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The influence of forest regrowth, original canopy cover and tree size on saproxylic beetles associated with old oaks

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Abstract

Abandoned management has caused many sites with free-standing, large oaks (*Quercus robur*) to become more shaded. This study shows how forest regrowth affects beetle species associated with old oaks in south-eastern Sweden. Beetles were trapped by pitfall traps placed in hollows and window traps placed near hollows in oak trunks in pasture woodlands. We assessed the influence of forest regrowth, tree size and original canopy cover on the species richness of saproxylic beetles (a total of 120 species identified) and the occurrence of 68 saproxylic beetle species in particular. Species richness was greatest in stands with large, free-standing trees. Large girth as well as low canopy cover increased frequency of occurrence for several species. Forest regrowth was found to be detrimental for many beetle species. As most localities with endangered beetles living in old oaks are small and isolated, ongoing management and the restoration of abandoned pasture woodlands should have a high priority in nature conservation.

Keywords: Saproxylic beetles; Quercus robur; Pasture woodland; Forest regrowth; Tree hollow; Microclimate

1. Introduction

In Europe, old-growth temperate deciduous forests have declined to a very small fraction of their original extent (Hannah et al., 1995), and this has caused very old trees to be much more scarce. Up until the 19th century, old trees were also widespread in pasture woodlands (Kirby et al., 1995), but abandoned management and changes of land use have caused a severe reduction of these habitats (e.g. Nilsson, 1997a; Kirby and Watkins, 1998). Therefore, many species dependent on old deciduous trees have remnant distributions with small, isolated populations (e.g. Harding and Rose, 1986; Speight, 1989). One such group are beetles that have a restricted dispersal capacity and are dependent on hollow trees (Speight, 1989; McLean and Speight, 1993; Nilsson and Ericson, 1997). In Sweden, large oaks (*Quercus robur*) sustain the most diverse fauna of beetles associated with old trees (Palm, 1959). The largest oaks (in trunk diameter, not in height) have formerly grown more or less in the open in wooded meadows (mainly used for hay-making) and, more lately, in pasture woodlands (mainly used for grazing) (Eliasson and Nilsson, 2000). As agriculture has changed drastically in the last few decades, many pasture woodlands have been abandoned (Nilsson, 1997a), and this has caused the habitats containing sunexposed old trees to decrease, in favour of shadier woods. This might be detrimental to the beetle fauna, since it is generally held among entomologists that beetles associated with old oaks prefer sun-exposed trees (e.g. Palm, 1959; Gärdenfors and Baranowski, 1992). However, there is a lack of quantitative data to support this view (but see Ranius and Nilsson, 1997; Lott, 1999). The present study considers how current management, original canopy cover and tree size affect the frequency of saproxylic beetles in old, hollow oaks. The first aim was to examine how the frequency of occurrence of beetles relates to original canopy cover. We would expect that there are species preferring large, free-standing oaks, but is there also an assemblage of species associated with shadier woods? The second aim was to assess how the beetle fauna is influenced by forest regrowth and whether the beetles are affected indifferent ways depending on which microhabitat they are associated with. The third aim was to study the preference for characteristics of individual trees that could explain the difference in frequency of occurrence between stands. Are the higher frequencies in stands with large, free-standing trees a result of preference for large girths or for sun-exposure?

2. Study plots, material and methods

2.1. Study plots

This study was performed in one of the few remaining landscapes in Northern Europe with a high density of old oaks, which is situated in the province of Östergötland, south-eastern Sweden (Antonsson and Wadstein, 1991). Here, plots were studied in a 12 × 16 km area with Bjärka-Säby as its centre (15 km south from Linköping, 58°16´N, 15 ° 46´E). We surveyed the beetle fauna of hollow oaks in 18 plots, each with an area of 0.5-8 ha. The plots were selected to obtain three groups of six plots differing in original canopy cover. The 'original cover' was assessed by measuring the canopy of

mature and old trees, i.e. by ignoring the cover produced by young trees that had invaded former open woodland. Thus, six plots contained mainly originally free-standing oaks (vertical coverage of the canopy: 10-30%), another six contained originally half-open pasture woodland (30-70% coverage) and the remaining six contained originally closed pasture woodland (70-90% coverage). Each category was subdivided so that three plots were still affected by grazing while the other three were regrown due to natural regeneration of deciduous trees. These young deciduous trees were 5-10 m high and mainly in dense stands, even though glades and patches with sparser canopy cover occured frequently. According to the category division above, the plots were characterized by two variables: ORIGINAL CANOPY COVER and FOREST REGROWTH. Moreover, for each tree with traps seven variables were estimated that might influence the results if they correlated with the two variables on the plot level (Table 1).

2.2. Beetle trapping

We set traps in and near hollows of oak trunks to survey saproxylic beetles living in old oaks, especially those associated with wood mould, but other saproxylic beetles associated with old oaks were also studied. Wood mould is fungi-infested loose wood in hollows, often with remains of bird nests and insect fragments. In each plot, we selected five living oaks with hollow trunks for trapping. The trees were chosen at random among those hollow trees where we were able to set traps. To be suitable for pitfall trapping, the entrance to the hollow had to be wide enough and not more than 7 m from the ground and the wood mould surface not too far from the entrance. In each tree, one pitfall trap and one window trap were set. The pitfall traps were plastic jars with a top diameter of 65 mm, placed with the opening level with the wood mould in the hollows. Each window trap consisted of a 30×40 cm wide transparent plastic plate with a tray underneath. Window traps were placed beside or in front of the entrance of the hollow. Glycol and water was used as preservative in all traps and detergent added to eliminate surface tension. The traps were placed in the trees 6-13 May and removed 8-16 August in 1994 and were examined every third week. All saproxylic beetle species can be caught within this period, even though a few individuals are active earlier and later than this (own obs.). This study includes beetles living in dead wood, saproxylic fungi, wood mould and animal nests in mature and old oaks. The beetles were identified by Nicklas Jansson, except Ampedus and Cryptophagidae which were identified by Rickard Andersson (formerly Baranowski). The following taxa include some saproxylic species, but they were not analyzed as they are difficult to identify or regarded as being of limited interest for this study: Anaspidae, Dasytinae, Euglenidae, Latridiinae, Nitudulidae, Ptilidae, Staphylinidae (except Staphylininae and Omaliinae) and Throscidae. The beetle species were divided into groups with regard to their microhabitat in trees (Table 2). The microhabitats of each species were obtained by consulting Swedish entomologists, in particular Rickard Andersson (pers. comm.), but also Bengt Ehnström (pers. comm.), Palm (1959) and our own observations.

3

2.3. Statistical analyses

The number of trees per plot with each species present was studied in relation to ORIGINAL CANOPY COVER and FOREST REGROWTH using analysis of covariance. The total number of species per tree, and for each of the six microhabitat groups were summed for each plot and analyzed similarly. Characteristics of trees with traps were estimated (Table 1) and analysis of their correlation with ORIGINAL CANOPY COVER and FOREST REGROWTH revealed three statistically significant relations: TRUNK DIAMETER was much greater in plots with low ORIGINAL CANOPY COVER (Spearman coefficient, C=-0.767, P<0.001), and SURROUNDING COVER increased with increasing ORIGINAL CANOPY COVER (C=0.381, P<0.001) and was higher in plots with FOREST REGROWTH (C=0.326, P=0.002). TRUNK DIAMETER and SURROUNDING COVER may therefore influence the correlation between species occurrence and characteristics of plots. Consequently, the presence (1) and absence (0) of each species were analyzed in relation to these two variables with multiple logistic regression (Hosmer and Lemeshow, 1989), and number of species in different microhabitats per tree were analyzed with multiple linear regression. The correlation between species richness and SURROUNDING COVER and TRUNK DIAMETER was further explored by comparing the number of species in trees divided into categories varying in these characteristics. Possible differences in occurrence patterns between redlisted and other species were controlled for by analyzing correlations not only with total number of species, but also with these two groups separately. All statistical analyses were carried out by use of SPSS 6.1.

2.4. Weather

The mean temperature was lower than normal in May and June, but higher than normal in July and August (Temperature, May, June, July, August 1994: 9.8, 13.4, 20.5, 16.7°C, mean 1960-1990: 10.5, 15.0, 16.2 and 15.3°C, respectively. Data from SMHI, Meteorological station of Malmslätt, 20 km from Bjärka-Säby).

3. Results

3.1. Species richness

In total, we found and indentified 120 saproxylic beetle species associated with mature or old oaks (Table 2). Among these species, 40% were on the Swedish red list. The number of identified beetle species per plot (five trees) varied between 36 and 58 (mean=47.4, S.D.=7.5) and per tree between 7 and 34 (mean=20.0, S.D.=6.3). We considered that a species must be present in at least five trees out of the 90 in order to analyze its occurrence in particular. This was the case for 68 species (Table 3), and among these, 41% were on the Swedish red list.

3.2. Plot differences: canopy cover and forest regrowth

The frequency of occurrence of saproxylic beetle species was higher in plots that were originally open (low ORIGINAL CANOPY COVER) and were still grazed (FOREST REGROWTH=0) (Table 4). Beetles associated with fruiting bodies of saproxylic fungi were the only group that showed a slight tendency to positive correlation with FOREST REGROWTH. Frequency of presence increased significantly with ORIGINAL CANOPY COVER for one species and decreased for four species. Furthermore, frequency of presence was lower in plots with FOREST REGROWTH for 10 species, whereas it was higher for one (Table 3). There was no assemblage of species associated with originally shadier forest. One single species - *Hypebaeus flavipes* - had greater frequency of occurrence in stands with higher original canopy cover. This seemed to be due to its preference for thinner trunks, as the species in the analysis at the per tree level was associated with thinner trunks and an open surrounding (Table 3). STAND SIZE was positively correlated with ORIGINAL CANOPY COVER (P=0.007) so an analysis of covariance was made between the number of species per plot in relation to STAND SIZE, ORIGINAL CANOPY COVER and FOREST REGROWTH. Since no significant effect was found we were satisfied that species richness was not affected by the number of large hollow oaks around our sample plots.

3.3. Tree effects: trunk diameter and surrounding cover

Low SURROUNDING COVER and large TRUNK DIAMETER were similar in importance for the frequency of occurrence of species (Tables 3 and 5). Species predominantly occurring in originally more open stands were affected both by surrounding cover and trunk diameter; of the four species significantly preferring originally low canopy cover, one preferred sunexposed trees and three preferred large girths (Table 3). Free-standing trees sustained higher species richness than trees situated in half-open or shaded conditions, whereas the difference between the two latter categories was small. Species richness was lower especially for trees with the thinnest trunks, whereas the difference was smaller between trees of intermediate and large girths (Table 6). Beetles associated with hollows and fruiting bodies of saproxylic fungi obtained the strongest positive correlation with large girths, but beetles in all microhabitats showed this trend. In general, red-listed species showed the same trends in their occurrence patterns as other species (Tables 4 and 6).

4. Discussion

4.1. Characteristics on plot and tree level

Grazed stands contained more saproxylic beetle species (Tables 3 and 4), probably because increased sun exposure makes the microclimate warmer. In grazed land, the habitat is more open not just because of grazing itself, but also because shrubs and young trees arecut to increase grass growth. The group of beetles that were most negatively affected by forest regrowth, were those associated with

animal nests (Table 4). This suggests that the preference for sun exposure for some species could also be because bird nests in tree hollows are more frequent in open areas. Due to better food availability for birds in open habitats, birds occupy a higher proportion of hollows near agricultural land than inside forests (Johnsson et al., 1993). Beetles associated with fruiting bodies of saproxylic fungi (group 4) prefer trees with large girths and a surrounding with a dense canopy cover (Table 5). One explanation could be that such trunks benefit saproxylic fungi by maintaining better moisture conditions, whereas another possibility is that such trees provide more entries able for the fungi to colonize. Both these conditions are important for the colonization of saproxylic fungi (Rayner and Boddy, 1988). The girths of the trunks are not affected by forest regrowth in the last few decades, but the trunks are thinner in originally shadier forests. Therefore, large oaks subject to forest regrowth might be the most suitable for beetles associated with fruiting bodies of saproxylic fungi. The preference for sun-exposed oaks has been considered by several Swedish entomologists (Palm, 1959; Gärdenfors and Baranowski, 1992; Jonsell et al., 1998) and is currently studied in Britain (Alexander, 1999; Lott, 1999) but most European studies on saproxylic beetles do not discuss any such preference (e.g. Dajoz, 1980; Harding and Rose, 1986; Speight, 1989; Hyman, 1992). Among the Swedish studies, only Palm (1959) records the habitat preference for single species and allows comparisons with the present study. The proportion of species preferring sun exposure and shade according to Palm (1959) is consistent with the present study, but his conclusions regarding individual species is partly contradictory with ours (Table 7). He studied more tree species in a broader climatic range, which may explain the differences in habitat preference compared to our study. It is impossible to look closer at this result, however, because he did not include quantitative data in his report. Studies on single species that include quantitative estimates are in better agreement with the present study (*Osmoderma eremita*: Ranius and Nilsson, 1997; *Grynocharis oblonga*: Nilsson, 1997b). Consequently, conclusions about habitat preferences must be based on quantitative analysis of data, not simply observations, so that the generality of the conclusions can be determined and further tested. Only then will we gain firm knowledge of the habitat characteristics favoured by saproxylic beetles. It is possible that the occurrence of some species are weakly correlated with the studied variables of sun exposure, that are affected by management, but still thespecies prefer a warm microclimate. A study on Osmoderma eremita showed that the frequency of occurrence is higher in hollows with the entrance facing south or west (Ranius and Nilsson, 1997). The orientation of the entrance is also a characteristic that affects sun exposure and microclimate (Kelner-Pillault, 1974), although the association between occurrence of O. eremita and canopy cover was rather weak in that study, as well as the present study. As the activity of beetles generally increases with increased temperature (e.g. Chiverton, 1988; Luff, 1982), catchability might be higher in sun-exposed trees. However, this study was performed in a summer with warmer weather than average, and therefore we think it was warm enough for all species to be catchable this year, even in trees with a cooler microclimate. The study area is situated near the northern distribution limit for many of the studied species, and the climate is cooler there than in the centre of their

distribution range in Europe. According to Martin (1989), beetles living in hollow trees prefer sun-exposed trees when near the northern limits of their distribution, but further south they occupy shadier habitats as well. Studies on butterflies in Britain and France have shown that in the cooler climate of Britain, butterflies are confined to habitats with warmer microclimates than in France (Thomas, 1993). Thus, the species in this study might be less strongly associated with open habitats further south in Europe, but we know of no relevant studies. Presently, some saproxylic beetles are confined to large free-standing oaks, which are a mainly man-made habitat. How could these species exist before man began managing the landscape? One explanation could be that the beetles were capable of occupying cooler microhabitats in the past because of warmer climates in general, in congruence with Thomas' (1993) hypothesis regarding thermophilous butterflies in Britain. Beetles associated with old oaks probably increased their range and reached their highest abundances in Scandinavia in the mid Holocene (8000-4000 B.P.) because broadleaf deciduous forests was much more extensive then than today (Huntley, 1988). As it was a few degrees warmer in the summer at that time than today (Huntley and Prentice, 1988), saproxylic beetles might were able to live even in dense forests then. Possibly, when the climate cooled, some species were able to sustain themselves exclusively in habitats with warmer microclimate created by man. It is also possible, however, that the species are originally adapted to warmer microhabitats which occurred even in primary woodlands (Warren and Key, 1991). Sun-exposed sites occur naturally in precipices (Ek et al., 1995), along rivers and sea-shores. Large glades could also be a result of grazing by large herbivores (Owen-Smith, 1987) and catastrophic events (Warren and Key, 1991). Beetles may prefer larger trunks because the larger the girth, the more stable the microclimate. Alternatively the stage of decay of a trunk may influence its suitability. When a hollow tree ages, the trunk diameter increases, but other characteristics of the tree also change, for example, the entrance size and volume of the hollow increase (Kelner-Pillault, 1974). This study suggests that most species prefer trees of intermediate or late stages of the successional decay of living, hollow trunks.

4.2. Conclusions for nature conservation

Plantations and natural regeneration of formerly open pasture woodlands cause existing old trees to die prematurely because of shading and competition for soil moisture and nutrients (Key and Ball, 1993; Alexander et al., 1996). We found that some saproxylic beetle species are also harmed by forest regrowth. There is a tendency for red-listed species to be more negatively affected by cessation of grazing than other beetle species (Table 4). Thus, to preserve the rarer saproxylic beetle fauna it is important to continue the management of areas with old oaks. This study shows that even where management has been abandoned in the last few decades most species still occur, albeit many of them in lower abundance. This is partly because the sites are heterogenous, and therefore some oaks remain sunexposed for a few decades even without management. Such sites should be restored, to delay the deaths of the trees and decrease risk of extinction of endangered beetle species. Restoration of regrown

sites should include cutting of shrubs and young trees and resumption of grazing. The cutting should be done with care, as dramatic changes of the microclimate could lead to death of the oaks (Alexander et al., 1996). Another problem is that Formica spp. often colonize hollow oaks if the surrounding canopy cover suddenly decrease (own obs.). We do not know the consequences of the presence of these ants, but there is circumstantial evidence that suggests they have a great impact as predators on forest invertebrates, including saproxylic beetles (Gösswald, 1990). If grazing has been abandoned for several decades, young trees should be cut in the immediate surrounding of the old trees, but usually not in other parts of the site. On the other hand, in sites where grazing has ceased more recently, a complete restoration including cutting of most shrubs and young trees could be done in one step. When the forest regrowth is in intermediate successional stages, fast-growing tree species (in our study plots ash (*Fraxinus excelsior*), aspen (*Populus tremula*) and birch (*Betula verrucosa*)) should be removed first, as these are the worst competitors for the old oaks. In many other sites in Sweden, the old oaks are surrounded by planted Norway spruce (*Picea abies*), and these must also be cut down. Slow-growing tree species (like younger oaks) could be removed later or be saved. It is usually not appropriate to cut down mature oaks, as it is desirable to have many oaks which can take over the role as hollow trees in the future. At many sites the number of hollow oaks are very small and there are gaps in the generation structure (Britain: Key and Ball, 1993; Sweden: own obs., e.g. Jansson and Tingvall, 1998). In small stands, the number of old trees needs to increase if the beetle fauna is to be sustained in the long run, as stand size (Ranius, 2000) and historical continuity (Nilsson and Baranowski, 1997) have been found to be important factors for the occurrence of some rare saproxylic beetles associated with tree hollows. Where there are problems with age gaps, decay could be initiated prematurely, by injuring younger trees. For example chain-saws or explosives could be used to produce shattered trunks or branch stumps which could initiate the formation of trunk hollows (Key and Ball, 1993; Alexander et al., 1996). The effects of such a treatment might be similar to that of the traditional use of oaks. There are Swedish documents from the 18th century indicating that rot holes commonly arose in oaks when branches were cut down (Eliasson and Nilsson, 2000). There are a few species that tend to increase when management ceases, mostly species associated with fruiting bodies of saproxylic fungi. Even in a grazed pasture woodland, however, there are often denser patches which make survival possible even for these species. Moreover, among the species of the present study, those associated with fruiting bodies of saproxylic fungi have fewer species on the red list compared to other groups of saproxylic beetles (Table 2).

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Table 1

Description of estimated variables

Name	Description
Variables of each plot	
ORIGINAL CANOPY COVER	Vertical coverage of the canopy (10-30%=0, 30-70%=1, 70-90%=2) (continuous)
FOREST REGROWTH	If the plot is still managed by grazing (=0) or regrown (=1) (categorical)
STANDARD SIZE	The stand size, divided into two categories: small (=0) or large (=1), with 50 hollow oaks within a radius of 1 km as a limit
Name of each sampled tree hollow	
AMOUNT OF WOOD MOULD	The amount of wood mould, divided into two categories: small (=0) or large (=1) amounts, with about 10 l as a limit (categorical)
AREA OF ENTRANCE	Area of the entrance to the hollow (cm2) (continuous)
SURROUNDING COVER	If the tree is situated in an open, half open or shaded surrounding, i.e. whether the vertical projection of foliage in the surrounding of the tree is <25% (free-standing=0), 25-75% (half-open=1) or >75% (shaded=2) (continuous)
DIRECTION (SUNSHINE)	The direction of the entrance in relation to the sun (value increasing with increased nearness to the most sun exposed compass direction: NE=1, N or E=2, NW or SE=3, W or S=4, SW=5) (continuous)
DIRECTION (UPWARDS)	If the entrance is directed more or less vertically (=0) or horizontally (=1) (categorical)
HEIGHT OF ENTRANCE	The height of the entrance above the ground (m) (continuous)
TRUNK DIAMETER	Trunk diameter of the tree at 1.3 m height (m) (continuous)

Table 2
Beeatle species trapped and determined in this study[a]

1. Rotten wood in any part of the trunks, even on the outside of the trunk
Alosterna tabacicolor
Ampedus balteatus
Ampedus nigroflavus R
Ampedus pomorum
Calambus bipustulatus R
Cerylon ferrugineum
Cerylon histeroides
Cis fagi
Cryptophagus badius
Cryptophagus scanicus
Ctesias serra
Dorcatoma chrysomelina
Dorcatoma flavicornis R
Euplectus piceus
Euplectus punctatus
Grynocharis oblonga R
Hypebaeus flavipes R
Hypulus quercinus R
Malachius bipustulatus
Megatoma undata
Melanotes castanipes
Melanotes erythropus
Mycetaea subterranea
Mycetochara flavipes
Mycetochara linearis
Mycetophagus piceus R
Paromalus flavicornis
Ptinus rufipes
Rhyncolus ater
Rhyncolus sculpturatus
Sinodendron cylindricum
Tillus elongatus R
Trichoceble memnonia
Uloma culinaris R
Xyletinus longitarsus R
Xyletinus pectinatus R

2. Rotten wood in trunks, exclusively from the inside, in hollows. Not associated with animal nests
Allecula morio R
Ampedus cardinalis R
Ampedus hjorti R

Cryptophagus confusus R
Cryptophagus labilis
Cryptophagus populi R
Cryptophagus quercinus R
Dendrophilus punctatus
Elater ferrugineus R
Euplectus bescidicus R
Euplectus karsteni
Euplectus nanus
Gnorimus nobilis R
Korynetes coeruleus
Locola marmorata R
Mycetochara axillaris R
Mycetochara humeralis R
Mycetophagus populi R
Osmoderma eremita R
Pentaphyllus testaceus R
Plectophloeus nitidus R
Plegaderus caesus R
Prionychus ater R
Procraerus tibialis R
Pseudocistela ceramboides R
Ptinus fur
Ptinus subpilosus
Rhizophagus cribratus R
Stenichnus godarti
Tenebrio opacus R

3. Animal nests in tree hollows
Anthrenus museorum
Anthrenus scrophulariae
Atomario morio
Attagenus pellio
Batrisodes adnexus R
Batrisodes venustus
Cryptophagus micaceus R
Dermestes lardarius
Hapalarea pygmaea R
Globicornis nigripes R
Gnathoncus buyssoni
Gnathoncus nidorum R
Nemadus colonoides R
Palorus depressus
Quedius brevicornis
Quedius cruentus
Quedius scitus
Scraptia fuscula R
Scydmaenus hellwigi

Tenebrio molitor
Trox scaber
Velleius dilatatus R

4. Fruiting bodies of saproxylic fungi
Atomaria alpina R
Atomaria bella
Atomaria umbrina
Cryptophagus dentatus
Dacne bipustulata
Diaperis boleti
Eledona agricola
Endomychus coccineus
Hallomenus binotatus
Mycetina cruciata
Mycetophagus quadriguttatus R
Orchesia micans
Orchesia undulata
Triplax aenea
Triplax russica

5. Dead, dry wood in trunks
Agrilus biguttatus R
Anobium nitidum
Anobium rufipes
Corticeus fasciatus R
Gastrallus immarginatus R
Hadrobregmus pertinax
Hedobia imperialis
Lyctus linearis
Lymexylon navale R
Phymatodes testaceus
Xestobium rufovillosum

6. Branches of old oaks
Agrilus laticornis
Agrilus sulcicollis
Agrilus viridis
Conopalpus testaceus
Grammoptera ustulata R
Leiopus nebulosus

[a] *Division in ecological groups according to their microhabitat. Taxonomy according to Lundberg (1995). Red-listed species (Ehnström et al., 1993) are marked with an* R.

13

Table 3
Analysis of occurrence of 68 saproxylic beetle species[a]

Species	Mean	Analysis of covariance		Logistic regression	
		(A)	(B)	(C)	(D)
Agrilus sulcicollis	0.39	0.083	-0.111	-1.02	-0.89
Allecula morio	2.22	-0.750	-1.333*	-1.31***	0.58
Alosterna tabacicolor	1.11	-0.167	0.667	-0.29	0.08
Ampedus balteatus	0.67	-0.667***	-0.667*	-0.40	1.53*
Ampedus cardinalis	0.94	-0.167	-0.333	0.29	0.60
Ampedus hjorti	0.89	-0.250	-0.222	-0.12	0.81
Anobium nitidum	0.78	-0.250	-0.444	-0.25	0.66
Anobium rufipes	0.28	0.000	0.111	-0.61	0.27
Anthrenus museorum	1.33	-0.250	-0.778	-0.58	0.76
Anthrenus scrophulariae	0.39	-0.417	-0.333	-1.42*	0.18
Atomaria morio	2.00	-0.167	-0.222	0.07	0.09
Cerylon ferrugineum	0.44	0.000	0.444	0.66	0.48
Cerylon histeroides	1.33	-0.083	0.222	-0.23	-0.37
Conopalpus testaceus	1.06	-1.000*	-0.778	-1.16***	0.26
Cryptophagus badius	1.39	-0.083	-0.111	0.64	1.46*
Cryptophagus dentatus	1.06	0.167	1.000*	0.86	0.70
Cryptophagus micaceus	3.00	-0.250	0.222	0.94**	0.83
Cryptophagus quercinus	1.00	-0.250	0.000	0.32	0.93
Cryptophagus scanicus	3.72	0.000	-0.111	0.10	0.23
Ctesias serra	3.78	-0.333	-0.889	-0.65	0.33
Dendrophilus punctatus	2.06	0.333	-0.556	0.10	-0.59
Diaperis boleti	1.33	-0.167	-0.667	0.009	0.47
Dorcatoma chrysomelina	3.56	-0.417	-0.444	0.19	1.05
Dorcatoma flavicornis	2.50	0.000	-1.444*	-0.48	-0.67
Elater ferrugineus	0.44	0.000	0.444	-0.14	1.10
Eledona agricola	0.39	-0.083	0.333	-0.69	-0.60
Euplectus karsteni	0.67	0.000	-0.111	-0.09	0.69
Gastrallus immarginatus	1.50	0.500	0.111	-0.44	-1.38*
Globicornis rufitarsis	1.00	-0.083	1.500***	-0.61	0.005
Gnathoncus buyssoni/nannetensis	2.61	0.333	-0.556	-0.22	-1.11*
Grammoptera ustulata	0.33	-0.250	0.000	-0.73	0.96
Grynocharis oblonga	0.28	-0.417**	-0.111	-1.06	3.24**
Hapalarea pygmaea	0.67	-0.500	0.667	0.29	1.94**
Hypebaeus flavipes	1.00	0.667*	-0.222	-0.77*	-2.02**
Leiopus nebulosus	0.39	0.083	-0.111	1.20	0.15
Liocola marmorata	0.72	0.000	0.333	-0.39	-0.91
Lymexylon navale	0.72	-0.083	0.111	-0.26	0.59
Megatoma undata	1.39	-0.333	-0.556	-0.53	0.51
Melanotus castanipes	0.72	0.000	0.778	0.81	0.59
Melanotus erythropus	0.67	-0.167	-0.889	-0.20	0.07
Mycetochara humeralis	1.33	0.500	0.667	-0.08	-0.61
Mycetochara linearis	1.50	-0.167	0.333	-0.64*	-0.49
Mycetophagus piceus	3.11	0.583	-0.667	-0.15	-0.76
Nemadus colonoides	0.44	-0.250	0.222	0.56	-0.21
Orchesia micans	0.33	-0.250	0.000	-1.31*	1.69

Osmoderma eremita	1.56	-0.083	-0.444	-0.14	-0.04
Paromalus flavicornis	0.33	-0.167	0.444	1.09	2.59*
Pentaphyllus testaceus	0.28	0.083	0.111	-1.33*	-1.33
Phymatodes testaceus	1.00	-0.083	0.000	0.39	0.70
Plegaderus caesus	0.44	0.083	-0.667*	-0.52	-0.97
Prionychus ater	2.44	-0.500	-0.667	-0.40	0.58
Procraerus tibialis	0.67	0.167	-0.889**	-0.41	-0.30
Pseudocistela ceramboides	1.78	-0.083	-0.444	-0.06	-0.16
Ptinus fur	4.06	-0.417	-1.000*	-0.36	1.82*
Ptinus rufipes	2.89	-0.333	0.222	0.03	0.38
Ptinus subpilosus	4.78	0.167	0.000	2.04*	0.32
Quedius brevicornis	0.67	0.167	0.000	-0.65	-1.59
Quedius cruentus	0.61	-0.333	-0.333	0.32	0.05
Quedius scitus	0.56	0.167	0.222	0.43	0.32
Rhyncolus ater	0.44	-0.250	0.000	-0.25	0.50
Scraptia fuscula	2.50	0.167	-2.333**	-0.40	-0.38
Tenebrio molitor	1.06	-0.167	-1.000*	-0.71*	0.71
Tenebrio opacus	0.61	-0.667*	-0.667	-0.67	2.21**
Tillus elongatus	0.50	0.333	-0.111	-0.54	-1.06
Trichoceble memnonia	2.33	0.000	-0.667	0.15	1.08*
Trox scaber	1.39	-0.500	-1.444*	-0.64*	-0.40
Velleius dilatatus	2.17	0.000	-0.111	0.15	-0.07
Xestobium rufovillosum	3.11	0.167	-0.889	-0.30	0.12

[a] Column 1 gives mean number of trees per plot with species present (five trees sampled in each plot). Columns 2 and 3 give analysis of covariance between this mean number and FOREST REGROWTH using ORIGINAL CANOPY COVER as covariate: A=coefficient of covariate, B=difference in mean number of trees in plots grazed and ungrazed (n=18 plots). Columns 4 and 5 give coefficients from multiple logistic regression between presence and absence of species and (C) SURROUNDING COVER and (D) TRUNK DIAMETER (n=90 trees). See Section 2.3. *, P<0.05; **, P<0.01; ***, P<0.001.

Table 4
Analysis of covariance between number of species occurrences of saproxylic beetles and (1)
ORIGINAL CANOPY COVER (covariate) and (2)
FOREST REGROWTH (factor)[a]

| | ORIGINAL CANOPY COVER | | | FOREST REGROWTH | |
Group	Mean[b]	B	P	Diff.	P
1	35.3	-2.92	NS[d]	-3.89	NS
2	28.9	-3.75	**	-4.22	*
3	21.0	-2.50	NS	-7.11	*
4	4.4	-1.08	NS	1.67	NS
5	8.2	-0.08	NS	-1.89	NS
6	2.3	-1.25	**	-1.33	NS
Red-listed[c]	37.3	-3.17	NS	-8.22	**
Not red-listed	62.7	-8.42	*	-8.56	NS
Total	100.1	-11.58	*	-16.78	*

[a] Species divided into six groups: (1) Rotten wood in any part of the trunks, even on the outside. (2) Rotten wood in trunks, exclusively from the inside, in hollows. Not associated with animal nests. (3) Animal nests in tree hollows. (4) Fruiting bodies of saproxylic fungi. (5) Dead, dry wood in trunks. (6) Branches of old oaks.
[b] Mean=Mean number of species occurrences per plot (i.e. number of species per tree summed for each plot), B=coefficient, P=significance, Diff.=difference between plots with forest regrowth and plots still grazed in mean number of species occurrences. n=18.
[c] Red-listed according to Ehnström et al. (1993).
[d] NS, not significant; *, P<0.05; **, P<0.01.

Table 5
Multiple linear regression between number of saproxylic beetle species per tree and (A) SURROUNDING COVER and (B) TRUNK DIAMETER[a]

Group	SURROUNDING COVER			TRUNK DIAMETER	
	Mean[b]	B	P	B	P
1	7.06	-0.63	NS[d]	1.23	NS
2	5.78	-0.51	NS	1.39	*
3	4.20	-0.32	NS	0.49	NS
4	0.88	0.37	**	0.71	**
5	1.63	-0.27	NS	0.03	NS
6	0.47	-0.26	**	0.06	NS
Red-listed[c]	7.47	-0.83	*	1.09	NS
Not red-listed	12.54	-0.78	NS	2.81	**
Total	20.02	-1.61	NS	3.90	*

[a] Species divided into six groups: (1) Rotten wood in any part of the trunks, even on the outside. (2) Rotten wood in trunks, exclusively from the inside, in hollows. Not associated with animal nests. (3) Animal nests in tree hollows. (4) Fruiting bodies of saproxylic fungi. (5) Dead, dry wood in trunks. (6) Branches of old oaks.
[b] Mean=mean number of species per tree. B=coefficient, P=significance. n=90.
[c] Red-listed according to Ehnström et al. (1993).
[d] NS, not significant; *, $P<0.05$; ** $P<0.01$.

(NOTE THAT THERE ARE ERRORS IN THE PUBLISHED VERSION OF THIS TABLE. THIS IS A CORRECTED VERSION)

Table 6
Number of saproxylic beetle species per tree, with the trees divided into categories of different TRUNK DIAMETER and SURROUNDING COVER[a]

Variable	n	Mean	S.D.
TRUNK DIAMETER			
<0.8 m	22	17.1	4.8
0.8-1.0 m	12	20.9	5.0
1.0-1.2 m	25	20.3	6.7
1.2-1.4 m	13	20.7	6.1
>1.4 m	18	22.1	7.4
SURROUNDING COVER			
Free-standing	21	23.8	5.3
Half-open	30	19.0	6.8
Shaded	39	18.7	5.7

[a] n=number of hollow oaks, Mean=mean number of species per tree, S.D.=standard deviation of number of species per tree.

Table 7
Species preferring sun exposure and shade, according to Palm (1959) and the present study[a]

		This study		
		Sun	Indifferent	Shade
Palm (1959)	Sun	Anthrenus scrophulariae Hypebaeus flavipes	Agrilus sulcicollis Ampedus balteatus Ampedus cardinalis Ampedus hjorti Anthrenus museorum Phymatodes testaceus Procraerus tibialis Tillus elongatus	
	Indifferent	Conopalpus testaceus Mycetochara linearis Orchesia micans Pentaphyllus testaceus Tenebrio molitor Trox scaber		Ptinus subpilosus
	Shade	Allecula morio		

[a] Preferences according to this study are achieved from the statistical significant relations with SURROUNDING COVER. All species studied specifically in the present study are potentially included, except *Cryptophagus micaceus*, as it was not studied by Palm (1959). Species indifferent in both studies are excluded.