Saproxylic beetle species in logging residues: which are they and which residues do they use?

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Small-diameter wood is largely overlooked when considering substrates used by saproxylic insects. Large amounts of such wood have always been retained after felling, in the form of logging residues. However, recent interest in renewable energy sources has made the extraction of such logging residues profitable. If this continues, saproxylic insects will have less substrate in which to breed. To determine which species of saproxylic beetles (Coleoptera) may be affected, this study investigated the fauna of four tree genera (aspen, birch, oak and spruce), three diameter classes (1-15 cm) and two decay stages of logging residues in southern Sweden. The aim was to determine which species were present in the wood, and to describe their associations with different categories of residue. The beetles were collected by rearing them out from 794 wood samples. In total, 49 109 beetles were found, belonging to 160 species; of these 22 are, or used to be red listed in Sweden. Fifty-six of the species were sufficiently frequent to allow statistical analysis of their substrate associations and these are presented species-wise. Only four species exhibited no significant association with host tree species and only eight did not vary on the basis of decay stage. Species in more decayed wood were less specific with respect to tree species association. Thirty-five species displayed a significant relationship with diameter class. Species associated with the thinnest wood categories and with a preference for sun-exposure, for example three buprestids recorded here, are expected to be the most severely affected by the harvesting of logging residues.

Key words: Coleoptera, Bioenergy wood, FWD, Logging residues, Saproxylic, Slash, Substrate associations.

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INTRODUCTION

The removal of dead wood has been identified as one major reason for forestry presenting a threat to many species (Esseen et al. 1997). This is because many thousands of species are saproxylic, i.e. they depend on dead wood for the successful completion of their life cycles (Siitonen 2001, deJong et al. 2004). Beetles (Coleoptera) is the most species rich group of saproxylic insects that has been reasonably well studied. Previous research is valuable when evaluating the effects of nature conservation measures. However, relatively little research has focused on the fauna of small-diameter wood, because, until recently, such wood was not commercially interesting (Jonsell 2008). It was retained within the forest, so the species using it have not been regarded as suffering from any shortage of breeding substrate; conservationists have, therefore, generally overlooked it. This situation is now changing. Increasing concerns about global warming, resulting from combustion of fossil fuels, have opened up the market for renewable fuels; in Scandinavia, at least, these may largely consist of logging residues (Lundborg 1998). This will inevitably mean that the amount of decaying wood, an already a restricted resource, will decrease.

In assessing the risks to biodiversity of harvesting logging residues, it is important to know which species are found in this wood. It is also important to know whether there are differences in species assemblages associated with the different types of forest fuels. Such data exist for many species, at least in the form of the personal knowledge of beetle collectors. However, such data are generally anecdotal, and often vague. Despite this, such information is often used in conservation planning (Berg et al. 1994, Dahlberg & Stokland 2004, Tikkanen et al. 2006). Quantitative studies of saproxylic species and their habitat associations are, therefore, very valuable (Haila 1994), not least for logging residues, which are under-represented in the published research. In this paper, I present information on the species found in a large-scale survey of logging residues in southern Sweden. An overview of the survey, listing species numbers in various categories of wood, is presented in Jonsell et al. (2007). Here, the actual species behind these numbers are presented and their associations with logging residues of different decay stages, tree genera and diameters are described.

The specific questions addressed are: which beetle species are found in logging residues on clear cuts in south Sweden? Of these, are any red-listed? What associations are there between species and different types of logging residues?

MATERIAL & METHODS

Samples of logging residue wood were collected in the years 2002-2004 from 60 clear cuts in southern Sweden. The wood was collected during three different time periods (sampling series); between these, there are some differences in the categories of wood collected and the sites sampled (the details can be found in Jonsell et al. 2007). The first and the second sampling series included only part of the categories and consisted in total of 182 samples. The third sample serie was the largest including 612 samples from clear cuts located at 14 different sites (Figure 1). At each of these sites all wood categories were represented (except in some occasions when specific categories could not be found). At each site (except in serie two), wood was sampled from one one-summer-old and one 3-5 year-old clear cut. Sometimes more than two clear cuts were visited on a site to find samples of all wood-categories (see below). The clear cuts were selected on the basis of region, age since cutting and tree-species composition.

Three main factors were compared: tree species (four species), diameter (three classes), and substrate age (two ages). Rearing method (two types) was an additional factor in the analyses. From each clear cut we sampled two to four tree species: aspen (*Populus tremula* L.), birch (*Betula pubescens* Ehrh. and *B. verrucosa* Ehrh.), oak (*Quercus robur* L.), and spruce (*Picea abies* (L.) Karst.). For each tree species, we collected samples from two or three different diameter classes: 1-4 cm, 4-8 cm and 8-15 cm. From each clear cut, we sampled two bundles of each combination of tree species and diameter class, giving a total of 24 bundles of wood to represent each sampled clear cut. However, in sampling series number one and

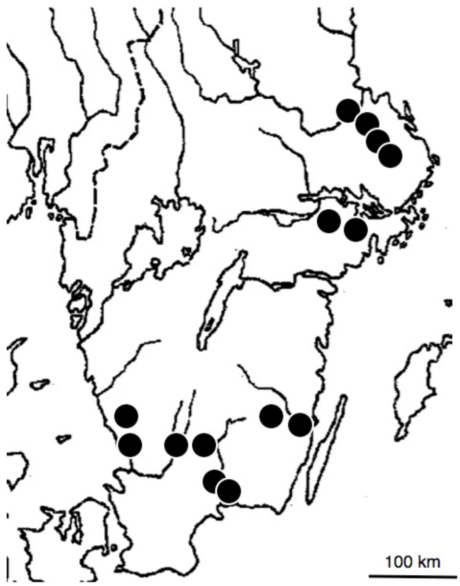

Figure 1. Location of the sampling sites of the largest sampling series (series three) in southern Sweden.

Table 1. Saproxylic beetle species reared out of logging residues on clear cuts in southern Sweden. First data column encompass species from all samples, while the two others only include samples from the third sample series (see Fig. 1). Names and systematical order according to Lundberg and Gustafsson (1995).

Species	Red-list cat 2000-2005	All Samples No of samples	Sample serie three No of sites	Sample serie three No of inds
Anisotoma humeralis (Fabricius,1792)	-	1	1	1
Phosphuga atrata (Linnaeus,1758)	-	2	2	2
Gabrius splendidulus (Gravenhorst,1802)	-	3	3	8
Gabrius expectatus Smetana,1952	-	1	1	1
Quedius xanthopus Erichson,1839	-	1	1	1
Bibloporus bicolor (Denny,1825)	-	4	3	7
Tyrus mucronatus (Panzer,1803)	-	7	5	9
Acrulia inflata (Gyllenhal,1813)	-	5	4	5
Phloeonomus sjoebergi Strand,1937	-	1	1	1
Phloeocharis subtilissima Mannerheim, 1830	-	61	13	115
Sepedophilus littoreus (Linnaeus, 1758)	-	1	1	1
Phloeopara corticalis (Gravenhorst, 1802)	-	19	9	29
Dadobia immersa (Erichson, 1837)	-	55	11	119
Dinaraea aequata (Erichson, 1837)	-	19	9	35
Leptusa pulchella (Mannerheim, 1830)	-	6	5	6
Leptusa fumida (Erichson, 1839)	-	47	11	102
Leptusa ruficollis (Erichson, 1839)	-	25	8	49
Anomagnathus cuspidatus (Erichson, 1839)	-	44	12	102
Homalota plana (Gyllenhal, 1810)	-	2	2	3
Cyphea curtula (Erichson, 1837)	NT–NT	1		
Placusa depressa Mäklin, 1845	-	1	1	1
Trichius fasciatus (Linnaeus, 1758)	-	4	4	12
Platycerus caprea (De Geer, 1774)	NT–0	2	2	2
Lygistopterus sanguineus (Linnaeus, 1758)	-	18	8	37
Denticollis linearis (Linnaeus, 1758)	-	4	3	4
Denticollis borealis (Paykull, 1800)	NT–NT	2	2	3
Melanotus castanipes (Paykull, 1800)	-	2	2	3
Microrhagus lepidus Rosenhauer, 1847	NT–NT	2	1	8
Microrhagus pygmaeus (Fabricius, 1792)	-	1	1	8
Anthaxia quadripunctata (Linnaeus, 1758)	-	20	7	64
Anthaxia godeti Gory, 1841	-	1	1	1
Chrysobothris affinis (Fabricius, 1794)	-	23	7	70
Agrilus angustulus (Illiger, 1803)	-	36	8	450
Agrilus sulcicollis Lacordaire, 1835	-	27	6	75
Agrilus betuleti (Ratzeburg, 1837)	-	42	12	136
Agrilus viridis (Linnaeus, 1758)	-	9	4	18
Agrilus suvorovi populneus Schaefer, 1946	-	43	7	277
Anthrenus museorum (Linnaeus, 1761)	-	1	1	1
Ptinus fur (Linnaeus, 1758)	-	4	3	3
Ernobius mollis (Linnaeus, 1758)	-	2	1	3
Anobium thomsoni (Kraatz, 1881)	-	2	1	4
Hylecoetus dermestoides (Linnaeus, 1761)	-	2	1	1
Nemozoma elongatum (Linnaeus, 1761)	-	17	9	27
Thanasimus formicarius (Linnaeus, 1758)	-	2	1	3
Dasytes niger (Linnaeus, 1761)	-	52	12	75
Dasytes cyaneus (Fabricius, 1775)	-	28	10	41
Dasytes plumbeus (Müller, 1776)	-	34	8	37
Malachius bipustulatus (Linnaeus, 1758)	-	2	1	1
Epuraea pygmaea (Gyllenhal, 1808)	-	1	1	1
Epuraea rufomarginata (Stephens, 1830)	-	4	2	4
Glischrochilus quadripunctatus (L., 1758)	-	3	1	1
Rhizophagus dispar (Paykull, 1800)	-	23	12	30
Rhizophagus bipustulatus (Fabricius, 1792)	-	6	5	6
Dendrophagus crenatus (Paykull, 1799)	NT–0	1	1	1
Laemophloeus muticus (Fabricius, 1781)	NT–VU	1	1	1
Cryptolestes ferrugineus (Stephens, 1831)	-	1	1	2
Cryptolestes alternans (Erichson, 1846)	-	1	1	1
Cryptophagus corticinus Thomson, 1863	-	2		
Dacne bipustulata (Thunberg, 1781)	-	6	3	4
Cerylon fagi Brisout de Barneville, 1867	-	5	3	8
Cerylon histeroides (Fabricius, 1792)	-	4	3	17
Cerylon ferrugineum Stephens, 1830	-	4	4	14
Cerylon deplanatum Gyllenhal, 1827	NT–0	1	1	1
Orthoperus punctatus Wankowicz, 1865	-	2	1	3
Orthoperus mundus Matthews, 1885	-	3	3	8
Latridius hirtus Gyllenhal, 1827	-	2	2	2
Latridius minutus (Linnaeus, 1767)	-	15	4	12
Enicmus testaceus (Stephens, 1830)	-	1	1	1
Enicmus transversus (Olivier, 1790)	-	1	1	1
Dienerella elongata (Curtis, 1830)	-	14	6	43
Aridius nodifer (Westwood, 1839)	-	1	1	3
Corticaria lapponica (Zetterstedt, 1838)	NT–0	1		
Corticaria rubripes Mannerheim, 1844	-	1	1	1
Cis comptus Gyllenhal, 1827	-	6	5	60
Cis hispidus (Paykull, 1798)	-	136	14	1687
Cis setiger Mellie, 1848	-	8	3	52
Cis micans (Fabricius, 1792)	NT–NT	23	4	314
Cis boleti (Scopoli, 1763)	-	82	13	540
Cis rugulosus Mellie, 1848	NT–NT	3	1	8
Cis punctulatus Gyllenhal, 1827	-	21	7	95

Table 1. continued

Species	Red-list cat 2000-2005	All Samples No of samples	Sample serie three No of sites	Sample serie three No of inds
Ennearthron cornutum (Gyllenhal, 1827)	-	1	1	1
Orthocis alni (Gyllenhal, 1813)	-	57	14	107
Orthocis vestitus (Mellie, 1848)	-	2	2	4
Orthocis festivus (Panzer, 1793)	-	29	8	128
Sulcacis affinis (Gyllenhal, 1827)	-	135	14	1917
Octotemnus glabriculus (Gyllenhal, 1827)	-	73	11	488
Synchita humeralis (Fabricius, 1792)	-	33	10	85
Bitoma crenata (Fabricius, 1775)	-	56	14	130
Litargus connexus (Fourcroy, 1785)	-	11	5	23
Pyrochroa coccinea (Linnaeus, 1761)	-	3	2	12
Schizotus pectinicornis (Linnaeus, 1758)	-	98	14	250
Salpingus planirostris (Fabricius, 1787)	-	7	4	8
Salpingus ruficollis (Linnaeus, 1761)	-	4	4	4
Anidorus nigrinus (Germar, 1831)	-	3	2	3
Corticeus linearis (Fabricius, 1790)	-	32	13	80
Anaspis bohemica Schilsky, 1898	-	3	2	6
Anaspis marginicollis Lindberg, 1925	-	1	1	1
Anaspis thoracica (Linnaeus, 1758)	-	2	2	2
Anaspis rufilabris (Gyllenhal, 1827)	-	4	4	4
Anaspis flava (Linnaeus, 1758)	-	3	2	5
Tomoxia bucephala Costa, 1854	-	3	3	4
Mordella holomelaena Apfelbeck, 1914	-	32	11	68
Curtimorda maculosa (Naezen, 1794)	-	4	4	4
Orchesia micans (Panzer, 1794)	-	1	1	16
Orchesia undulata Kraatz, 1853	-	19	7	97
Abdera triguttata (Gyllenhal, 1827)	-	2	2	4
Rhagium mordax (De Geer, 1775)	-	10	7	13
Rhagium inquisitor (Linnaeus, 1758)	-	1	1	1
Anoplodera rubra (Linnaeus, 1758)	-	1	1	1
Anoplodera sanguinolenta (Linnaeus, 1761)	-	1	1	1
Leptura quadrifasciata Linnaeus, 1758	-	13	8	24
Leptura melanura Linnaeus, 1758	-	2	2	2
Molorchus minor (Linnaeus, 1758)	-	15	8	18
Callidium aeneum (De Geer, 1775)	NT–NT	1	1	1
Pyrrhidium sanguineum (Linnaeus, 1758)	NT–NT	5	2	3
Phymatodes testaceus (Linnaeus, 1758)	-	5	2	23
Poecilium alni (Linnaeus, 1767)	NT–NT	1		
Xylotrechus rusticus (Linnaeus, 1758)	-	22	9	55
Xylotrechus antilope (Schönherr, 1817)	NT–NT	5	1	5
Clytus arietis (Linnaeus, 1758)	-	13	7	23
Plagionotus arcuatus (Linnaeus, 1758)	-	26	7	81
Monochamus sutor (Linnaeus, 1758)	-	1	1	1
Pogonocherus hispidulus (P.&Mitterpacher,1783)	NT–0	2	2	6
Pogonocherus fasciculatus (De Geer, 1775)	-	30	10	119
Acanthoderes clavipes (Schrank, 1781)	NT–0	21	7	32
Leiopus nebulosus (Linnaeus, 1758)	-	17	5	41
Leiopus punctulatus (Paykull, 1800)	EN–VU	2	1	2
Saperda scalaris (Linnaeus, 1758)	-	23	8	29
Saperda perforata (Pallas, 1773)	NT–0	5	3	7
Allandrus undulatus (Panzer, 1795)	-	22	12	32
Dissoleucas niveirostris (Fabricius, 1798)	NT–0	2	1	2
Platystomus albinus (Linnaeus, 1758)	-	19	12	29
Choragus horni Wolfrum, 1930	VU–NT	1	1	1
Rhyncolus ater (Linnaeus, 1758)	-	7	6	9
Magdalis duplicata Germar, 1819	-	1	1	1
Magdalis violacea (Linnaeus, 1758)	-	25	10	70
Magdalis carbonaria (Linnaeus, 1758)	-	50	11	155
Magdalis cerasi (Linnaeus, 1758)	-	1	1	1
Hylobius abietis (Linnaeus, 1758)	-	1	1	1
Pissodes pini (Linnaeus, 1758)	-	1	1	2
Trachodes hispidus (Linnaeus, 1758)	-	13	6	45
Hylurgops palliatus (Gyllenhal, 1813)	-	1	1	1
Xylechinus pilosus (Ratzeburg, 1837)	-	4	2	4
Phloeotribus spinulosus (Rey, 1883)	-	4	4	14
Scolytus ratzeburgi Janson, 1856	-	4	2	4
Scolytus intricatus (Ratzeburg, 1837)	-	38	9	1185
Pityogenes chalcographus (Linnaeus, 1761)	-	296	14	34399
Pityogenes quadridens (Hartig, 1834)	-	6	3	19
Pityogenes bidentatus (Herbst, 1783)	-	19	8	138
Orthotomicus suturalis (Gyllenhal, 1827)	-	2	2	2
Ips typographus (Linnaeus, 1758)	-	6	5	8
Dryocoetes autographus (Ratzeburg, 1837)	-	32	11	117
Crypturgus spp.	-	61	12	540
Trypodendron domesticum (Linnaeus, 1758)	-	6	4	53
Trypodendron lineatum (Olivier, 1795)	-	1	1	1
Xyleborus dispar (Fabricius, 1792)	-	18	3	550
Xyleborinus saxesenii (Ratzeburg, 1837)	NT–NT	4	2	12
Trypophloeus bispinulus Eggers, 1927	-	5	3	6
Trypophloeus grothii (Hagedorn, 1904)	NT–NT	12	4	807
Pityophthorus micrographus (Linnaeus, 1758)	-	64	13	2080

two, at the beginning of the project, only two tree species and two diameters were sampled per clear cut. In addition, it was sometimes impossible to find all four tree-species within a clear cut. In such cases we tried to sample the missing tree species from a nearby clear cut, but there are missing data at some sites. The substrate age could be compared, since about half of the clear cuts were one summer old and the rest 3-5 years-old. All clear cuts were paired: one from each age class, at a distance of 1-3 km.

The wood we collected was chosen so that each sample contained wood from different parts of the clear cut. Usually, small-diameter wood is aggregated in piles by the harvester, in which case we sampled wood from five different piles spread out across the clear cut. Only wood with bark was sampled, because many saproxylic beetle species live under the bark. Wood that fitted into the categories described above was selected subjectively from each pile. It was cut into 50 cm long pieces and packed together in 25-35 cm diameter bundles. The bundles contained similar bark surface areas for each diameter class (on average, ranging from 86 to 116 dm^2, Jonsell et al. 2007). Consequently, the volume of solid wood was largest for the coarsest diameter class (averages ranging from 6.4 to 26.3 dm^3 Jonsell et al. 2007). Especially in the early stages of wood decay, the surface area is probably a better descriptor of the amount of habitat than wood volume, because most species live in the space between the bark and the wood. The bundles were taken to the laboratory, where the insects were reared in a greenhouse at 20 °C. There were some deviations from this temperature, especially during warm days in the summer, but all samples within the same rearing cohort were exposed to the same temperature regime. The rearings continued for at least three months.

For practical reasons, we had to use two types of rearing containers: textile sacks and wooden boxes (Jonsell & Hansson 2007). To account for the possible effects of using different rearing containers, one of each bundle type (site, tree species and diameter combination) was enclosed in each type of container. The effect of rearing container was also included in the regression models. When rearing in textile sacks, the bundles of wood were hung from the ceiling by a string then wrapped in a cotton sack with metal wires on the inside to prevent the wood coming into contact with the sack. The insects were collected in a plastic vial attached to a plastic funnel at the bottom of the sack. The remaining wood bundles were placed in boxes made of plywood. Insects were collected in a glass vial inserted in one gable end. At the end of the rearing period, the debris in the bottom of each wooden box was also inspected for insects, since not all insects were caught in the vials.

All saproxylic beetles were determined to species by the authors, according to the nomenclature of Lundberg & Gustafsson (1995). Beetles were classified as saproxylic or not by help of Palm (1959), Hansen (1964) and Koch (1989-1992). Red-listed species were classified according to Gärdenfors (2000, 2005).

Statistics

Associations of individual species with environmental variables were analysed using multiple regression models, including all four variables: age of the clear cut, tree species, diameter class and rearing method. The number of specimens in each sample was the dependent variable. A variable was judged to significantly explain a substrate association if its effects had a probability <0.05 when it was added last to the full model (Type 3 tables in the SAS software). Poisson regression was used, since it is suitable for analysing count data, especially when many results have a value of zero (Quinn & Keough 2002). However, some species, especially *Agrilus* spp., ciids and bark beetles, frequently emerged either in large numbers or were totally absent. This does not fit the Poisson distribution and causes "overdispersion" in the model, implying that levels of significance are likely to be overestimated. For such species, where the deviance/df exceeded 2, the deviance was rescaled, using the command DSCALE in SAS, so that the deviance/df=1. The same procedure was used for species that were "underdispersed", with a deviance/df less than 0.5. 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. In such cases, the statistical significance of the difference between categories were analysed univariately, using a Fisher exact test in a contingency table. The analyses were conducted using SAS (1989-96).

RESULTS

In total, 49 109 saproxylic beetles were found, belonging to 160 species (Table 1). This included 22 red-listed species according to the red-list of 2000 and 14 according the the red list of 2005 (Table 1). 56 species were sufficiently numerous to be analysed for their microhabitat associations (Table 2, Appendix). Six species were found on all 14 sites of sample series three: *Cis hispidus*, *Orthocis alni*, *Sulcacis affinis*, *Bitoma crenata*, *Schizotus pectinicornis* and *Pityogenes chalcographus* (Table 1). The last of these was also the most abundant, with a total of almost 35 000 individuals.

Most of the 56 species for which habitat associations were investigated exhibited a significant association with the age of the wood (Table 2). Eight species displayed no association, 28 species were associated with 3-5 year-old wood and 20 were associated with one summer old wood.

Most beetle species were also significantly associated with one or more tree species – only four species displayed no significant association (Table 2). Of these one, *Phloeopara corticalis*, also exhibited no association to decay-stage. All tree species had at least some beetle species specifically associated with them: spruce had twelve specialists, oak had four and aspen and birch had three each. In the younger wood, more beetles exhibited host specificity than in the older wood (Table 3).

The different species were less clearly associated with particular diameter classes: 21 species exhibited no associaton (Table 2). Of the others, 19 species were associated with the coarser wood categories, and 21 species with the smaller-diameter wood. There were no correlations between diameter class association and either decay class or tree species association.

DISCUSSION

Species found in logging residues

A large number of saproxylic beetle species were found in the residues. The species composition is not dramatically different from the composition in coarser wood. However, direct comparisons with other studies are complicated, since methods, wood quality and other factors differ. This has been discussed more thoroughly in Jonsell (2008) and Jonsell et al. (2007), so here the focus is on the species themselves. One can conclude that logging residues support a diverse fauna of saproxylic beetles.

Several of the species are red-listed, and it is pertinent to ask whether species that occur in logging residues - a very common type of wood - really should be red-listed. I suggest such a classification can be appropriate; indeed the design of this study probably increased the likelihood of finding such species. This was because we did not survey the most common tree species, but we restricted our survey to sites where oak and aspen occurred. The presence of these tree species usually indicates that the sites have a higher conservation value than the average managed forest in Sweden. Moreover, half of the sites were chosen specifically to target biodiversity hot-spots in Sweden (cf Nilsson 2001, Lindbladh et al. 2007). The three red listed species classified as more threatened than NT (on either version of the red-list) were found in these regions: *Laemophloeus muticus* was recorded from the Båtfors-area in northern Uppland; *Leiopus punctulatus* from the Vällen-area in eastern Uppland; and *Choragus horni* from the Hornsö area in Småland. On the other hand, the most frequent species from the year 2000 red-list,

Table 2. Associations of 56 saproxylic beetle species with various categories of logging residue. An association means that there was a significant variable effect in multiple regression analyses (Appendix). Tree species in parentheses are secondary hosts, i.e. hosts with a parameter estimate (see Appendix) less than half that of the highest, but with more than single occurrences.

Species	n	obs.	Decay stage	Diameter	Tree species
Phloeocharis subtilissima	744	61	Old	No assoc.	Deciduous
Phloeopara corticalis	294	19	No assoc.	No assoc.	No assoc.
Dadobia immersa	744	55	Old	No assoc.	Birch and Oak
Leptusa fumida	744	47	Old	No assoc.	Deciduous
Leptusa ruficollis	744	25	Old	No assoc.	No assoc.
Anomagnathus cuspidatus	744	44	No assoc.	Coarse	Aspen (and deciduous)
Lygistopterus sanguineus	376	8	Old	No assoc.	No assoc.
Anthaxia quadripunctata	202	20	No assoc.	Coarse	Spruce
Chrysobothris affinis	365	3	Young	Thin	Oak (and birch)
Agrilus angustulus	131	36	Young	Thin	Oak
Agrilus sulcicollis	131	27	Young	Coarse	Oak
Agrilus betuleti	234	42	Young	Thin	Birch
Agrilus suvorovi	177	43	Young	No assoc.	Aspen
Nemozoma elongatum	333	17	No assoc.	No assoc.	Spruce
Dasytes niger	744	52	Old	Thin	Spruce and birch
Dasytes cyaneus	744	28	Old	Thin	Aspen and oak
Dasytes plumbeus	744	34	Old	Thin	Oak and spruce
Rhizophagus dispar	744	23	Old	Coarse	Deciduous
Latridius minutus	744	15	Young	Thin	Aspen (and deciduous)
Dienerella elongata	450	14	No assoc.	Coarse	Not oak
Cis hispidus	744	136	Old	Coarse	Aspen and birch
Cis micans	744	23	Old	Coarse	Aspen and birch
Cis boleti	376	82	Old	Coarse	Deciduous
Cis punctulatus	112	21	Old	Coarse	Spruce
Orthocis alni	744	57	Old	Thin	No assoc.
Orthocis festivus	567	29	Old	Coarse	Birch and Oak
Sulcacis affinis	744	135	Old	Coarse	Deciduous
Octotemnus glabriculus	744	73	Old	Coarse	Deciduous
Synchita humeralis	411	33	Old	No assoc.	Birch (and aspen)
Bitoma crenata	744	56	Old	Coarse	Deciduous
Schizotus pectinicornis	376	98	Old	Coarse	Deciduous
Corticeus linearis	613	32	Young	No assoc.	Spruce
Mordella holomelaena	376	32	Old	Thin	Oak, birch (and aspen)
Orchesia undulata	376	19	Old	Coarse	Oak (and deciduous)
Leptura quadrifasciata	189	13	Old	No assoc.	Birch (and aspen)
Molorchus minor	202	15	No assoc.	No assoc.	Spruce
Xylotrechus rusticus	411	22	Young	Coarse	Aspen
Clytus arietis	187	13	Old	Thin	Oak (and birch)
Plagionotus arcuatus	56	26	Young	Coarse	Oak
Pogonocherus fasciculatus	202	30	Young	No assoc.	Spruce
Acanthoderes clavipes	542	21	Old	Coarse	Birch (and aspen)
Leiopus nebulosus	365	17	Young	No assoc.	Oak (and birch)
Saperda scalaris	365	23	No assoc.	Coarse	Oak and birch
Allandrus undulatus	744	22	Young	Thin	Aspen (and birch)
Platystomus albinus	542	19	Old	Thin	Birch
Magdalis violacea	202	25	Young	Thin	Spruce
Magdalis carbonaria	234	50	Young	Thin	Birch
Trachodes hispidus	450	13	Old	Thin	Birch and Oak
Scolytus intricatus	56	38	Young	No assoc.	Oak
Pityogenes chalcographus	90	296	Young	No assoc.	Spruce
Pityogenes bidentatus	90	19	Young	No assoc.	Spruce
Dryocoetes autographus	744	32	Young	Coarse	Spruce
Crypturgus spp.	436	61	Old	Coarse	Spruce
Xyleborus dispar	542	18	Young	No assoc.	Oak (and birch)
Trypophloeus grothii	100	12	Young	Thin	Aspen
Pityophthorus micrographus	90	64	Young	No assoc.	Spruce

Acanthoderes clavipes (recorded on seven of the sites included in this survey), was deleted from the revised 2005 red-list. This decision is thus supported by data presented here. Some red-listed species, e.g. *Cis micans* and *Trypophloeus grothii*, were very abundant and more than 300 individuals were recorded. However, they occurred at only four of the sites. Species restricted in their distribution may deserve their entry on the red-list even though they are abundant on the sites where they do occur. Also, the current increase in the harvesting of logging residues may reduce the habitat available for these species, suggesting that they should remain on the red-list.

It has been suggested that many of the saproxylic species in boreal forests depend on disturbances; originally these mainly consisted of fires (Kouki et al. 2001, Lindhe & Lindelöw 2004). This has implications for species in logging residues,

Table 3. Number of species associated with each decay stage and number of tree species (Compiled from Table 2 – species with no association with a specific decay stage are excluded). There is a significant difference in the distribution between columns (contingency table, $\chi 2=26.2$, df=3, p<0.0001).

Number of tree species	Wood one summer old	Wood 3-5 yrs old
One	16	3
Two	4	9
Three	0	13
Four	0	3

since the vast majority of sun-exposed fine wood is created during clear cutting (Jonsell 2008). One group of true sun-lovers are the buprestids (Palm 1959), six species of which were frequent enough to be analysed statistically here. Three of these (*Chrysobotris affinis, Agrilus angustulus* and *A. betuleti*) were associated with the small-diameter wood. This suggests that these species in particular may decrease if logging residues are harvested on a large scale. Other similar examples could probably be drawn from other families on the species list if there were better data on species' responses to sun-exposure.

Affinity to tree species

Spruce had a higher number of specialist species than any of the deciduous tree species. This is because spruce is more different from the deciduous trees than they are from each other (cf Jonsell et al. 1998). In addition, the level of decay affected the host affinities, since host specificity was lower in decayed wood than in recently dead wood. This is probably because many of the secondary host specific metabolites, which defend against herbivores, are still present when the primary consumers arrive. After some years, these metabolites have degraded, and then other parameters have a greater impact on the species composition. Fungal flora is one very important factor (cf Jonsell et al. 2005). Fungal fruiting bodies exhibit a similar pattern of greater host specificity early in the decay process (Jonsell & Nordlander 2004).

Individual species biology

For many of the species listed in Table 2, the associations with the substrate variables are rather well known, and they correspond to more anecdotal data presented, for example, in Palm (1959) and Ehnström & Axelsson (2002). This includes most of the species of high interest to forest entomologists, such as Scolytinae, Buprestidae, and Cerambycidae. Since it is not particularly useful to repeat data already in the literature, the following section focuses on species for which the results here add to our knowledge of species biology. The comments follow the systematic order of Table 2.

In general the Staphylinids were not particularly specialised. *Phloeopara corticalis* was probably the greatest generalist in this study, since it occurred in both decay stages and in all tree species at frequencies that were not significantly different. Several other staphylinids were, however, associated with one, two or three of the deciduous tree species, but none were associated with spruce.

Among the buprestids, *Chrysobotris affinis* was associated with thin wood. Previous authors (Palm 1959, Brechtel & Kostenbader 2002) have recorded that this species makes use of small-diameter wood, but here it exhibited a significant association with such wood. This is surprising for such a large species. A similar preference is less surprising for the small *Agrilus* species, of which *A. betuleti* has a well known association with thin twigs (Ehnström & Axelsson 2002). However, contrary to what is suggested by Ehnström & Axelsson (p 473), there is an overlap in the diameter use with *Agrilus viridis*, which also occurs in birch. The two *Agrilus* species on oak made use of different diameter classes, so that *A. angustulus* was mainly found on thin wood and *A. sulcicollis* mainly on coarse wood. A third species that is suspected to live on oak, *A. laticornis*, (Brechtel & Kostenbader 2002, Ehnström & Axelsson 2002) was not found during this investigation, although several of the sites lay within its known range. The species must either be very rare, or must use some other type of wood for breeding. It has been suggested that this species mainly breeds in the dead top twigs of living trees (Niehuis 2004).

Little is known about the larval biology of species in the genus *Dasytes*; Palm (1959) assigned the larvae of each species to a number of different tree species. Here they were all associated with the thinner diameter classes on older clear cuts, but they all had different host associations. *D. niger* was most common in spruce and birch, whereas *D. cyanea* tended to be found in oak and aspen. *Dasytes plumbeus* was most common in oak and spruce.

Ciid species are fungivores and they often have strong associations with specific hosts (Jonsell & Nordlander 2004). Five of the eight ciid species analysed belong to the assemblage that uses *Trametes*-species and closely related taxa as hosts (Orledge & Reynolds 2005), namely *C. hispidus, Cis micans, C. boleti, Sulcacis affinis* and *Octotemnus glabriculus*. Since these fungi only grow on deciduous trees, the beetles were not found on spruce. However, *Cis micans* was found only in association with aspen, and *C. hispidus* was associated with aspen and birch. This is probably because these beetle species use somewhat different host fungi, which in turn use different host trees. The exact host species for these *Cis*-species are not known, and these results suggest that they are probably not as uniform as one may expect from the literature (Reibnitz 1999, Orledge & Reynolds 2005). These differences may, however also depend on factors other than host specificity (Guevara et al. 2000). *Orthocis festivus* lives on *Stereum* species (Orledge & Reynolds 2005) and its association with birch and oak correlates with the host trees of the more common *Stereum* species in Sweden (Ryman & Holmåsen 1984). *Cis punctulatus* is a specialist on *Trichaptum* (Reibnitz 1999, Jonsell et al. 2005, Orledge & Reynolds 2005), which occurs almost exclusively on conifers. *Orthocis alni* exhibited no preference for particular tree species; its putative host fungi is *Auricularia* (Orledge & Reynolds 2005).

Among the ciids, almost all species were associated with coarse wood, although the number of occurrences was rather similar between diameter classes. However, many more individuals were reared from the coarse wood. The single ciid exception was *Orthocis alni*, which was associated with fine wood.

The biology of *Allandrus undulatus* is little known (Ehnström & Axelsson 2002). Here we found it rather frequently on young clear cuts, and it was strongly associated with small-diameter aspen (and birch) wood. It was also widely distributed and found on 12 of the 14 sites. The beetle family to which it belongs, the Anthribidae, is generally associated with ascomycetes (Crowson 1984), but apparently this species requires a very early primary coloniser, since it was found mainly on the young clear cuts. It might even be the agent that disperses the fungus, in the same way as has been suggested for *Daldinia loculata* (Johannesson et al. 2001). In that case, the fungus occurs endophytically in live, healthy trees in the form of inactive mycelia. When the trees die, insects trigger the decay of the wood and the formation of fruiting bodies, by dispersing asexual conidia between trees. This may explain why a fungivorous beetle is associated with recently dead wood.

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Appendix. Poisson regression models for the 56 species occurring in more than 11 samples. p-values are shown for each variable (capital letters) based on the likelihood ratio statistics. For each category, numbers show the predicted odds to have an occurrence as compared to the reference category for each variable. These are AGE=Young, TREE=Spruce, DIAM=Thin and METHOD=Sack, unless otherwise noted.

Species	Variable	p-value	Category	Odds
Phloeocaris subtilissima				
	df, error=736		Deviance/df=0.7445	
	AGE	0.0001	Old	2.9
	TREE	0.0001	Aspen	4
			Birch	2.7
			Oak	6.3
	DIAM	0.1652	Coarse	1.7
			Medium	0.8
	METHOD	0.0001	Box	0.11
Phloeopora corticalis				
	df, error=288		Deviance/df=0.504	
	AGE	0.7083	Old	1.2
	TREE	0.7015	Aspen	1.9
			Birch	1.8
			Oak	1.3
	DIAM	0.0548	Medium	2.3
Dadobia immersa				
	df, error=736		Deviance/df=0.7401	
	AGE	0.0001	Old	5.2
	TREE	0.0005	Aspen	0.9
			Birch	2.1
			Oak	2.4
	DIAM	0.5098	Coarse	0.6
			Medium	0.9
	METHOD	0.0001	Box	0.17
Leptusa fumida				
	df, error=736		Deviance/df=0.5747	
	AGE	0.0001	Old	3.9
	TREE	0.0001	Aspen	5.8
			Birch	4.8
			Oak	7.3
	DIAM	0.9131	Coarse	0.8
			Medium	0.9
	METHOD	0.0001	Box	0.03
Leptusa ruficollis				
	df, error=736		Deviance/df=0.4534	
	AGE	0.0012	Old	2.6
	TREE	0.8914	Aspen	0.9
			Birch	0.8
			Oak	1
	DIAM	0.6175	Coarse	2
			Medium	1
	METHOD	0.0001	Box	0.07

Appendix. continued

Species	Variable	p-value	Category	Odds
Orthocis alni				
	df, error=736		Deviance/df=0.595	
	AGE	0.0001	Old	26.7
	TREE	0.2758	Aspen	1.4
			Birch	0.8
			Oak	0.9
	DIAM	0.0006	Coarse	0.2
			Medium	1.1
Orthocis festivus				
	df, error=560		Deviance/df=0.9984	
	AGE	0.0001	Old	23.3
	TREE	0.0001	Birch[a]	8.6
			Oak[a]	10.6
	DIAM	0.0001	Coarse	3.4
			Medium	4.2
	METHOD	0.0001	Box	0.1
	[a]) Spruce is the reference			
Sulcacis affinis				
	df, error=736		Deviance/df=8.689	
	AGE	0.0001	Old	249.7
	TREE	0.0001	Aspen	61.9
			Birch	55.4
			Oak	13.3
	DIAM	0.0001	Coarse	7.5
			Medium	1.6
	METHOD	0.0001	Box	0.4
Octotemnus glabriculus				
	df, error=736		Deviance/df=2.3289	
	AGE	0.0001	Old	168.9
	TREE	0.0001	Aspen	49.3
			Birch	23.2
			Oak	7.4
	DIAM	0.0001	Coarse	7.4
			Medium	2.7
	METHOD	0.0001	Box	0.13
Synchita humeralis				
	df, error=405		Deviance/df=1.5143	
	AGE	0.0001	Old	4.1
	TREE	0.0001	Aspen[a]	0.3
	DIAM	0.0225	Coarse	0.4
			Medium	1.3
	METHOD	0.0001	Box	0.3
	[a]) Birch is the reference			

Appendix. continued

Species	Variable	p-value	Category	Odds
Anomognathus cuspidatus				
	df, error=736		Deviance/df=0.6523	
	AGE	0.1239	Old	1.3
	TREE	0.0001	Aspen	97.8
			Birch	13.4
			Oak	18.6
	DIAM	0.0001	Coarse	6
			Medium	2.2
	METHOD	0.0001	Box	0.06
Lygistopterus sanguineus				
	df, error=369		Deviance/df=0.5462	
	TREE	0.1014	Aspen	0.7
			Birch	2.3
			Oak	1.1
	DIAM	0.1599	Coarse	1.3
			Medium	2.2
	METHOD	0.0246	Box	0.4
Anthaxia quadripunctata				
	df, error=197		Deviance/df=0.5227	
	AGE	0.4595	Old	0.7
	DIAM	0.0052	Coarse	3.5
			Medium	0.2
	METHOD	0.0459	Box	0.2
Chrysobotris affinis				
	df, error=359		Deviance/df=1.2497	
	AGE	0.0001	Old	0.03
	TREE	0.0001	Birch[a]	0.13
	DIAM	0.0001	Coarse	0.3
			Medium	0.5
	METHOD	0.8726	Box	1
	[a]) Oak is the reference			
Agrilus angustulus				
	df, error=126		Deviance/df=13.7756	
	AGE	0.01	Old	0.4
	DIAM	0.0007	Coarse	0.5
			Medium	0.17
	METHOD	0.2008	Box	0.6
Agrilus sulcicollis				
	df, error=126		Deviance/df=3.1614	
	AGE	0.0001	Old	0.16
	DIAM	0.0406	Coarse	2.9
			Medium	2.8
	METHOD	0.3943	Box	0.7
Agrilus betuleti				
	df, error=229		Deviance/df=1.4116	
	AGE	0.0001	Old	0.03
	DIAM	0.0001	Coarse	0.04
			Medium	0.14
	METHOD	0.0353	Box	1.5

Appendix. continued

Species	Variable	p-value	Category	Odds
Agrilus suvurovi				
	df, error=172		Deviance/df=8.1772	
	AGE	0.0001	Old	0.15
	DIAM	0.0001	Coarse	0.8
			Medium	3.8
	METHOD	0.7706	Box	1.1
Nemozoma elongatum				
	df, error=327		Deviance/df=0.5474	
	AGE	0.457	Old	0.8
	TREE	0.0001	Oak[a]	0.12
	DIAM	0.1505	Coarse	0.6
			Medium	1.9
	METHOD	0.0001	Box	0.11
	[a]) Spruce is the reference			
Dasytes niger				
	df, error=736		Deviance/df=0.4227	
	AGE	0.0001	Old	72.1
	TREE	0.0001	Aspen	0.5
			Birch	0.8
			Oak	0.3
	DIAM	0.0001	Coarse	0.3
			Medium	0.8
	METHOD	0.1978	Box	0.8
Dasytes cyaneus				
	df, error=736		Deviance/df=0.3712	
	AGE	0.0001	Old	3.4
	TREE	0.0001	Aspen	2.9
			Birch	1
			Oak	2.7
	DIAM	0.0001	Coarse	0.08
			Medium	0.5
	METHOD	0.0001	Box	0.4
Dasytes plumbeus				
	df, error=736		Deviance/df=0.2942	
	AGE	0.0001	Old	2.9
	TREE	0.0001	Aspen	0.3
			Birch	0.18
			Oak	1.1
	DIAM	0.0001	Coarse	0.3
			Medium	0.16
	METHOD	0.0623	Box	0.7
Rhizophagus dispar				
	df, error=736		Deviance/df=0.2543	
	AGE	0.0001	Old	5.2
	TREE	0.0001	Aspen	8.5
			Birch	19.6
			Oak	6.3
	DIAM	0.0001	Coarse	3.6
			Medium	2.9
	METHOD	0.0001	Box	0.3

Appendix. continued

Species	Variable	p-value	Category	Odds
Lathridius minutus				
	df, error=736		Deviance/df=0.2135	
	TREE	0.0001	Aspen	14.8
			Birch	4.5
			Oak	1.6
	AGE	0.0005	Old	0.5
	DIAM	0.0063	Coarse	0.3
			Medium	0.9
	METHOD	0.1666	Box	0.7
Dienerella elongata				
	df, error=443		Deviance/df=0.857	
	AGE	0.7335	Old	1.1
	TREE	0.0002	Aspen	2.6
			Birch	2.5
			Oak	0.3
	DIAM	0.0001	Coarse	22.6
			Medium	17.5
Cis hispidus				
	df, error=736		Deviance/df=6.1709	
	AGE	0.0001	Old	86.2
	TREE	0.0001	Aspen	46.6
			Birch	20.5
			Oak	1.7
	DIAM	0.0001	Coarse	8.5
			Medium	3.7
	METHOD	0.4957	Box	0.9
Cis micans				
	df, error=736		Deviance/df=2.3553	
	AGE	0.0001	Old	298.6
	TREE	0.0001	Aspen	51.7
			Birch	3.1
			Oak	0.4
	DIAM	0.0001	Coarse	42.5
			Medium	1.7
	METHOD	0.0225	Box	0.3
Cis boleti				
	df, error=369		Deviance/df=5.7919	
	TREE	0.0001	Aspen	43.4
			Birch	14.1
			Oak	10.4
	DIAM	0.0001	Coarse	13.5
			Medium	7.4
	METHOD	0.0001	Box	0.3
Cis punctulatus				
	df, error=108		Deviance/df=2.5543	
	DIAM	0.0012	Coarse	11.5
			Medium	6
	METHOD	0.0162	Box	0.3

Appendix. continued

Species	Variable	p-value	Category	Odds
Bitoma crenata				
	df, error=736		Deviance/df=0.7798	
	AGE	0.0001	Old	8.6
	TREE	0.0001	Aspen	2.5
			Birch	5.9
			Oak	3.4
	DIAM	0.0001	Coarse	7.2
			Medium	2.7
	METHOD	0.0001	Box	0.06
Schizotus pectinicornis				
	df, error=369		Deviance/df=1.7812	
	TREE	0.0001	Aspen	29.4
			Birch	75.5
			Oak	42.4
	DIAM	0.0001	Coarse	3
			Medium	3.5
	METHOD	0.0017	Box	0.5
Corticeus linearis				
	df, error=606		Deviance/df=0.4837	
	AGE	0.0001	Old	0.16
	TREE	0.0001	Aspen[a]	0.012
			Birch[a]	0.019
	DIAM	0.0007	Coarse	1.1
			Medium	2.6
	METHOD	0.0034	Box	0.5
	[a]) Spruce is the reference			
Mordella holomeleana				
	df, error=369		Deviance/df=0.8835	
	TREE	0.0001	Aspen	6.9
			Birch	43
			Oak	30.3
	DIAM	0.0186	Coarse	0.4
			Medium	0.8
	METHOD	0.0018	Box	2.4
Orchesia undulata				
	df, error=369		Deviance/df=1.3131	
	TREE	0.0001	Aspen	3.2
			Birch	3.5
			Oak	59.6
	DIAM	0.0001	Coarse	2.4
			Medium	0.5
	METHOD	0.0004	Box	4.5
Leptura quadrifasciata				
	df, error=184		Deviance/df=0.649	
	TREE	0.0209	Aspen[a]	0.3
	DIAM	0.123	Coarse	3
			Medium	1.6
	METHOD	0.1789	Box	2.4
	[a]) Birch is the reference			

Appendix. continued

Species	Variable	p-value	Category	Odds
Molorchus minor				
	df, error=197		Deviance/df=0.5085	
	AGE	0.1553	Old	0.5
	DIAM	0.1033	Coarse	0.15
			Medium	0.7
	METHOD	0.2676	Box	0.6
Xylotrechus rusticus				
	df, error=405		Deviance/df=0.6365	
	AGE	0.0001	Old	0.16
	TREE	0.0001	Aspen[a]	45.8
	DIAM	0.0001	Coarse	183.9
			Medium	14
	METHOD	0.1916	Box	0.5
	a) Birch is the reference			
Clytus arietis				
	df, error=182		Deviance/df=0.55	
	TREE	0.0001	Birch[a]	0.06
	DIAM	0.0253	Coarse	0.5
			Medium	0.2
	METHOD	0.1643	Box	2
	a) Oak is the reference			
Plagionotus arcuatus				
	df, error=126		Deviance/df=3.2369	
	AGE	0.0001	Old	0.04
	DIAM	0.0001	Coarse	12.1
			Medium	4.5
	METHOD	0.0027	Box	0.3
Pogonochaerus fasciculatus				
	df, error=197		Deviance/df=2.1382	
	AGE	0.0001	Old	0.03
	DIAM		Medium	2.2
			klen	1
	METHOD	0.9291	Box	1
Acanthoderes clavipes				
	df, error=535		Deviance/df=0.3097	
	AGE	0.0001	Old	37
	TREE	0.0001	Aspen[a]	1.9
			Birch[a]	9.1
	DIAM	0.0113	Coarse	2
			Medium	1.9
	METHOD	0.1307	Box	0.7
	a) Oak is the reference			
Leiopus nebulosus				
	df, error=359		Deviance/df=0.5259	
	AGE	0.0001	Old	0.13
	TREE	0.0001	Birch[a]	0.09
	DIAM	0.1586	Coarse	1.8
			Medium	0.9
	METHOD	0.001	Box	7.2
	a) Oak is the reference			

Appendix. continued

Species	Variable	p-value	Category	Odds
Saperda scalaris				
	df, error=359		Deviance/df=0.482	
	AGE	0.1931	Old	1.6
	TREE	0.0165	Birch[a]	0.4
	DIAM	0.0007	Coarse	7.1
			Medium	8.4
	METHOD	0.2203	Box	1.8
	a) Oak is the reference			
Allandrus undulatus				
	df, error=736		Deviance/df=0.2528	
	AGE	0.0001	Old	0.04
	TREE	0.0001	Aspen	8.2
			Birch	4
			Oak	0.8
	DIAM	0.0001	Coarse	0.07
			Medium	0.2
	METHOD	0.3443	Box	0.8
Platystomus albinus				
	df, error=535		Deviance/df=0.3502	
	AGE	0.0001	Old	5.2
	TREE	0.0001	Aspen[a]	0.5
			Birch[a]	9.3
	DIAM	0.0001	Coarse	0.11
			Medium	0.6
	METHOD	0.0001	Box	0.4
	a) Oak is the reference			
Magdalis violacea				
	df, error=197		Deviance/df=1.0225	
	AGE	0.0001	Old	0.03
	DIAM	0.0017	Coarse	0.4
			Medium	0.3
	METHOD	0.0753	Box	1.8
Magdalis carbonaria				
	df, error=229		Deviance/df=2.3956	
	AGE	0.0001	Old	0.04
	DIAM	0.0001	Coarse	0.12
			Medium	0.4
	METHOD	0.4523	Box	1.2
Trachodes hispidus				
	df, error=443		Deviance/df=0.6253	
	AGE	0.0001	Old	6.6
	TREE	0.0001	Aspen	0.3
			Birch	4.7
			Oak	7.3
	DIAM	0.0001	Coarse	0.2
			Medium	1.2

Appendix. continued

Species	Variable	p-value	Category	Odds
Scolytus intricatus				
	df, error=52		Deviance/df=73.1408	
	DIAM	0.7065	Coarse	0.6
			Medium	0.7
	METHOD	0.2328	Box	0.5
Pityogenes calchographus				
	df, error=86		Deviance/df=433.8005	
	DIAM	0.0687	Coarse	0.5
			Medium	1.5
	METHOD	0.0001	Box	0.2
Pityogenes bidentatus				
	df, error=86		Deviance/df=6.79	
	DIAM	0.2237	Coarse	0.17
			Medium	0.5
	METHOD	0.0003	Box	0.14
Pityphthorus micrographus				
	df, error=86		Deviance/df=66.6317	
	DIAM	0.0119	Coarse	1.1
			Medium	3.9
	METHOD	0.0001	Box	0.12
Trypophloeus grothii				
	df, error=75		Deviance/df=20.3945	
	DIAM	0.0001	Medium	0.01
	METHOD	0.0001	Box	395
Crypturgus spp.				
	df, error=430		Deviance/df=5.0351	
	TREE	0.0001	Birch	0.3
	AGE	0.0001	Old	31.7
	DIAM	0.0001	Coarse	3.9
			Medium	5.7
	METHOD	0.0056	Box	0.5
Xyleborus dispar				
	df, error=535		Deviance/df=6.0477	
	TREE	0.0001	Aspen[a]	0.004
			Birch[a]	0.04
	AGE	0.0001	Old	0.09
	DIAM	0.5634	Coarse	0.6
			Medium	1
	METHOD	0.0001	Box	0.16
	[a]) Oak is the reference			
Dryocoetes autographus				
	df, error=736		Deviance/df=0.9441	
	AGE	0.0001	Old	0.2
	TREE	0.0001	Aspen	0.17
			Birch	0.06
			Oak	0.12
	DIAM	0.0001	Coarse	16.4
			Medium	2.9
	METHOD	0.3106	Box	1.5