and sieving than between emergence traps and window traps or between window traps and sieving (ANOVA;  $F = 45$ ,  $P < 0.0001$ ).

By emergence trapping and sieving, a total of 81 saproxylic species were captured. Of these, 35 were captured by both methods. Eighteen percent of the species caught by emergence traps live mainly inside wood, compared with



**Fig. 2.** Species accumulation curves for saproxylic beetles sampled from Norway spruce logs (shaded and sun-exposed) with three different methods (mean  $\pm$  SD). A sample includes beetles collected in emergence traps on stem sections representing 0.5 m<sup>2</sup> of bark over a whole vegetation period (May–October), in window traps in July, or by sieving 0.5 m<sup>2</sup> of bark in May.



7% of the species caught by sieving ( $\chi^2 = 7.1$ ,  $P < 0.01$ ; Appendix A). Among the 104 obligate saproxylic species collected in window traps, 56 were unique to window traps, while 48 were also collected either by sieving or in emergence traps.

The seasonal distribution of species richness varied among methods (Fig. 3). Emergence traps caught significantly more species during the first half of the season than during the second half (ANOVA;  $F = 28.6$ ,  $P < 0.0001$ ). Sieving collected a significantly higher number of species in spring and autumn than in summer (ANOVA;  $F = 8.3$ ,  $P < 0.001$ ). In window traps the number of saproxylic species had a clear peak in late June – early July (ANOVA;  $F = 33.8$ ,  $P < 0.0001$ ).

The Sørensen similarity indices for sieved samples taken in spring and autumn did not differ from the similarity between samples from the same season but from different sites (ANOVA;  $F = 0.24$ ,  $P = 0.84$ ). Among the 16 most common species, all were present during the whole season (*i.e.*, all of the three periods spring (May,  $n = 30$ ), summer (June–August,  $n = 60$ ), and autumn (September–October,  $n = 36$ )).

Species richness of saproxylic beetles was higher in logs (both shaded and sun-exposed) than in high stumps (Table 3, Fig. 4). This result was consistent across all methods, which was also indicated by the nonsignificant

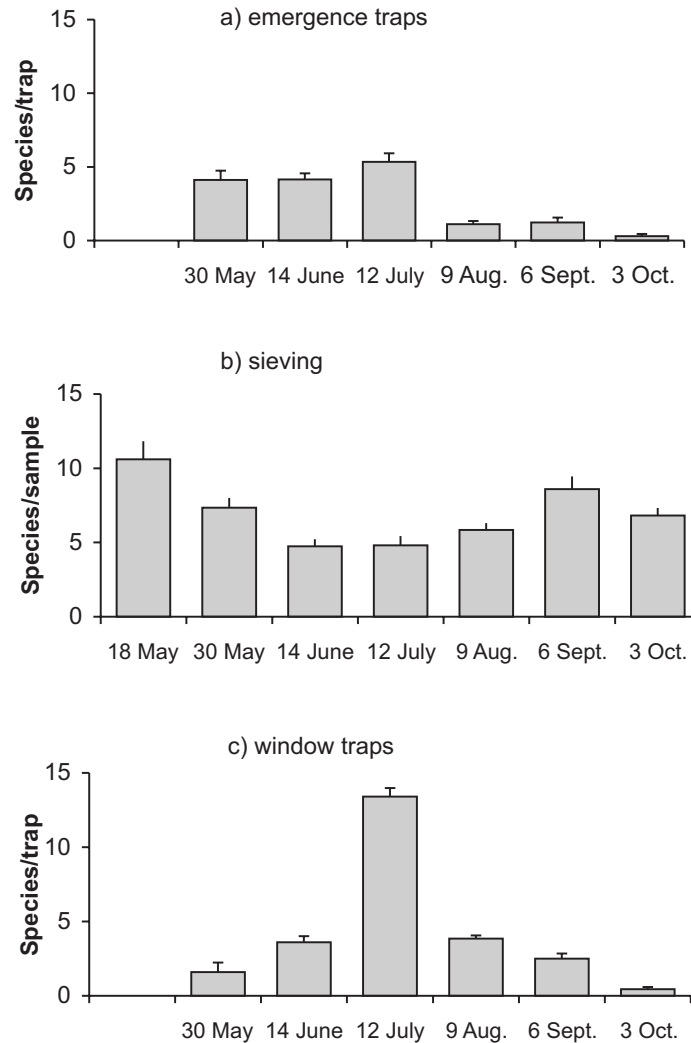
interaction “method  $\times$  substrate” (Table 3). However, if analyses were done separately for each sampling method, samples from window traps did not differ among substrates (ANOVA,  $F = 2.33$ ,  $P = 0.12$ ), but samples obtained by the other two methods did (emergence traps,  $F = 7.16$ ,  $P < 0.005$ ; sieving,  $F = 14.7$ ,  $P < 0.0001$ ). Independently of dead wood type, fewer species were collected with sieving than with the other methods (Fig. 4).

Red-listed species occurred in all three types of dead wood and were sampled by all three methods. The results were inconsistent among methods; for instance, most of the red-listed species collected in window traps were collected on high stumps, but sieving collected only one red-listed species in this substrate (Table 4). Four red-listed species were collected in large numbers ( $>10$  individuals), and these species were collected mainly by sieving (Table 4).

## Discussion

We found great differences in the number of beetles captured by the three methods and in the methods’ capabilities to specifically sample saproxylic beetles, so our study confirms the results of earlier studies (Siitonen 1994; Økland 1996; Hammond 1997; Ranius and Jansson 2002). All methods have their advantages and disadvantages, and the preferred method

**Fig. 3.** Numbers of saproxylic beetle species in logs of Norway spruce, per trap or per sample, by date that traps were emptied or samples were taken (mean  $\pm$  SE): (a) emergence traps, (b) sieving, and (c) window traps.



depends on the resources available and the aim of the study.

Emergence traps are probably the most reliable and complete method when single dead wood objects are to be studied, but they are labour-intensive (Table 5), especially during construction of the traps. The *ex situ* type of emergence trap used here seems to be substantially more efficient than the *in situ* type used by Økland (1996). Økland (1996) argues that the low efficiency makes the method useless for statistically meaningful samples. He collected 164 saproxylic beetles belonging to 50 species from 167 emergence traps that each enclosed Norway spruce logs along a length of 75 cm,

while we collected 1400 saproxylic beetles belonging to 67 species in only 30 traps.

Sieving primarily catches the subset of saproxylic species that live between bark and wood. Clearly, it will underestimate species richness because beetles mainly living inside the wood are rarely captured (Siitonen 1994). However, the large numbers of individuals and species caught, with less effort than that required for emergence traps, and the fact that the collected species assemblage is known may make sieving the favoured method. In this study, all methods yielded about the same number of red-listed species, but most red-listed individuals were collected with sieving (Table 4).

**Table 3.** Test of differences (see Fig. 4) among methods and Norway spruce objects with regard to number of saproxylic beetle species per sample (ANOVA).

	<i>F</i> value	Significance	Pairwise comparisons
Model	9.1	****	
Method	20.1	****	E > S****, E = W, W > S****
Substrate type	14.6	****	SL = EL, SL > HS****, EL > HS***
Interaction	0.9	NS	

**Note:** A sample includes beetles collected in emergence traps on stem sections representing 0.5 m<sup>2</sup> of bark over a whole vegetation period (May–October), in window traps in July, or by sieving 0.5 m<sup>2</sup> of bark in May. Pairwise comparisons with least square means (*P* values). Methods: E, emergence traps; S, sieving; W, window traps. Substrate types: SL, shaded logs; EL, exposed logs; HS, high stumps. Significance levels: \*, *P* < 0.05; \*\*, *P* < 0.01; \*\*\*, *P* < 0.001; \*\*\*\*, *P* < 0.0001; NS, not significant.

**Fig. 4.** Number of saproxylic beetle species collected from different types of Norway spruce dead wood (mean ± SE). A sample includes beetles collected in emergence traps on stem sections representing 0.5 m<sup>2</sup> of bark over a whole vegetation period (May–October), in window traps in July, or by sieving 0.5 m<sup>2</sup> of bark in May. The difference between types of dead wood and methods was tested with two-way ANOVA (see Table 3).

Sieving is destructive because of the bark peeling, but not to the same extent as emergence traps applied *ex situ*, where pieces of wood are actually cut out and moved.

Window traps collect many species, but a majority of these are not associated with the dead wood to which the trap is attached (Table 2; Siitonen 1994). This nonspecificity also applies to many of the saproxylic species collected. For example, our window traps on Norway spruce caught several species that develop mainly on deciduous trees (Appendix A). This is probably one of the reasons for the low similarity in saproxylic species composition between window traps and the other two methods.

The large number of species caught by window traps might actually be a problem when processing insect samples, because more species mean more identification work. Species

identification is much easier for samples from emergence traps and sieving, as these methods yield a lower number of species and among them a much higher proportion are of interest (*i.e.*, living in the surveyed substrate).

A surprisingly large fraction of the species caught by sieving (18%) and emergence traps (16%) were non-saproxylic species (Table 2; Appendix A). Some of these species were found in substantial numbers and probably had not been accidentally sampled but use dead wood for protection, hibernation, or larval development, for example. For species for which larvae were found, a more appropriate classification would probably be facultative saproxylic. Often, we do not have much information on the habitat of individual species, and the only way to acquire such information is to use methods



**Table 4.** Occurrence of red-listed beetle species (according to Gärdenfors 2000): total number of samples with species present, total number of individuals over the whole season, and number of individuals by sampling method and substrate.

Red-listed species	Total no. of samples with species	No. of individuals														
		Window traps						Emergence traps						Sieving		
		Total	Shaded log	Exposed log	High stump	High stump	Total	Shaded log	Exposed log	High stump	High stump	Shaded log	Exposed log	High stump	High stump	
<i>Atomaria alpina</i>	1	2	0	0	2	0	0	0	0	0	0	0	0	0	0	0
<i>Atomaria badia</i>	11	17	0	1	0	0	0	2	2	10	1	1	1	1	1	1
<i>Atomaria subangulata</i>	5	10	0	4	0	0	0	0	0	2	4	0	0	0	0	0
<i>Callidium coriaceum</i>	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0
<i>Dendrophagus crenatus</i>	9	17	2	0	0	0	0	2	0	2	11	0	0	0	0	0
<i>Ennearthron laricinum</i>	4	7	0	0	0	0	0	0	5	1	1	1	0	0	0	0
<i>Globicornis emarginata</i>	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Hapalarea clavigera</i>	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Harminius undulatus</i>	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0
<i>Mycetochara obscura</i>	1	2	0	0	0	0	0	0	2	0	0	0	0	0	0	0
<i>Prinus sexpunctatus</i>	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Stagetus borealis</i>	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Zilora ferruginea</i>	1	13	0	0	0	0	0	0	0	0	13	0	0	0	0	0
Total no. of individuals		74	2	5	6	0	0	4	10	15	31	1	1	1	1	1
Total no. of individuals per method			13		14				47							

**Table 5.** Estimated working time (minutes) for taking one sample by each method.

Task	Method		
	Emergence	Sieving	Window
Establishment in the field	60	0	10
Taking sample	5	20	5
Handling and sorting	15	30	20
Trap dismounting	10	0	5
Total	90	50	40
Minimum no. of visits	2	1	2
Time for identification	Short	Short	Long

**Note:** Handling and sorting includes extraction in Tullgren funnels (only sieving) and extracting beetles in coarse samples by hand from debris under microscope (all methods). Time for preparation of traps, travelling, and searching for suitable positions for sampling in the field is excluded from the estimates.

such as emergence trapping and sieving rather than window trapping.

The seasonal pattern in species richness of samples varied strongly among methods (Fig. 3). The differences may be explained by the life history of the majority of saproxylic beetles. During the short growing season in boreal forests, insects have a limited time to grow as larvae, pupate, emerge, disperse, and reproduce, especially because most species are univoltine (Danks and Footit 1989). Many species disperse by flight during the earliest warm part of the season, which is the reason for the clear peak in the window trap samples from June to July. For many species, the adults emerge from the pupae during autumn but remain in the wood or under the bark until next summer, before the dispersal phase (Saalas 1917; Palm 1951). The observed similarity in species composition between spring and autumn samples from sieving would be the result if such a life history is common.

Emergence traps collected most species during the first part of the year. In comparison with the individuals collected by other methods, a greater portion of individuals collected by emergence trapping were larvae (21%). These probably leave the wood to search for a place in the soil to pupate.

Artificial high stumps had a lower species richness than logs. This difference was consistent across all three methods (Fig. 3). However, if only data from window traps were used, the relation was not statistically significant (whereas it was highly significant for both of the other two methods). This indicates that window traps are less efficient in detecting

differences in species richness between types of dead wood.

In studies on aspen (*Populus* spp.; Salicaceae), more species were found on sun-exposed than on shaded dead wood (Martikainen 2001; Sverdrup-Thygeson and Ims 2002). We did not find the same result for Norway spruce, probably because Norway spruce is a more shade-tolerant, secondary successional tree (Esseen *et al.* 1997). Therefore, it may be that a larger proportion of insect species associated with Norway spruce prefer shade, in comparison with insects associated with deciduous trees such as aspen and birch (*Betula* spp.; Betulaceae) (Jonsell and Eriksson 2001; Wikars 2002).

It might be expected that window traps collect beetles more efficiently in open areas, because flight activity is higher when the microclimate is warmer. However, our results do not support this hypothesis; no difference in species richness was found between sun-exposed and shaded logs, either with window traps or with the other methods (Fig. 4).

Some red-listed saproxylic beetles were found also in artificial high stumps on clearcuts (Table 4), which agrees with the results from other studies (*e.g.*, Lindhe and Lindelöv 2004). The quality of dead wood in standing dead trees probably differs from that in downed logs in several respects (*e.g.*, because of slower decay rate; Storaunet and Rolstad 2002). Moreover, artificially created high stumps have died at the same time of year and in the same way, and this probably makes them more homogenous in comparison with logs that may have different histories and thus differences in, for example,

the decomposition process. Jonsell and Weslien (2003) concluded that although artificial high stumps are used as a substrate by some saproxylic beetles, it is desirable to also leave logs to diversify the available dead wood on clearcuts. Our study confirms that there are red-listed species that live in high stumps, and thus the creation of this substrate seems to be useful for at least some saproxylic species.

To conclude, the aim of the sampling should always determine the method used. If the aim is to yield a species list as complete as possible from an area, window traps are useful, especially in combination with other methods. If the goal is to evaluate how useful different substrates are, as in this study, it is obviously better to use emergence traps or sieving, because it is not desirable to collect beetles that are not developing in the substrate. Although emergence trapping requires a larger initial effort (construction of traps, establishment in the field), it is more efficient than sieving and it is the only way to sample the whole assemblage of saproxylic beetles.

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### References

- Ahti, T., Hämet-Ahti, L., and Jalas, J. 1968. Vegetation zones and their sections in northwestern Europe. *Annales Botanici Fennici*, **5**: 169–211.
- Baev, P.V., and Penev, L.D. 1995. BIODIV software. Version 5.1 [computer program]. Pensoft, Sofia, Bulgaria.
- Berg, Å., Ehnström, B., Gustafsson, L., Hallingbäck, T., Jonsell, M., and Weslien, J. 1994. Threatened plant, animal, and fungus species in Swedish forests: distribution and habitat associations. *Conservation Biology*, **8**: 718–731.
- Colwell, R.K. 2000. EstimateS. Statistical estimation of species richness and shared species from samples. Version 6b1a [computer program]. Available from <http://viceroy.eeb.uconn.edu/estimates>.
- Dahlberg, A., and Stokland, J.N. 2004. Vedlevande arters krav på substrat. Rapport No. 7. Skogsstyrelsen, Jönköping, Sweden. [In Swedish.]
- Danks, H.V., and Footit, R.G. 1989. Insects of the boreal zone of Canada. *The Canadian Entomologist*, **121**: 625–690.
- Esseen, P.A., Ehnström, B., Ericson, L., and Sjöberg, K. 1997. Boreal forests. *Ecological Bulletins*, **46**: 16–47.
- Fridman, J., and Walheim, M. 2000. Amount, structure and dynamics of dead wood on managed forestland in Sweden. *Forest Ecology and Management*, **131**: 23–36.
- Gärdenfors, U. (Editor). 2000. The 2000 red list of Swedish species. Swedish Threatened Species Unit, Uppsala, Sweden.
- Hammond, H.E.J. 1997. Arthropod biodiversity from *Populus* coarse woody material in north-central Alberta: a review of taxa and collection methods. *The Canadian Entomologist*, **129**: 1009–1033.
- Jonsell, M., and Eriksson, P. 2001. A comparison of the saproxylic beetle fauna on spruce wood and birch high-stumps between the Båtfors forest reserve and its surroundings. *Entomologisk Tidskrift*, **122**: 107–122. [In Swedish with English summary.]
- Jonsell, M., and Nordlander, G. 1995. Field attraction of Coleoptera to odours of the wood-decaying polypores *Fomitopsis pinicola* and *Fomes fomentarius*. *Annales Zoologici Fennici*, **32**: 391–402.
- Jonsell, M., and Weslien, J. 2003. Felled or standing retained wood — it makes a difference for saproxylic beetles. *Forest Ecology and Management*, **175**: 425–435.
- Jonsell, M., Weslien, J., and Ehnström, B. 1998. Substrate requirements of red-listed saproxylic invertebrates in Sweden. *Biodiversity and Conservation*, **7**: 749–764.
- Jonsson, B.G., Kruys, N., and Ranius, T. 2005. Ecology of species living on dead wood — lessons for dead wood management. *Silva Fennica*, **39**(2): 289–309.
- Kaila, L. 1993. A new method for collecting quantitative samples of insects associated with decaying wood or wood fungi. *Entomologica Fennica*, **4**: 21–23.
- Koch, K. 1989. Die Käfer Mitteleuropas. Ökologie 2. Goecke & Evers, Krefeldt.
- Lindhe, L., and Lindelöw, Å. 2004. Cut high stumps of spruce, birch, aspen and oak as breeding substrates for saproxylic beetles. In *Conservation through management — cut wood as substrate for saproxylic organisms*. Edited by A. Lindhe. Ph.D. thesis, Swedish University of Agricultural Sciences, Uppsala, Sweden.
- Lundberg, S., and Gustafsson, B. 1995. *Catalogus Coleopterorum Sueciae*. Naturhistoriska Riksmuseet, Stockholm.
- Martikainen, P. 2001. Conservation of threatened saproxylic beetles: significance of retained aspen *Populus tremula* on clearcut areas. *Ecological Bulletins*, **49**: 205–218.

- Martikainen, P., Siitonen, J., Punttila, P., Kaila, L., and Rauh, J. 2000. Species richness of Coleoptera in mature managed and old-growth forests in southern Finland. *Biological Conservation*, **94**: 199–209.
- Økland, B. 1996. A comparison of three methods of trapping saproxylic beetles. *European Journal of Entomology*, **93**: 195–209.
- Owen, J.A. 1989. An emergence trap for insects breeding in dead wood. *British Journal of Entomology and Natural History*, **2**: 65–67.
- Palm, T. 1946. Coleoptärfaunan i en jämtländsk lavgranskog. I. Träd- och trädsvampfaunan. *Entomologisk Tidskrift*, **67**: 109–139.
- Palm, T. 1951. Die Holz- und Rindenkäfer der Nordschwedischen Laubbäume. *Meddelanden från Statens Skogsforskningsinstitut*, **40**(2).
- Ranius, T., and Jansson, N. 2002. A comparison of three methods to survey saproxylic beetles associated with old oaks. *Biodiversity and Conservation*, **11**: 1759–1771.
- Renvall, P. 1995. Community structure and dynamics of wood-rotting Basidiomycetes on decomposing conifer trunks in northern Finland. *Karstenia*, **35**: 1–51.
- Saalas, U. 1917. Die Fichtenkäfer Finnlands 1. *Annales Academiae Scientiarum Fennicae Series A*, **VIII**: 1.
- Siitonen, J. 1994. Decaying wood and saproxylic Coleoptera in two old spruce forests: a comparison based on two sampling methods. *Annales Zoologica Fennici*, **31**: 89–95.
- Siitonen, J. 2001. Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. *Ecological Bulletins*, **49**: 11–42.
- Siitonen, J., and Saaristo, L. 2000. Habitat requirements and conservation of *Pytho kolwensis*, a beetle species of old-growth boreal forest. *Biological Conservation*, **94**: 211–220.
- Speight, M.C.D. 1989. Saproxylic invertebrates and their conservation. Council of Europe, Strasbourg.
- Storaunet, K.O., and Rolstad, J. 2002. Time since death and fall of Norway spruce logs in old-growth and selectively cut boreal forest. *Canadian Journal of Forest Research*, **32**: 1801–1812.
- Sverdrup-Thygeson, A., and Ims, R.A. 2002. The effect of forest clear-cutting in Norway on the community of saproxylic beetles on aspen. *Biological Conservation*, **106**: 347–357.
- Väisänen, R., Biström, O., and Heliövaara, K. 1993. Sub-cortical Coleoptera in dead pines and spruces: is primeval species composition maintained in managed forests? *Biodiversity and Conservation*, **2**: 95–113.
- Weslien, J. 1992. The arthropod complex associated with *Ips typographus* (L.) (Coleoptera, Scolytidae): species composition, phenology, and impact on bark beetle productivity. *Entomologica Fennica*, **3**: 205–213.
- Wikars, L.-O. 2002. Dependence on fire in wood-living insects; an experiment with burned and unburned spruce and birch logs. *Journal of Insect Conservation*, **6**: 1–12.

## Appendix A

**Table A1.** Beetle taxa collected in a survey of 30 Norway spruce (*Picea abies*) objects using emergence traps (E), bark sieving (S), and window traps (W) during one growing season in central Sweden.

Taxon	Saproxylic*	Comments <sup>†</sup>	No. of individuals			
			E	S	W	Total
<b>Carabidae</b>						
<i>Notiophilus biguttatus</i> (Paykull, 1779)	no		0	3	1	4
<i>Carabus violaceus</i> L., 1758	no		0	0	2	2
<i>Cychrus caraboides</i> (L., 1758)	no		0	1	0	1
<i>Pterostichus oblongopunctatus</i> (Fabr., 1787)	no		0	0	2	2
<i>Calathus micropterus</i> (Duftschmid, 1812)	no		0	1	16	17
<i>Amara nigricornis</i> Thomson, 1857	no		0	0	1	1
<i>Dromius fenestratus</i> (Fabr., 1794)	fac.		0	0	1	1
Carabidae sp. (larvae)	no		0	7	0	7
<b>Hydrophilidae</b>						
<i>Hydrophilidae</i> sp.	no		0	0	2	2
<b>Sphaeritidae</b>						
<i>Sphaerites glabratus</i> (Fabr., 1792)	fac.		0	0	10	10

Table A1 (continued).

Taxon	Saproxyllic*	Comments <sup>†</sup>	No. of individuals			
			E	S	W	Total
<b>Histeridae</b>						
<i>Gnathoncus buyssoni</i> Auzat, 1917	fac.	iw, d	0	0	1	1
<b>Ptiliidae</b>						
<i>Pteryx suturalis</i> (Heer, 1841)	obl.		3	13	9	25
<i>Acrotrichis</i> sp.	no		1	0	11	12
<b>Leiodidae</b>						
<i>Anisotoma humeralis</i> (Fabr., 1792)	obl.		0	1	22	23
<i>Anisotoma axillaris</i> Gyllenhal, 1810	obl.		0	0	8	8
<i>Anisotoma castanea</i> (Herbst, 1792)	obl.		0	0	28	28
<i>Anisotoma glabra</i> (Kugelann, 1794)	obl.		0	0	4	4
<i>Agathidium rotundatum</i> (Gyllenhal, 1827)	fac.		0	4	3	7
<i>Agathidium confusum</i> Brisout de Barneville, 1863	fac.		0	4	9	13
<i>Agathidium arcticum</i> Thomson, 1862	fac.		0	0	2	2
<i>Agathidium nigripenne</i> (Fabr., 1792)	obl.		0	0	1	1
<i>Agathidium pisanum</i> Brisout de Barneville, 1872	obl.		1	34	3	38
<i>Agathidium</i> sp. (larvae)	fac.		0	2	0	2
<b>Catopidae</b>						
<i>Catopidae</i> sp.	no		0	0	10	10
<b>Scydmaenidae</b>						
<i>Stenichnus bicolor</i> (Denny, 1825)	obl.		0	7	0	7
<b>Silphidae</b>						
<i>Nicrophorus</i> sp.	no		0	0	3	3
<b>Staphylinidae</b>						
<i>Gabrius splendidulus</i> (Gravenhorst, 1802)	fac.		3	9	21	33
<i>Philonthus puella</i> Nordmann, 1837	fac.		0	0	3	3
<i>Philonthus succicola</i> Thomson, 1860	no		0	0	1	1
<i>Philonthus addendus</i> Sharp, 1867	fac.		0	0	1	1
<i>Philonthus tenuicornis</i> Mulsant et Rey, 1853	no		0	0	1	1
<i>Quedius maurus</i> (Sahlberg, 1830)	fac.		0	0	1	1
<i>Quedius tenellus</i> (Gravenhorst, 1806)	no		1	7	14	22
<i>Quedius xanthopus</i> Erichson, 1839	fac.		5	1	12	18
<i>Quedius plagiatus</i> (Mannerheim, 1843)	fac.		7	8	7	22
<i>Quedius fulvicollis</i> (Stephens, 1833)	no		0	0	1	1
<i>Quedius boops</i> (Gravenhorst, 1802)	no		0	0	1	1
<i>Quedius</i> sp.	no		0	2	0	2
<i>Nudobius lentus</i> (Gravenhorst, 1806)	obl.		0	0	4	4
<i>Othius lapidicola</i> Kiesenwetter, 1848	fac.		1	0	2	3
<i>Atrecus pilicornis</i> (Paykull, 1790)	obl.		1	12	1	14
<i>Atrecus longiceps</i> (Fauvel, 1872)	obl.		5	3	0	8
<i>Lathrobium brunnipes</i> (Fabr., 1792)	no		0	1	0	1



Table A1 (continued).

Taxon	Saprophytic*	Comments <sup>†</sup>	No. of individuals			
			E	S	W	Total
<i>Bibloporus bicolor</i> (Denny, 1825)	obl.		4	12	1	17
<i>Euplectus nanus</i> (Reichenbach, 1816)	fac.		0	2	0	2
<i>Euplectus piceus</i> Motschulsky, 1835	fac.		0	5	0	5
<i>Euplectus decipiens</i> Raffray, 1910	obl.		0	9	0	9
<i>Euplectus punctatus</i> Mulsant, 1861	obl.		8	19	5	32
<i>Euplectus karsteni</i> (Reichenbach, 1816)	fac.		0	1	0	1
<i>Tyrus mucronatus</i> (Panzer, 1803)	fac.		0	1	1	2
<i>Megarathrus nitidulus</i> Kraatz, 1858	no		0	0	2	2
<i>Proteinus brachypterus</i> (Fabr., 1792)	fac.		0	0	2	2
<i>Acrulia inflata</i>	fac.		5	41	53	99
<i>Hapalarea linearis</i> (Zetterstedt, 1828)	obl.		1	9	1	11
<i>Hapalarea clavigera</i> (Luzé, 1906)	obl.		0	0	1	1
<i>Hapalarea</i> sp.	obl.		0	9	1	10
<i>Omalius rivulare</i> (Paykull, 1789)	fac.		0	0	3	3
<i>Omalius caesum</i> Gravenhorst, 1806	no		0	0	1	1
<i>Omalius rugatum</i> Mulsant et Rey, 1880	fac.		0	2	9	11
<i>Phloeonomus lapponicus</i> (Zetterstedt, 1838)	obl.		0	1	2	3
<i>Phloeonomus pusillus</i> (Gravenhorst, 1806)	obl.		0	0	1	1
<i>Deliphrum tectum</i> (Paykull, 1789)	no		0	0	10	10
<i>Anthobium melanocephalum</i> (Illiger, 1794)	no		0	0	1	1
<i>Eucnecosum brachypterus</i> (Gravenhorst, 1802)	no		2	0	0	2
<i>Eucnecosum brunnescens</i> (J. Sahlberg, 1871)	no		3	0	0	3
<i>Anthophagus omalinus</i> Zetterstedt, 1828	no		1	1	8	10
<i>Anthophagus caraboides</i> (L., 1758)	no		0	0	2	2
<i>Coryphium angusticolle</i> Stephens, 1834	fac.		0	7	1	8
<i>Scaphisoma agaricinum</i> (L., 1758)	fac.		0	1	19	20
<i>Scaphisoma inopinatum</i> Löbl, 1967	obl.		0	0	1	1
<i>Scaphisoma boleti</i> (Panzer, 1793)	obl.		0	0	1	1
<i>Oxytelus laqueatus</i> (Marsham, 1802)	no		0	0	1	1
<i>Mycetoporus lepidus</i> (Gravenhorst, 1806)	fac.		0	0	3	3
<i>Mycetoporus ?brucki</i> Pandelle, 1869	no		0	1	0	1
<i>Ischnosoma splendidum</i> (Gravenhorst, 1806)	no		0	2	0	2
<i>Bryoporus cernuus</i> (Gravenhorst, 1806)	no		0	0	1	1
<i>Lordithon lunulatus</i> (L., 1761)	fac.		0	0	90	90
<i>Lordithon speciosus</i> (Erichson, 1839)	obl.		0	0	4	4
<i>Bolitobius cingulatus</i> Mannerheim, 1830	no		0	1	0	1
<i>Sepedophilus littoreus</i> (L., 1758)	fac.		0	3	3	6
<i>Sepedophilus testaceus</i> (Fabr., 1792)	fac.		2	1	0	3
<i>Tachyporus chrysomelinus</i> (L., 1758)	no		0	0	1	1
<i>Tachinus rufipes</i> (L., 1758)	no		0	0	1	1
<i>Tachinus pallipes</i> Gravenhorst, 1806	no		0	0	225	225
<i>Tachinus proximus</i> Kraatz, 1855	no		0	0	3	3
<i>Tachinus subterraneus</i> (L., 1758)	no		0	0	1	1
<i>Tachinus laticollis</i> Gravenhorst, 1802	no		0	0	21	21

Table A1 (continued).

Taxon	Saproxyllic*	Comments <sup>†</sup>	No. of individuals			
			E	S	W	Total
<i>Tachinus marginellus</i> (Fabr., 1781)	no		0	0	1	1
<i>Tachinus elongatus</i> Gyllenhal, 1810	no		0	0	3	3
<i>Aleochara fumata</i> Gravenhorst, 1802	no		0	0	147	147
<i>Aleochara moerens</i> Gyllenhal, 1827	fac.		0	0	35	35
<i>Oxygoda nigricornis</i> Motschulsky, 1860	no		0	0	1	1
<i>Oxygoda vittata</i> Märkel, 1842	fac.		0	0	1	1
<i>Oxygoda ?skalitzkyi</i> Bernhauer, 1902	no		0	0	2	2
<i>Oxygoda umbrata</i> (Gyllenhal, 1810)	no		0	0	1	1
<i>Oxygoda alternans</i> (Gravenhorst, 1802)	no		0	1	237	238
<i>Oxygoda annularis</i> Mannerheim, 1830	no		1	0	0	1
<i>Oxygoda soror</i> Thomson, 1855	no		0	0	1	1
<i>Oxygoda haemorrhoea</i> Mannerheim, 1830	no		0	0	1	1
<i>Acrostiba borealis</i> Thomson, 1858	no		0	0	3	3
<i>Thyasophila wockii</i> (Schneider, 1862)	fac.		2	0	0	2
<i>Haploglossa villosula</i> (Stephens, 1832)	fac.		0	0	1	1
<i>Haploglossa marginalis</i> (Gravenhorst, 1806)	fac.		0	0	1	1
<i>Haploglossa</i> sp.	fac.		0	0	1	1
<i>Mniusa incrassata</i> (Mulsant <i>et</i> Rey, 1852)	fac.		0	1	0	1
<i>Schistoglossa</i> sp.	no		0	0	1	1
<i>Liogluta micans</i> (Mulsant <i>et</i> Rey, 1852)	no		1	4	0	5
<i>Liogluta microptera</i> Thomson, 1867	no		0	0	1	1
<i>Geostiba circellaris</i> (Gravenhorst, 1806)	fac.		0	2	0	2
<i>Dadobia immersa</i> (Erichson, 1837)	obl.		5	9	1	15
<i>Philhygra</i> sp.	no		0	0	2	2
<i>Atheta subtilis</i> (Scriba, 1866)	no		1	1	49	51
<i>Atheta myrmecobia</i> (Kraatz, 1856)	no		0	3	6	9
<i>Atheta fungi</i> (Gravenhorst, 1806)	no		0	1	1	2
<i>Atheta amplicollis</i> (Mulsant <i>et</i> Rey, 1873)	no		0	0	3	3
<i>Atheta flavipes</i> (Gravenhorst, 1806)	no		0	0	41	41
<i>Atheta eremita</i> (Rye, 1866)	no		0	0	1	1
<i>Atheta cinnamoptera</i> (Thomson, 1856)	no		0	0	2	2
<i>Atheta aeneipennis</i> (Thomson, 1856)	no		0	0	12	12
<i>Atheta intermedia</i> (Thomson, 1852)	no		0	0	6	6
<i>Atheta pilicornis</i> (Thomson, 1852)	fac.		0	0	4	4
<i>Atheta boleticola</i> J. Sahlberg, 1876	no		0	0	10	10
<i>Atheta crassicornis</i> (Fabr., 1792)	no		0	0	65	65
<i>Atheta paracrassicornis</i> Brundin, 1954	no		0	0	84	84
<i>Atheta nigricornis</i> (Thomson, 1852)	fac.		3	0	46	49
<i>Atheta nigrifula</i> (Gravenhorst, 1802)	fac.		0	0	6	6
<i>Atheta picipes</i> (Thomson, 1856)	fac.		0	0	16	16
<i>Atheta</i> sp.	no		1	0	7	8
<i>Anopleta corvina</i> (Thomson, 1856)	no		0	0	2	2
<i>Anopleta depressicollis</i> (Fauvel, 1872)	no		0	0	1	1
<i>Dinaraea arcana</i> (Erichson, 1839)	obl.		24	46	2	72
<i>Lyprocorrhe anceps</i> (Erichson, 1837)	no		1	0	0	1

**Table A1** (continued).

Taxon	Saproxyllic*	Comments <sup>†</sup>	No. of individuals			
			E	S	W	Total
<i>Zyras humeralis</i> (Gravenhorst, 1802)	no		1	0	0	1
<i>Zyras cognatus</i> (Märkel, 1842)	fac.		0	0	1	1
<i>Gyrophana strictula</i> Erichson, 1839	obl.		0	2	0	2
<i>Gyrophana boleti</i> (L., 1758)	obl.		1	0	0	1
<i>Gyrophana</i> sp.	fac.		0	1	1	2
<i>Bolitochara mulsanti</i> Sharp, 1875	obl.		0	3	1	4
<i>Leptusa pulchella</i> (Mannerheim, 1830)	obl.		120	815	22	957
<i>Leptusa fumida</i> (Erichson, 1839)	obl.		4	25	2	31
<i>Leptusa</i> sp. (larvae)	obl.		282	163	3	448
<i>Autalia impressa</i> (Olivier, 1795)	fac.		0	0	22	22
<i>Autalia longicornis</i> Scheerpeltz, 1947	no		0	0	25	25
<i>Autalia puncticollis</i> Sharp, 1864	no		0	0	1	1
<i>Holobus apicatus</i> (Erichson, 1837)	no		0	2	0	2
<i>Cypha ?tarsalis</i> (Luze, 1902)	no		0	0	1	1
Staphylinidae sp. (larvae)	fac.		12	31	0	43
<b>Scirtidae</b>						
<i>Cyphon</i> sp.	no		1	0	1	2
<b>Scarabaeidae</b>						
<i>Geotrupes stercorarius</i> (L., 1758)	no		0	0	3	3
<i>Aphodius</i> sp.	no		1	0	1	2
<i>Potosia cuprea metallica</i> (Herbst, 1786)	no		0	0	73	73
<i>Trichius fasciatus</i> (L., 1758)	obl.	iw, d	0	0	1	1
<b>Lycidae</b>						
<i>Dictyoptera aurora</i> (Herbst, 1784)	obl.	iw	0	0	3	3
<i>Pyropterus nigroruber</i> (De Geer, 1774)	obl.	iw	0	0	3	3
<i>Lygistopterus sanguineus</i> (L., 1758)	obl.	d	0	0	9	9
<b>Cantharidae</b>						
<i>Rhagonycha limbata</i> Thomson, 1864	no		0	0	3	3
<i>Rhagonycha atra</i> (L., 1767)	no		0	0	2	2
<i>Absidia rufotestacea</i> (Letzner, 1845)	obl.		0	0	5	5
<i>Absidia schoenherrri</i> (Dejean, 1837)	obl.		0	0	3	3
<i>Malthodes dispar</i> (Germar, 1824)	obl.	iw	0	2	5	7
<i>Malthodes guttifer</i> Kiesenwetter, 1852	obl.	iw	4	0	0	4
<i>Malthodes brevicollis</i> (Paykull, 1798)	obl.	iw	0	1	0	1
<i>Malthodes</i> sp.	obl.	iw	2	0	1	3
Cantharidae sp. (larvae)	obl.		20	86	2	108
<b>Elateridae</b>						
<i>Athous subfuscus</i> (Müller, 1764)	obl.		0	0	10	10
<i>Harminius undulatus</i> (De Geer, 1774) (larvae)	obl.		0	1	0	1
<i>Ampedus tristis</i> (L., 1758)	obl.	iw	0	0	3	3
<i>Ampedus nigrinus</i> (Herbst, 1784)	obl.	iw	3	0	6	9
<i>Melanotus castanipes</i> (Paykull, 1800)	obl.	iw	0	0	1	1

**Table A1** (continued).

Taxon	Saproxyllic*	Comments <sup>†</sup>	No. of individuals			
			E	S	W	Total
<i>M. castanipes</i> (larvae)	obl.	iw	6	6	0	12
<b>Throscidae</b>						
<i>Trixagus</i> sp.	no		0	0	1	1
<b>Buprestidae</b>						
<i>Anthaxia quadripunctata</i> (L., 1758)	obl.		0	0	1	1
<i>Chrysobothris chrysostigma</i> (L., 1758)	obl.	iw	1	0	0	1
<b>Dermestidae</b>						
<i>Globicornis emarginata</i> (Gyllenhal, 1808)	obl.	iw	0	0	1	1
<i>Globicornis</i> sp. (larvae)	obl.	iw	2	0	0	2
<i>Anthrenus museorum</i>	no		0	0	1	1
<b>Anobiidae</b>						
<i>Ptinus sexpunctatus</i> Panzer, 1795	obl.	iw	0	0	1	1
<i>Ptinus subpilosus</i> Sturm, 1837	obl.		0	0	1	1
<i>Ernobius explanatus</i> (Mannerheim, 1843)	obl.		5	2	3	10
<i>Anobium thomsoni</i> (Kraatz, 1881)	obl.	iw	1	0	0	1
<i>Hadrobregmus pertinax</i> (L., 1758)	obl.	iw	0	0	1	1
<i>Stagetus borealis</i> Israelsson, 1971	obl.	iw	0	0	1	1
<i>Dorcatoma punctulata</i> Mulsant et Rey, 1864	obl.		0	0	2	2
Anobiidae sp. (larvae)	obl.		0	25	0	25
<b>Trogossitidae</b>						
<i>Ostoma ferruginea</i> (L., 1758)	obl.	iw	5	16	2	23
<i>Thymalus limbatus</i> (Fabr., 1787)	obl.	iw	1	0	0	1
<b>Cleridae</b>						
<i>Thanasimus</i> sp. (larvae)	obl.		1	1	0	2
<b>Melyridae</b>						
<i>Dasytes niger</i> (L., 1761)	obl.		0	0	3	3
<i>Dasytes obscurus</i> Gyllenhal, 1813	obl.		0	0	3	3
<b>Nitidulidae</b>						
<i>Carpophilus marginellus</i> Motschulsky, 1858	no		0	0	1	1
<i>Epuraea</i> sp.	fac.		0	2	17	19
<i>Meligethes</i> sp.	no		0	0	11	11
<i>Soronia grisea</i> (L., 1758)	obl.		0	0	7	7
<i>Pocadius ferrugineus</i> (Fabr., 1775)	fac.		0	0	1	1
<i>Thalycra fervida</i> (Olivier, 1790)	no		0	0	10	10
<i>Glischrochilus hortensis</i> (Geoffroy, 1785)	obl.		0	0	20	20
<i>Glischrochilus quadripunctatus</i> (L., 1758)	obl.		0	0	6	6
<i>Pityophagus ferrugineus</i> (L., 1761)	obl.		0	0	1	1
<b>Aspidiphoridae</b>						
<i>Sphindus dubius</i> (Gyllenhal, 1808)	obl.		1	0	1	2
<i>Arpidiphorus orbiculatus</i> (Gyllenhal, 1808)	obl.		0	0	6	6

**Table A1** (continued).

Taxon	Saproxyllic*	Comments <sup>†</sup>	No. of individuals			
			E	S	W	Total
<b>Monotomidae</b>						
<i>Rhizophagus ferrugineus</i> (Paykull, 1800)	obl.		0	0	1	1
<i>Rhizophagus dispar</i> (Paykull, 1800)	obl.		29	94	10	133
<i>Rhizophagus</i> sp. (larvae)	obl.		3	0	0	3
<b>Cucujidae</b>						
<i>Dendrophagus crenatus</i> (Paykull, 1799)	obl.		2	4	2	8
<i>D. crenatus</i> (larvae)	obl.		0	9	0	9
<b>Cryptophagidae</b>						
<i>Pteryngium crenatum</i> (Fabr., 1798)	obl.		0	1	5	6
<i>Cryptophagus abietis</i> (Paykull, 1798)	fac.		5	7	0	12
<i>Cryptophagus lapponicus</i> Gyllenhal, 1827	fac.	iw	0	0	1	1
<i>Cryptophagus scanicus</i> (L., 1758)	fac.	iw	2	0	6	8
<i>Cryptophagus</i> sp.	fac.		0	0	3	3
<i>Spavius glaber</i> (Gyllenhal, 1808)	no		0	0	1	1
<i>Atomaria contaminata</i> Erichson, 1846	fac.		0	0	16	16
<i>Atomaria fuscata</i> (Schönherr, 1808)	no		0	0	1	1
<i>Atomaria nigrirostris</i> Stephens, 1830	no		0	0	1	1
<i>Atomaria alpina</i> Heer, 1841	obl.		0	0	2	2
<i>Atomaria subangulata</i> J. Sahlberg, 1926	obl.		0	6	4	10
<i>Atomaria bescidica</i> Reitter, 1877	no		0	0	3	3
<i>Atomaria badia</i> Erichson, 1846	obl.		4	11	2	17
<i>Atomaria bella</i> Reitter, 1875	obl.		0	1	7	8
<i>Atomaria pulchra</i> Erichson, 1846	fac.		0	0	2	2
<i>Atomaria atrata</i> Reitter, 1875	no		0	0	1	1
<b>Erotylidae</b>						
<i>Triplax russica</i> (L., 1758)	obl.	d	0	0	12	12
<i>Triplax scutellaris</i> Charpentier, 1825	obl.	d	0	0	1	1
<i>Dacne bipustulata</i> (Thunberg, 1781)	obl.	d	0	0	3	3
<b>Cerylonidae</b>						
<i>Cerylon histeroides</i> (Fabr., 1792)	obl.		10	16	9	35
<i>Cerylon ferrugineum</i> Stephens, 1830	obl.		3	8	6	17
<b>Endomychidae</b>						
<i>Endomychus coccineus</i> (L., 1758)	obl.	d	0	1	2	3
<b>Coccinellidae</b>						
Coccinellidae sp.	no		0	0	1	1
Coccinellidae sp. (larvae)	no		0	0	1	1
<b>Corylophidae</b>						
<i>Orthoperus punctulatus</i> Reitter, 1876	obl.		1	2	0	3
<i>Orthoperus atomus</i> (Gyllenhal, 1808)	fac.		0	0	2	2
<b>Lathridiidae</b>						
<i>Latridius minutus</i> (L., 1767)	fac.		0	0	5	5



Table A1 (continued).

Taxon	Saproxyllic*	Comments <sup>†</sup>	No. of individuals			
			E	S	W	Total
<i>Enicmus fungicola</i> Thomson, 1868	obl.		0	0	1	1
<i>Enicmus rugosus</i> (Herbst, 1793)	obl.		0	1	9	10
<i>Dienerella filum</i> (Aube, 1850)	fac.		1	0	0	1
<i>Corticaria longicornis</i> (Herbst, 1793)	fac.		0	1	0	1
<i>Corticaria crenicollis</i> Mannerheim, 1844	obl.		2	0	0	2
<i>Corticaria orbicollis</i> Mannerheim, 1853	obl.		1	1	0	2
<i>Corticaria abietorum</i> Motschulsky, 1867	fac.		1	1	1	3
<i>Corticaria polypori</i> J. Sahlberg, 1900	obl.		1	0	0	1
<i>Corticaria longicollis</i> (Zetterstedt, 1838)	fac.		0	11	3	14
<i>Corticarina obfuscata</i> Strand, 1937	fac.		0	0	2	2
<b>Byturidae</b>						
<i>Byturus</i> sp.	no		1	0	8	9
<b>Cisidae</b>						
<i>Cis alter (nitidus)</i> Silfverberg, 1991	obl.		0	2	0	2
<i>Cis glabratus</i> Mellie, 1848	obl.		8	2	1	11
<i>Cis comptus</i> Gyllenhal, 1827	obl.		0	2	0	2
<i>Cis hispidus</i> (Paykull, 1798)	obl.		0	1	1	2
<i>Cis boleti</i> (Scopoli, 1763)	obl.		2	4	10	16
<i>Cis punctulatus</i> Gyllenhal, 1827	obl.		24	192	2	218
<i>Cis punctulatus</i> (larvae)	obl.		0	30	0	30
<i>Cis dentatus</i> Mellie, 1848	obl.		1	1	0	2
<i>Cis bidentatus</i> (Olivier, 1790)	obl.		0	1	0	1
<i>Ennearthron laricinum</i> (Mellie, 1848)	obl.	iw	5	2	0	7
<i>Orthocis alni</i> (Gyllenhal, 1813)	obl.		0	1	0	1
<i>Orthocis festivus</i> (Panzer, 1793)	obl.		1	2	0	3
<i>Hadreule elongata</i> (Gyllenhal, 1827)	obl.	iw	15	3	3	21
Cisidae (larvae)	obl.		0	7	0	7
<b>Oedemeridae</b>						
<i>Oedemera virescens</i> (L., 1767)	no		0	0	14	14
<b>Pythidae</b>						
<i>Pytho depressus</i> (L., 1767)	obl.		1	1	0	2
<i>P. depressus</i> (larvae)	obl.		0	1	0	1
<b>Salpingidae</b>						
<i>Rabocerus foveolatus</i> (Ljung, 1823)	obl.	d	0	0	1	1
<i>Salpingus ruficollis</i> (L., 1761)	obl.	d	0	0	2	2
<b>Aderidae</b>						
<i>Euglenes nitidifrons</i> Thomson, 1886	obl.	iw	0	0	1	1
<b>Tenebrionidae</b>						
<i>Corticeus linearis</i> (Fabr., 1790)	obl.		0	0	1	1
<i>Mycetochara obscura</i> (Zetterstedt, 1838)	obl.	iw	2	0	0	2
<b>Scraptiidae</b>						
<i>Anaspis schilskyana</i> Csiki, 1915	obl.	iw	0	0	3	3

**Table A1** (continued).

Taxon	Saproxyllic*	Comments <sup>†</sup>	No. of individuals			
			E	S	W	Total
<i>Anaspis thoracica</i> (L., 1758)	obl.	iw	0	0	3	3
<i>Anaspis rufilabris</i> (Gyllenhal, 1827)	obl.	iw	2	0	4	6
<b>Mordellidae</b>						
<i>Curtimorda maculosa</i> (Naezen, 1794)	obl.	iw	0	0	19	19
<b>Melandryidae</b>						
<i>Hallomenus binotatus</i> (Quensel, 1790)	obl.		0	0	9	9
<i>Orchesia micans</i> (Panzer, 1794)	obl.	d	0	0	1	1
<i>Abdera triguttata</i> (Gyllenhal, 1827)	obl.		50	1	3	54
<i>Xylita laevigata</i> (Hellenius, 1786)	obl.	iw	0	0	5	5
<i>Zilora ferruginea</i> (Paykull, 1798)	obl.		0	6	0	6
<i>Z. ferruginea</i> (larvae)	obl.		0	7	0	7
<b>Cerambycidae</b>						
<i>Asemum striatum</i> (L., 1758)	obl.	iw	0	0	2	2
<i>Rhagium inquisitor</i> (L., 1758)	obl.		0	3	1	4
<i>R. inquisitor</i> (larvae)	obl.		0	86	0	86
<i>Acmaeops pratensis</i> (Laicharting, 1784)	obl.		0	0	1	1
<i>Leptura melanura</i> L., 1758	obl.	iw	0	0	1	1
<i>Callidium coriaceum</i> (Paykull, 1800)	obl.	iw	1	0	0	1
<i>Pogonochaerus fasciculatus</i> (De Geer, 1775)	obl.		1	0	1	2
<b>Chrysomelidae</b>						
<i>Syneta betulae</i> (Fabr., 1792)	no		0	0	2	2
<i>Phratora vittelinae</i> (L., 1758)	no		0	4	0	4
<i>Galeruca tanaceti</i> (L., 1758)	no		0	0	1	1
<b>Apionidae</b>						
<i>Apion</i> sp.	no		0	1	0	1
<b>Curculionidae</b>						
<i>Othiorhynchus scaber</i> (L., 1758)	no		0	3	11	14
<i>Othiorhynchus</i> sp.	no		0	0	1	1
<i>Polydrosus undatus</i> (Fabr., 1781)	no		0	0	8	8
<i>Dorytomus</i> sp.	no		0	0	1	1
<i>Anoplus plantaris</i> (Naezen, 1794)	no		0	0	1	1
<i>Rhyncolus ater</i> (L., 1758)	obl.	iw	16	21	0	37
<i>Hylobius piceus</i> (De Geer, 1775)	obl.		0	0	1	1
<i>Hylobius abietis</i> (L., 1758)	obl.		0	1	16	17
<i>Hylobius pinastri</i> (Gyllenhal, 1813)	obl.		0	0	1	1
<i>Pissodes pini</i> (L., 1758)	obl.		0	1	0	1
<i>Pissodes glyllenhalii</i> (Sahlberg, 1834)	obl.		1	0	0	1
<i>Hylurgops palliatus</i> (Gyllenhal, 1813)	obl.		0	1	9	10
<i>Hylurgops</i> sp.	obl.		0	1	0	1
<i>Hylastes</i> sp.	obl.		0	4	254	258
<i>Xylechinus pilosus</i> (Ratzeburg, 1837)	obl.		1	1	0	2
<i>Phloeotribus spinulosus</i> (Rey, 1883)	obl.		3	0	1	4

**Table A1** (concluded).

Taxon	Saproxyllic*	Comments <sup>†</sup>	No. of individuals			
			E	S	W	Total
<i>Polygraphus</i> sp.	obl.		0	3	1	4
<i>Pityogenes</i> sp.	obl.		1	5	4	10
<i>Orthotomicus</i> sp.	obl.		1	1	0	2
<i>Ips typographus</i> (L., 1758)	obl.		0	0	1	1
<i>Dryocoetes</i> sp.	obl.		94	142	42	278
<i>Dryocoetes</i> sp. (larvae)	obl.		0	8	0	8
<i>Crypturgus</i> sp.	obl.		619	2006	18	2643
<i>Crypturgus</i> sp. (larvae)	obl.		0	64	0	64
<i>Trypodendron lineatum</i> (Olivier, 1795)	obl.	iw	0	1	0	1
<i>Pityophthorus</i> sp.	obl.		1	0	0	1
<b>Total</b>			<b>1483</b>	<b>4298</b>	<b>2416</b>	<b>8197</b>

**Note:** Regarding the classification of taxa in categories, see Materials and methods.

\*no, do not develop in wood; fac., can develop in dead wood, but also in other substrates; obl., develop exclusively in dead wood.

<sup>†</sup>iw, species that develop or are mainly found inside dead wood; d, species that develop exclusively on deciduous tree species.