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Increased openness around retained oaks increases species richness of saproxylic beetles

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Abstract The decrease of old deciduous trees in northern Europe is a threat to the saproxylic fauna. In northern Europe, oak sustains the highest richness of saproxylic invertebrates, among which beetles is a large group. In order to preserve species associated with old trees, it has become common practice in commercial forestry to retain such trees at final felling. However, to create beneficial conditions for species associated with retained trees, the surrounding plantation has to be managed with regard to their specific demands. In the case of oak-associated species, including many red-listed species, several studies have shown that light is an important factor. The aim of this study was to analyze the effects of increased openness around oaks (*Quercus robur*) in spruce plantations (*Picea abies*) on species richness and abundance of oak-associated saproxylic beetles. The study was performed in nine spruce plantations located in southern Sweden, with mature oaks standing in a gradient of canopy openness. Beetles were collected from 54 oaks from May to September during two seasons, using window traps. The analyses revealed that increased openness around oaks increases species richness and abundance of oak-associated beetles. By including insolation angle in the analysis, we found that it is mainly the degree of openness directed south from the oak that has positive effects on beetle richness. These findings imply that it is desirable to maintain an open area around retained oaks, and that this area should be placed on the southern side of the oak to maximize the biodiversity benefit in relation to costs for the forest owner.

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Introduction

The general decrease of old growth deciduous trees in northern Europe poses a major threat to the existing saproxylic (dependent on dead or decaying wood) fauna (Hannah et al. 1995; Nilsson 1997). Throughout most of the Holocene, this part of Europe has been covered with mixed deciduous forests (Southwood 1961; Iversen 1973; Berglund and Digerfeldt 1976; Vera 2000; Sverdrup-Thygeson and Birkemoe 2009), however over the last thousand years these forests have gradually changed due to human interventions. In central and western Europe, many forests have been transformed into agricultural land (Emanuelsson 2009; Vera 2000). In northern Europe, the forested area is still comparatively large, although intensive forestry and expansion of monocultures of Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) (Bakke 1968) have dramatically changed the structure and composition of these forests, especially during the last century. (Lindbladh and Foster 2010; Aspenberg and Jansson 2011; Emanuelsson 2009). The abundance of broadleaved deciduous trees, in particular old trees (Diekmann 1996), has therefore decreased considerably (Hannah et al. 1995; Nilsson 1997), and several species groups associated with microhabitats and structures on such trees (e.g. cavities, dead wood, and coarse bark) have suffered great losses of habitat. Consequently, numerous species of invertebrates, birds, bats, fungi, and lichens have declined, and many are today threatened. This include, e.g. many saproxylic insect species (Jonsell et al. 1998; Brändle and Brandl 2001; Berg et al. 1994), among which beetles are a large group.

In order to preserve the species associated with ancient deciduous trees, it has during the last decades become a common practice in commercial coniferous forestry to retain a number of large deciduous trees at final felling (Gustafsson et al. 2010). The overall objective of retaining trees is to conserve or restore environmental values by maintaining or developing structurally complex managed forests. Retained trees may function as a refuge for many species by providing suitable habitat from which they can disperse to similar trees in the near surroundings (Franklin et al. 1997). This is especially crucial for species with a limited dispersal capacity (Ranius and Jansson 2000; Ranius and Hedin 2001; Löbel et al. 2006; Svensson et al. 2011; Ranius et al. 2011).

To create favorable conditions for retained trees and species connected to them, the surrounding stand has to be managed with regard to the specific demands of the tree and its associated fauna. Regarding Norway spruce, its initial growth is rapid and therefore spruce stands cast a dense shade even at a relatively young age (Pacala et al. 1996). Hence, light may soon be a limiting factor for the many invertebrate species that prefer a high level of insolation (Jonsell et al. 1998), e.g. several saproxylic beetle species (Ranius and Jansson 2000; Blennow et al. 2002; Koivula 2002; Bakke 1968). Studies have shown that beetle species dependent on high levels of insolation are often associated with shade-intolerant tree species (Jonsell et al. 1998; Lindhe et al. 2005). Oak (*Quercus* spp.) is an example of a shade intolerant species (Diekmann 1996; Vera 2000) and several studies have shown that light is an important factor for many species associated with oak (including red-listed species (Ranius and Jansson 2000; Lindhe et al. 2005). In addition, increased light may have indirect positive effects on many species, including red-listed, by promoting development of certain characteristics, such as large girth and coarse branches. It may also increase the differentiation of microclimate in the bark and trunk, structures that becomes more diverse as the tree ages (Niklasson and Nilsson 2005). Maintaining the insolation, however, adds economic costs due to extended forestry operations and losses of potential volumes of spruce wood. Hence, increased knowledge about the effect of insolation on species richness on retained trees in spruce plantations, should be beneficial both from an economical and ecological point of view.

In northern Europe, oak trees are of high conservational value since they sustain the highest species richness of saproxylic invertebrates, among which beetles is one of the major groups (Palm 1959), and several species are red-listed (Jonsell et al. 1998). Sweden hosts many globally threatened oak-associated species such as the beetle *Osmoderma eremita* (Ranius et al. 2005; Ranius and Jansson 2000), and therefore, it is important to maintain and restore oak habitats, and this should be extended to include retained oaks in commercial plantations.

The aim of this study was to analyze the effects of canopy openness on the richness and abundance of saproxylic beetles on retained oaks in spruce plantations. Several studies have investigated the effect of surrounding tree regeneration density, or canopy cover, on the oak-living beetle fauna in deciduous woodlands of high conservation value (Ranius and Jansson 2000; Franc and Götmark 2008), in beech forests (Müller and Gossner 2007), and in larch plantations (Ohsawa 2007). However, no study has focused on oak trees retained in spruce plantations and the effect of openness around those trees on the richness and composition of saproxylic beetle species.

We aimed to test the following hypotheses:

1. Increased canopy openness around retained oaks in spruce plantation has a positive effect on oak-associated saproxylic beetles, in terms of both species richness and abundance.
2. Other factors related to the oaks, such as increasing amounts of dead wood, increasing age, girth, and crown dimension should positively influence species richness and abundance of oak-associated saproxylic beetles on the retained oaks.

Materials and methods

Study areas

We performed the study in nine spruce stands (locations) in southern Sweden (Fig. 1) with retained mature oaks (*Quercus robur*) (Table 1). All stands were former wood pastures with first generation of spruce (*Picea abies* (L.) Karst.), and contained at least 90 % spruce trees and several scattered oaks. The spatial distribution of oaks within the stands varied among the locations and ranged between 0.35 and 4.30 ha. On all locations the spruces were planted, except for Strömsrum and Tönnersjö where they were naturally regenerated. The plantations were managed according to common Swedish silvicultural practices, i.e. with both pre-commercial and commercial thinning.

The stands were located in the nemoral (temperate) or boreo-nemoral zone (Ahti et al. 1968) (Fig. 1). The boreo-nemoral zone is a transition zone between the boreal and nemoral zone, and both oak and spruce have occurred here naturally in the past. This was not the case in the nemoral zone, and today spruce occurs here predominantly in plantations. The mean annual temperature in this region ranges typically between 5 and 8 °C, and the mean temperature between −4 and 0 °C in January and between 15 and 16 °C in July.

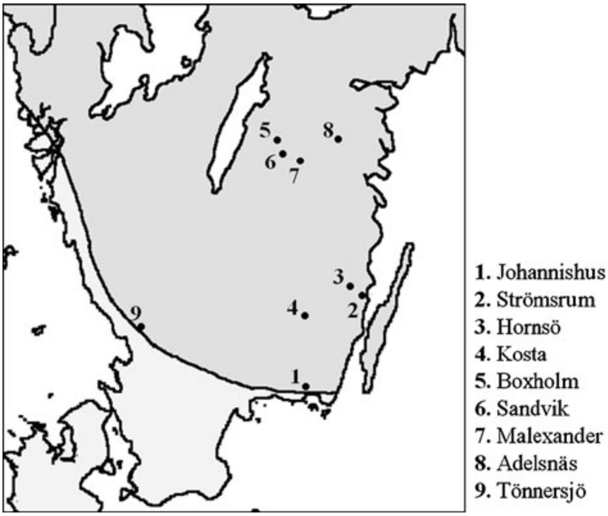


Fig. 1 The nine locations used in the study. All areas were located in the boreo-nemoral zone (*darker grey*), except for Johannishus and Tönnersjö, which were located at the border between the nemoral- (*lighter grey*) and the boreo-nemoral zones

There is a large variation in precipitation between the western (up to 1,200 mm/year) and the eastern (500 mm/year) part of the region. The growing period with a mean daily temperature above 5 °C lasts for about 180–240 days (Nilsson 1996). Coniferous species, such as Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*), are today the dominating tree species, and birch (*Betula pendula* and *Betula pubescens*), European aspen, (*Populus tremula*), oaks (*Quercus robur* and *Q. petraea*), and European beech (*Fagus sylvatica*), represent the dominating deciduous species (Nilsson 1996).

At each location, six oaks in gaps of different sizes were selected to obtain a gradient in openness around the trees, ranging from small gap to large gap. In the small gap, spruce trees grew under and/or through the crown of the oak, whereas the size of the large gap differed among the locations and ranged between three and eight meters outside the crown edge. The remaining four oaks on each location had gaps ranging four steps between the small and the large gap. In order to minimize variations due to other factors than openness, the six oaks on each location were selected to achieve a set of oaks as homogenous as possible regarding age (min. age approx. 100 years), DBH, height, vitality, amount of dead wood, and distance to the plantation edge. Furthermore, to avoid inter-correlation in insect composition among the sampled oaks, the trees were selected in order to achieve a selection of oaks with the tree crowns isolated by at least three rows of spruce (>3 m, depending on the initial spacing of each particular spruce stand).

Data sampling

Saproxylic beetles

Beetles were collected from the 54 oaks (nine locations, six oaks at each) from mid May to early September during 2008 and 2009, using window traps. The traps consisted of a plexiglass window (40 × 60 cm) tied to a funnel, and attached to each funnel was a bottle

Table 1 Data from the nine different spruce stands with mature standing oaks

Site	Coordinates (SE)	Size (ha)	Land use history	No oaks	Spruce age	Spruce stems/ha	Spruce BA/ha	Last thinning
Johannishus	N 56° 14.372′, E 15° 31.270′	1.55	WP	11	43/45	822	18,442	1997
Strömsrum	N 56° 55.560′, E 16° 27.817′	4.3	WP	18	Mixed	559	11,348	None
Hornsö	N 57° 0.959′, E 16° 14.016′	0.75	WP	20	70	929	14,113	1999
Kosta	N 56° 48.924′, E 15° 28.861′	2.5	Spruce forest	11	38	1,783	11,446	1998
Boxholm	N 58° 11.382′, E 15° 7.850′	1.35	WP	11	53	837	10,195	1997
Sandvik	N 58° 7.197′, E 15° 10.110′	1.6	WP	18	48	537	12,393	2002
Malexander	N 58° 4.132′, E 15° 21.423′	0.65	WP/Conifers	12	50	907	13,270	1999
Adelsnäs	N 58° 8.599′, E 15° 57.128′	0.35	WP	8	47	482	17,343	2000
Tönnersjö	N 56° 42.249′, E 13° 8.383′	0.4	WP	8	50, Mixed	1,459	11,138	None

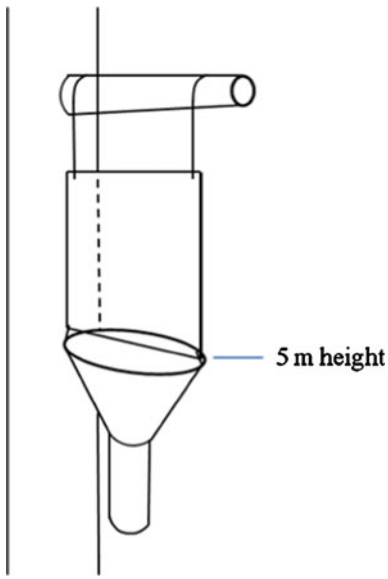
WP indicates that the stand is a former wood pasture. BA stands for basal area with propylene glycol (0.6 l, 60 %) and a few drops of detergent. The traps were mounted on branches on the southern side of the tree close to the trunk at a height of approximately 5 m (the height of the upper edge of the funnel), where the majority of dead branches generally was found. The plexiglass window was stabilized with wires so that the edge of the glass pointed in approximately 180° south, in order to reduce solar reflections as they might disturb the beetles and affect the sampling efficiency (Fig. 2). Once a month the traps were emptied and the beetles collected and stored in ethanol solution (60 %).

All saproxylic beetles (*Coleoptera*) were identified to species level by taxonomist Rickard Andersson (formerly Baranowski), Höör, Sweden. The beetles were divided into five groups based on their association with oak and spruce (using the host tree, and possibly other tree species as well, as larvae and/or adults) (Palm 1959; Dahlberg and Stokland 2004; Andersson (formerly Baranowski) 2010, pers. comm.): (1a) oak-associated species (138 species); (1b) oak-associated species with no association with spruce (87 species); (1c) oak-associated species with preference for oak (23 species); (2a) spruce-associated species (91 species); and (2b) spruce-associated species with no association with oak (40 species). Thus, the groups 1b and 1c are subgroups to group 1a, and group 2b subgroup to group 2a. We also recorded the number of red-listed species according to the red-list of Swedish species (Gärdenfors 2005).

Oak variables

For all oak trees selected for the study, we estimated age (through coring), DBH, height, crown radius (average of eight directions), and amount of dead wood. Age was estimated by dating tree rings from drill cores in laboratory, using standard dendrochronological methods (Stokes and Smiley 1968). For a few oaks, the core showed signs of rot and from those trees we took additional cores. Three oaks had larger holes in the trunk and these trees were cross-dated using disc samples from neighboring oaks of about the same DBH. As estimates of dead wood on the oaks, we measured several different factors related to

Fig. 2 The window traps were mounted on branches close to the oak trunk on the southern side, at a height of 5 m. The glass was fixed with the edge facing south



branches and trunk. Factors related to branches included the number of dead branches, as well as the average, maximum, and summed diameter of dead branches. For these estimates, only branches of min. diameter of 5 cm and min. length of 0.5 m were included. We also measured the height range of the majority (approx. ¾) of dead branches along the main trunk, and noted how these branches were dispersed in relation to compass direction (evenly, N, E, S, or W). Furthermore, we visually estimated the percentage of dead crown as the volume of dead branches in relation to total branch volume. As trunk related factors, we measured the area of dead stem surface (m^2) and the percentage of hollows (roughly estimated from the core samples).

Shade index as an estimation of canopy openness around oaks

The amount of solar radiation reaching the oak is determined by the openness around the tree. Measuring openness is complex however, as it is not simply determined by the size of the gap, but also by the density, height, and position of the surrounding spruce trees in relation to the sun. Hemispherical photography analysis, which is a method commonly used for analyzing canopy openness, could in this case provide an estimate of openness. However, when it comes to developing management advices and strategies, hemispherical photography analysis is not a straight-forward and appropriate tool to be used by forest managers as it does not provide basic information about stand characteristics. Another common way to estimate stand density is by using a relascope. This instrument does not provide detailed stand information though, such as the angle and distance to, or height of, the surrounding spruces. Therefore, to get more accurate estimates of the openness per se, we collected data on the spruce trees around the oaks. All spruce trees within a radius, r, were measured for DBH (two measurements, cross-measured) and height (h), as well as distance (d) and compass angle (α) measured from the center of the oak trunk to the center of the spruce stem. To get comparable data for the six oaks at each location (stand), the radius (r) used for the measurements was standardized. For this we measured the crown radius of each oak in eight directions and calculated the average of the four largest radii. Then we added 3 m to obtain a radius that contained data outside the oak crown. To get sufficient amounts of data, we decided that the additional 3 m should include at least three rows of spruce in each cardinal direction (N = 0°/360°; E = 90°; S = 180°; W = 270°), and if it did not, then more meters were added until three spruce rows were included. To standardize the radius for each location, r was set to equal the smallest obtained radii for the six oaks at each location, and only spruces within this radius were measured. From the

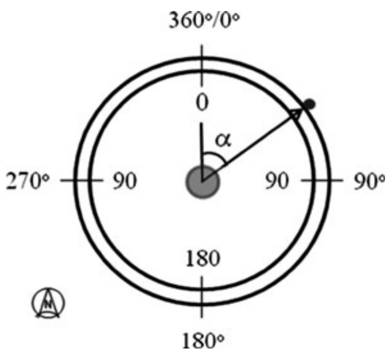


Fig. 3 The compass angle (α) from the oak (*large dot*) to a spruce tree (*small dot*). The outer circle shows the compass degree whereas the inner circle shows the grading of the spruces according to α, ranging between 0 and 180

spruce data we calculated a "shade index", SI, for each oak, as an estimate of the light regime influenced by the surrounding trees:

$$SI = \sum_{i=1}^{n} \left(\left(DBH^2/d \right) \times h \right)_i$$

where n is the number of spruces. The shade from the oak itself was roughly the same for all traps.

As the shape of the gap and the density of the spruce trees in different directions should affect the insolation in the gap, we graded each spruce from 0 to 180 according to α. The position (P) of spruces with α ranging from 180° to 360° was calculated by:

$$P = 180 - (\alpha - 180)$$

to obtain values between 0 and 180 (Fig. 3). The angular index, I_α with a theoretical range of values between 0 and 1, was calculated for each spruce:

$$I_\alpha = P/180$$

Including I_α in the model, we calculated the angular shade index, SI_α:

$$SI_\alpha = \sum_{i=1}^{n} \left(\left(DBH^2/d \right) \times h \times I_\alpha \right)_i$$

We also calculated the basal area/ha of spruce for each location and for this purpose we measured DBH of spruces on 24 plots. These plots were placed by the groups of four, one along each cardinal direction of the six study oaks. The plots had a radius of 5 m and were centered at a distance of 15 m from the oak. If overlapping with the gap trees, the plots were placed further away from the oak.

Statistical analyses

Species richness and abundance of the host-association groups (1a, 1b, 3b, 2a, 2b) and the red-listed species were tested against shade indices SI and SI_α with univariate linear regression analysis (12 response variables in total). The response variables showed Shapiro–Wilks non-normal distribution and were thus ln-transformed to obtain normal distribution.

The shade index among SI and SI_α which exhibited the highest significance (p) for the response variables in the univariate regression analysis was selected for statistical modeling with proc GLM (general linear models). To account for variability in the model, we also included location (class variable), age and DBH of the oaks, and one of the following dead wood variables; number of dead branches, average diameter of dead branches, diameter of the thickest dead branch, summed diameter of dead branches, percentage of dead crown, area of dead stem surface, percentage of hollows, and height range and cardinal direction of dead branches. In order to select the dead wood variable, we first tested each variable with univariate linear regression analysis and chose the variable which exhibited the highest significance for the response variables.

In order to account for differences in sample size between the oaks, we also used individual-based rarefaction adjusted species richness, calculated with freeware Biodiversity Pro (The Natural History Museum, London). Adjusted species richness was only calculated for oak associated beetles (groups 1a and 1b), however, group 1c was excluded due to its relatively low sample size with comparatively few species. For group 1a, an adjusted sample size of 11 individuals generated 50 observations (92.6 % of the study oaks) and a sample size of 21 generated 44 observations (81.5 % of the study oaks). For group 1b, a sample size of 11 individuals generated a dataset with 42 observations (77.8 % of the study oaks). For further analyses, only locations with at least three observations (oaks) were included. This resulted in 48 (sample size 11) and 40 (sample size 21) observations respectively for group 1a, and 39 observations for group 1b. These three datasets were tested against the angular shade index with proc GLM, including location as class variable. The adjusted data showed Shapiro–Wilks normal distribution.

All statistical modeling was performed using the SAS program version 9.2 (SAS Institute Inc., Cary, NC, USA).

Results

Sampled data

Saproxylic beetles

A total of 2,779 saproxylic beetles, belonging to 226 different species and 42 genera, were caught in the nine stands during two seasons (Table 2). The abundance and number of beetle species varied among the different locations (Table 3). Many of the beetle species (23 % of the total and 37 % of the oak-associated) were associated with both oak and spruce (Table 8 in Appendix). Dividing the beetles into different groups according to host tree association and preference gave the following outcome: in the total pool of species, 61 % were associated with oak (group 1a), 38 % were associated with oak and not with spruce (group 1b), and 10 % species had preference for oak (group 1c). Further, 40 % of the recorded species were associated with spruce (group 2a) and 18 % of the species were associated with spruce and not with oak (group 2b). Overall, the number of oak-associated species in the total pool of identified saproxylic beetles was higher than the number of spruce-associated species.

We identified 18 species (42 individuals) as red-listed (Table 4), which made 8 % of the total number of collected saproxylic beetle species. Among this group, 67 % of the species were associated with oak, which is somewhat higher than the figure for all 226 species in the study (61 %). As for all species, the richness of red-listed beetle species varied among the different locations (Table 3).

Table 2 The number of caught individuals, species, and genera of saproxylic beetles for each host association group

Count	Total	Oak	Oak, not spruce	Oak preference	Spruce	Spruce, not oak
Individuals	2,779	2,117	1,252	581	1,019	154
Species	226 (100)	138 (61)	87 (38)	23 (10)	91 (40)	40 (18)
Genera	42	39	33	12	27	14

The *numbers* in *parenthesis* refer to the percentage of species in each specific group out of the total number of species caught in the study

Table 3 The total number of beetle species (Sp) and the number of red-listed beetle species (Gärdenfors 2005) for each location

Location	Sp (Ind) (*SpAverage*)	Red-listed Sp (Ind)
Johannishus	140 (481) (*23*)	4 (5)
Strömsrum	145 (420) (*24*)	7 (15)
Hornsö	141 (345) (*24*)	7 (9)
Kosta	174 (634) (*29*)	3 (4)
Boxholm	85 (168) (*14*)	2 (3)
Sandvik	124 (281) (*21*)	1 (1)
Malexander	103 (280) (*17*)	0
Adelsnäs	144 (475) (*24*)	4 (5)
Tönnersjö	57 (123) (*10*)	0

The number of individuals (Ind) and the average number of species per trap (*SpAverage*) are shown in *parenthesis*

Table 4 The total number of red-listed species in the study, the red-list (RL) category, host tree, and location where the species was caught

Latin	Total	RL-category	Host tree	Location
Ampedus nigroflavus	1	NT	Oak (polyphag.)	4
Anoplodera sexguttata	2	NT	Oak (preferring)	3, 8
Calambus bipustulatus	5	NT	Oak (polyphag.)	1, 2, 8
Cis castaneus	2	NT	Oak, beech	4
Colydium elongatum	1	EN	Conif., fagus	3
Enedreytes sepicola	1	NT	Oak (polyphag.)	3
Lymexylon navale	2	NT	Oak (preferring)	1, 2
Magdalis armigera	1	NT	Elm	8
Malthinus facialis	1	NT	Polyphagus	2
Microrhagus lepidus	1	NT	Polyphagus	5
Notolaemus unifasciatus	1	VU	Oak (polyphag.)	2
Obrium brunneum	2	NT	Spruce, pine	2;3
Orchesia fasciata	5	NT	Oak (polyphag.)	3, 4, 5, 6
Orchesia minor	1	NT	Oak (polyphag.)	8
Phloiotrya rufipes	4	NT	Oak (polyphag.)	1, 3
Rhagium sycophanta	1	NT	Oak (polyphag.)	2
Xyleborus monographus	10	NT	Oak pref. (poly.)	1, 2
Zilora ferruginea	1	NT	Spruce, pine	3

Host tree association (Oak and Spruce) is according to (Dahlberg and Stokland 2004) and red-list (RL) category is according to (Gärdenfors 2005); VU Vulnerable, NT near threatened, EN endangered Oak species. For name of Location, see Fig. 1

Local variables

Age, DBH, height, and amount of dead wood on the study oaks varied across the locations (Table 5). The highest age was recorded in Kosta and the highest DBH in Strömsrum and Boxholm, both regarding maximum and average values. The lowest corresponding values

Table 5 Age, DBH, height, and diameter of the thickest dead branch of the oaks at each location

Site	Age (years)	Oak DBH (cm)	Height (m)	Thickest branch
Johannishus	145 (106–207)	75.3 (51–107)	21.7 (17.4–26.6)	23 (20–30)
Strömsrum	200 (171–225)	89.6 (80–109)	21.3 (17.5–25.5)	24 (20–30)
Hornsö	110 (97–116)	52.3 (45–66)	26.9 (24.8–30.0)	15 (10–20)
Kosta	275 (163–350)	73.8 (53–94)	16.9 (11.3–20.2)	23 (5–40)
Boxholm	152 (138–168)	87.0 (60–113)	17.9 (14.5–22.5)	31 (20–40)
Sandvik	125 (103–143)	71.7 (55–87)	20.6 (18.5–26.6)	24 (15–30)
Malexander	134 (104–186)	58.1 (51–73)	21.3 (17.2–25.2)	22 (15–30)
Adelsnäs	146 (130–164)	60.1 (43–75)	25.6 (24.0–27.5)	13 (5–20)
Tönnersjö	150 (115–242)	46.8 (34–69)	20.3 (18.9–21.9)	15 (10–20)

The values indicate average, whereas range is shown in *parenthesis*

Table 6 The angular shade index, SI_α, for the six study oaks at each location

Trap	Johannishus	Strömsrum	Hornsö	Kosta	Boxholm	Sandvik	Malexander	Adelsnäs	Tönnersjö
1	577	989	2,544	762	416	521	740	986	731
2	1,046	1,817	926	202	972	996	313	653	383
3	1,452	654	960	128	61	1,173	128	1,641	357
4	1,955	1,372	1,847	248	599	1,780	835	848	1
5	392	105	1,575	214	1,096	448	1,068	2,021	609
6	664	467	2,251	64	1,971	1,618	619	2,006	353

SI_α was calculated from DBH (diam), height (h), distance (d), and angular position (P) of spruce trees around the oak: $SI_\alpha = \Sigma(\text{diam}^2/d)h\text{P}/180$

were recorded in Hornsö. The average diameter of the thickest dead branch ranged among the locations between 13 and 31 cm, while the average estimate of dead crown ranged between 9 and 52 %. There was also a variation in shade index, both within and among the locations (Table 6).

Openness and species richness

The results from the GLM analyses revealed a significant decrease in *species richness* of oak associated species (group 1a) with increasing angular shade index (Fig. 4a) and a significant increase with increasing diameter of the thickest dead oak branch (Table 7). The response pattern remained similar for those species associated with oak and not with spruce (group 1b) (Fig. 4b); the angular shade index had a significant negative effect and the diameter of the thickest dead branch showed a significant positive effect on species richness. When testing species with preference for oak (group 1c), the angular shade index had a significant negative effect, while there was no significant effect of the diameter of the thickest dead branch. The species richness of beetles associated with spruce (group 2a) showed the same trend, with the angular shade index being significantly negative, while there was no significant effect of the diameter of the thickest dead branch. When testing those species that were associated with spruce and not with oak (group 2b), there was no significant response to any of the variables (Table 7) and this was also the case for the species richness of red-listed saproxylic beetles.

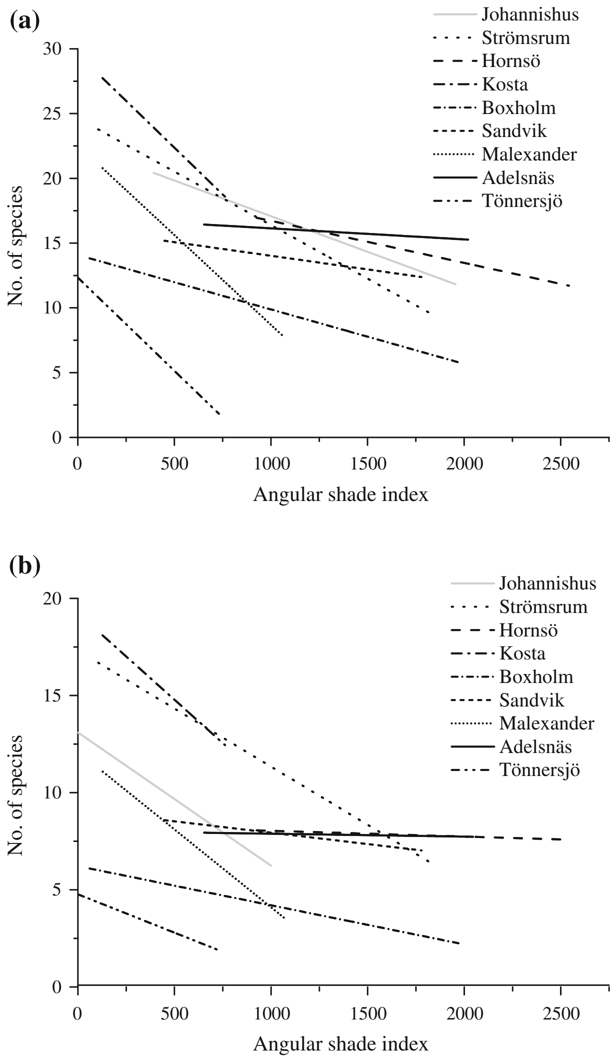


Fig. 4 Linear regression analysis shows that species richness of saproxylic oak-associated beetles decreased with increasing angular shade index, SI_α, of the retained oaks. The response to SI_α varied among the locations as indicated by the variation of the slope of the linear regression curves. **a** The response to increased SI_α for all saproxylic oak-associated species collected in the study. **b** The response of those species associated with oak and not with spruce. SI_α was calculated from DBH (diam), height (*h*), distance (*d*), and angular position (P) of spruce trees around the oak: $SI_\alpha = \Sigma(\mathrm{diam}^2/d)hP/180$

The rarefaction adjusted species richness of oak beetles (group 1a) showed a significant decrease with increasing angular shade index when testing both sample size 11 ($F = 12.13$, $p = 0.0012$) (Fig. 5a) and sample size 21 ($F = 6.32$, $p = 0.0171$) (Fig. 5b), whereas it was not significant for oak beetles not associated with spruce (group 1b).

Using beetle *abundance* as dependent variable in the GLM, we obtained similar patterns as revealed with analyses of species richness. Both oak-associated beetles (group

Table 7 The result from the GLM analyses, *F*-value and with *p* value (type III[a]), and the variance explained by the model (R^2)

	Oak		Oak, not spruce		Oak preference		Spruce		Spruce, not oak	
	F	*p*	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*
Species richness										
SI_{α}	11.18	0.0018	7.5	0.0091	4.48	0.0404	6.3	0.0161	0.04	0.8524
Age	1.4	0.2436	2.6	0.1148	0.36	0.55	0.04	0.8518	0.43	0.5136
DBH	1.17	0.2854	2.54	0.1185	0.13	0.7218	0.59	0.4485	0.99	0.3251
Thick. branch	6.56	0.0142	7.89	0.0076	1.89	0.1765	3.54	0.067	1.71	0.1985
Location	7.59	<0.0001	8.51	<0.0001	5.9	<0.0001	5.41	0.0001	1.47	0.1977
R^2 (Model)	0.677		0.71		0.602		0.544		0.298	
Abundance										
SI_{α}	4.87	0.0330	3.72	0.0607	2.52	0.1200	3.04	0.0886	0.01	0.9192
Age	2.53	0.1196	2.77	0.1038	2.09	0.1563	1.43	0.2388	0.37	0.5458
DBH	0.55	0.462	2.76	0.1042	0.39	0.5366	0.16	0.6957	0.25	0.6179
Thick. branch	1.26	0.2676	2.49	0.1225	0.00	0.9895	0.06	0.8002	1.96	0.1691
Location	7.50	<0.0001	5.99	<0.0001	7.63	<0.0001	5.3	0.0001	1.42	0.2185
R^2 (Model)	0.658		0.621		0.684		0.560		0.282	

The predictor variables used in the analyses were the angular shade index (SI_{α} Age (oak), DBH (oak), thickest dead branch (oak), and location (class variable)

[a] Type III denotes tests for individual coefficients

1a) and beetles associated with oak and not with spruce (group 1b) showed significant, or nearly significant, negative response to increasing angular shade index, and significant positive response to increasing diameter of thickest dead branch. However, there was no significant correlation between beetle abundance and the diameter of the thickest dead branch for the group of oak-preferring beetles (group 1c), and the spruce associated (group 2a and 2b) and the red-listed beetles showed no significant correlation to any of the tested variables (Table 7).

Discussion

Our study shows that mature standing oaks are important elements for conservation in spruce plantations, as they can sustain a diverse community of oak-associated saproxylic beetles, including red-listed species. We found that beetles on oaks in spruce plantations prefer light and open conditions, and that oaks with much dead wood favor a larger diversity of oak-associated beetle species compared to oaks with less or no dead wood.

We caught a substantial number of saproxylic oak-associated beetle species on the oaks in our study and this shows that oaks in dense spruce plantations host a rather species rich beetle assembly. This was not expected considering the oaks in our study were rather young relative to the species maximum age and located in dense spruce plantations with a distance of up to 100 m to the forest edge, which may isolate them from potential sources of dispersal, such as oaks standing freely in the open surroundings. During two seasons, we sampled 138 oak-associated species, of which 8 % were red-listed, the number of species per location ranging between 21 and 58. This can be compared to similar studies in

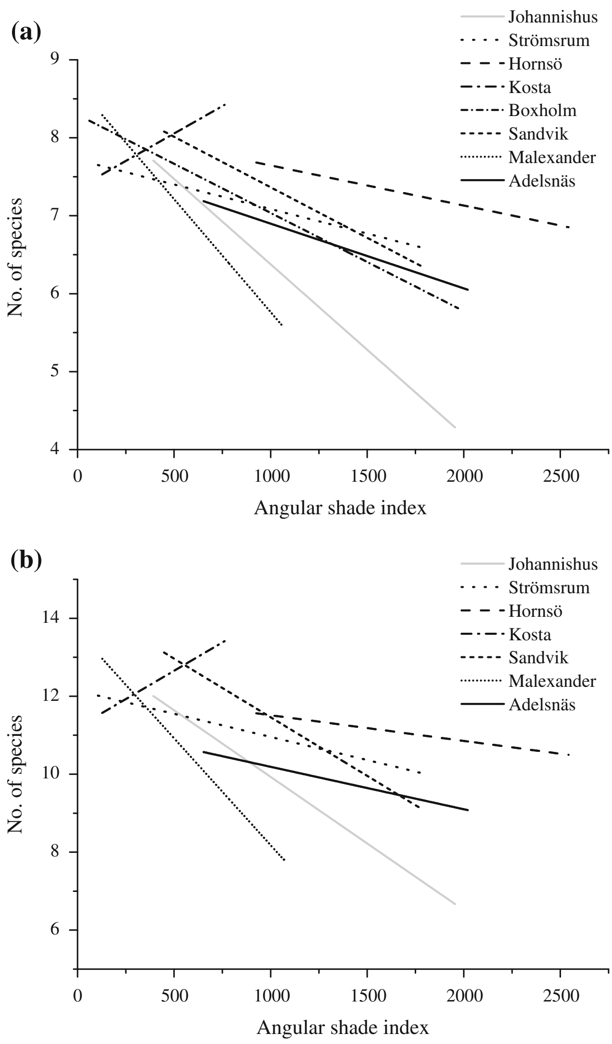


Fig. 5 Rarefaction adjusted species richness of saproxylic oak-associated beetles (group 1a), tested against SI_α angular shade index) with Linear regression analysis, shows a decrease with increasing SI_α. **a** The analyses with sample size 11, and **b** the analyses with sample size 21. SI_α was calculated from DBH (diam), height (*h*), distance (*d*), and angular position (P) of spruce trees around the oak: $SI_\alpha = \Sigma(\text{diam}^2/d)hP/180$

southern Sweden. Ranius and Jansson (2000) sampled 120 saproxylic beetle species associated with old oaks during one season. (In contrary to our study they excluded Scolytids and most of the Staphylinids). The beetles in their study were sampled with window and pitfall traps on 90 old oaks and the number of species varied between 36 and 58 per plot (5 trees). In another study from southern Sweden, Franc and Götmark (2008) sampled, during two seasons, 267 saproxylic oak-associated species in 22 oak stands, each stand being endowed with four window traps mounted to dead oak wood. The actual species number in their study varied between 31 and 88 per stand. Hence, in this context we believe our catch is rather high, considering the oaks in our study were overall younger and isolated in dense spruce plantations.

The effect of openness on species richness

Oaks in large gaps had overall higher species richness and abundance of oak-associated beetles than did oaks in small or no gaps. Larger gaps showed generally a larger increase in species richness and abundance of oak-associated beetles than of spruce-associated. This was expected as light is important for many species associated with oak (Ranius and Jansson 2000), and oak beetles should hence be favored by the light conditions in canopy gaps.

For the three groups of oak-associated beetles, species richness showed a more significant increase with increasing openness than did abundance, and this might be explained by prevailing variations in abundance among beetle species with different ecology and preference for openness. This was especially true for the group of oak-preferring beetles, and was most likely due to the impact of one single species, *Ptinus subpilosus*, which was clearly dominant in this group. *P. subpilosus* displayed a large variation in response to increasing openness. This could be explained by the fact that, although this species prefers oak, it is also associated with spruce and is thus likely more shade-tolerant than most of the remaining species in this group. Since it constituted as much as 64 % of the total species pool of oak-preferring beetles, it should have a substantial impact on how the abundance of this group was affected by openness.

The difference in response to openness between oak beetles and spruce beetles strengthens the idea that oak-associated beetles are attracted to light and open conditions even if the surrounding stand is dark and dense, which is in line with previous studies by e.g. Ranius and Jansson (2000). In their study, the oaks were located in overgrown or grazed pastures. In a study on high-stumps in spruce plantations, aspen and oak attracted a larger proportion of species favored by sun-exposed conditions, compared to high-stumps of spruce and birch (Lindhe et al. 2005). Franc and Götmark (2008) found that species richness of saproxylic oak beetles increased significantly on oaks in plots treated by partial harvesting compared to untreated oak plots.

We found 12 oak-associated species that were red-listed, which shows that oaks in spruce plantations can be used also by rare or threatened species. Three locations, Strömsrum, Kosta, and Johannishus, had more red-listed saproxylic beetles than the other locations. This is likely because both Strömsrum and Johannishus are located in a region with many red-listed saproxylic beetle species (Nilsson 2001), and the stand in Kosta had several dead oaks, both standing and lying.

By including the insolation angle in the analyses, we found that oaks standing in gaps more open south from the trunk attracted a larger number of oak-associated species, compared to oaks that were shaded by the plantation trees in that direction. This is reasonable, as it is likely the insolation in the gap rather than the openness per se, that is determinant of species richness of shade-intolerant beetles. We believe this finding has important implications for conservation as it allows for clearing strategies to maximize species richness benefit in relation to costs for the forest owner. When clearing around oaks, it should be important to consider which trees to cut regarding their position and compass direction in relation to the oak. In this way, it is possible to reduce the cost in terms of losses in potential timber volume.

The effect of dead wood

The saproxylic beetle fauna on sun-exposed oaks in spruce stands favored trees with dead wood structures. We are not aware of any other studies on the effect of dead wood amounts in the canopy of living trees on saproxylic insects. However, many studies have shown a positive relationship between the amount of dead wood on saproxylic organisms at a forest stand level (Lassauce et al. 2011; Martikainen et al. 2000) and therefore our result was rather expected.

We found that factors related to branches rather than to the trunk, or to hollows within the trunk, were important. In particular, increasing diameter of the thickest dead branch had positive effects on species richness of oak-associated beetles. This is reasonable as the oaks in our study were relatively young; the mean age was <200 years in seven out of nine stands in our study, whereas cavities are formed in oaks when they are between 200 and 400 years old (Ranius et al. 2009). Very few trees in our study had exposed dead wood on the trunk or hollows within the trunk, structures that are frequent in older trees.

Local variation in species richness

Species richness and abundance varied substantially among the locations. This might be explained by differences in the surroundings, on both stand-level and landscape-level, as environmental factors may affect the beetle composition. Such factors may be the local quantity of dead wood, local climate, and the tree composition in the near surroundings.

Some of the stands had overall more standing and lying dead wood, a factor that was clearly visible, but which we did not inventory as it was beyond the scope of this study. The amount of dead oak wood could however be important as it attracts several saproxylic beetle species. Moreover, some stands were located in a landscape or region with a relatively high density of mature and old oaks, while other stands were more isolated in a landscape heavily dominated by coniferous forests and with relatively few old oaks as potential sources for dispersal of oak-associated saproxylic beetles. According to other studies, both local, landscape and regional factors are important for local species richness of saproxylic oak-associated beetles in mixed oak-rich forests, such as the local quantity of dead oak wood (Götmark et al. 2011; Franc et al. 2007). However, species richness of red-listed oak-associated saproxylic beetles is mainly determined by landscape variables within 1 km (Franc et al. 2007; Götmark et al. 2011). There is also an increase in species richness from west to east in southern Sweden (Franc 2007), which may be explained by less yearly precipitation, more sunshine hours, and a higher mean annual temperature on the east coast, which may be beneficial for those species whose development is limited by climatic factors (Palm 1959). The climate may thus explain the overall low catch of beetles in Tönnersjö, the westernmost location in our study, which has substantially higher annual rainfall than the other areas (Nilsson 1996).

Window traps

There are challenges, though, to using window trap sampling for studies on saproxylic species as it may not reflect the true beetle community using the tree (Saint-Germain et al. 2006; Wikars et al. 2005). Beyond collecting species that use the oak, window traps can also collect flying beetles not using the substrates in the immediate surroundings of the trap, so called "tourists". The warm, sunlit conditions in gaps may further lure shade-intolerant beetle species, attracted by the openness and not by the oak substrate itself. However, a study by Sverdrup-Thygeson and Birkemoe (2009), analyzing the effect of substrate type on the sampling efficiency of window traps, showed that substrate is a determinant factor of species composition. Traps mounted on trunks of aspen, at different degrees of openness, caught more aspen-associated beetle species than did their freely mounted counterparts, and the difference was even larger for dead than for living trees. Moreover, one may argue that the overall higher species richness on oaks in larger gaps simply results from a higher beetle activity due to higher ambient temperatures in more open, sunlit conditions. This issue may yet be solved by individual-based rarefaction (Connor and McCoy 1979; Gotelli and Colwell 2001), in which the number of species is adjusted to the number of individuals caught. In our case, we obtained a similar result with rarefaction adjusted species richness as with total species richness when testing the group of all oak associated beetles (1a) against the angular shade index. However, the group of oak-associated beetles not associated with spruce (1b) did not respond significantly to increasing angular shade index. One explanation to this might be the smaller sample size in combination with fewer observations, obtained from rarefaction, for this group compared to group 1a. At any rate, our results strongly support the hypothesis that increased canopy openness around oaks in spruce plantations has a positive effect on species richness of oak-associated saproxylic beetles. Most likely, it is not the openness per se, but rather a combination of oak substrate and openness that is important. This is further supported by the fact that we found a positive effect of the amount of dead oak wood on species richness of saproxylic oak beetles.

Conclusions

Oaks in spruce plantations attract oak-associated saproxylic beetle species, and oaks standing more openly within the stand attract more oak-associated species than do oaks in smaller gaps. However, it appears it is the amount of sunlight reaching the oak, rather than the openness around it, that is determinant of species richness, since oaks in gaps more open south from the trunk generally attracted a higher species richness of oak-associated beetles compared to oaks shaded by the plantation trees. There was also a positive effect on species richness by the amount and dimension of dead branches on the oaks, the latter being the most determinant. This indicates that it is beneficial to maintain dead structures and that it is effective to save a few coarse branches. These findings have important implications for conservation as they allow for forestry practices to maximize the biodiversity benefit of oak-associated species and at the same time reduce the costs for the forest owner. When clearing around oaks, it is important to know which trees to remove, in terms of numbers and position in relation to the oak, in order to reduce losses in potential timber volume. Thus, retaining oaks with dead wood structures in spruce plantations, and expanding management operations to include clearing around the retained trees in a way that is cost-effective, could benefit the overall beetle diversity in the stand.

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Appendix

See Table 8.

Table 8 List of saproxylic beetles collected on 54 oak on 9 locations in southern Sweden May–September 2008–2009

Latin	Family	Total	No. of areas	RL category	Oak	Spruce
Acrulia inflata	Staphylinidae	1	1		x	x
Agathidium confusum	Leiodidae	9	3		x	
Agathidium rotundatum	Leiodidae	2	1		x	x
Agathidium seminulum	Leiodidae	3	2		x	x
Agrilus angustulus	Buprestidae	1	1		x	
Alosterna tabacicolor	Cerambycidae	47	9		p	x
Ampedus balteatus	Elateridae	18	3		x	
Ampedus hjorti	Elateridae	21	1		x	
Ampedus nigrinus	Elateridae	11	4		x	x
Ampedus nigroflavus	Elateridae	1	1	NT	x	
Ampedus pomorum	Elateridae	1	1		x	
Ampedus sp.	Elateridae	1	1			
Anaspis bohemica	Scraptiidae	1	1			
Anaspis flava	Scraptiidae	1	1			
Anaspis frontalis	Scraptiidae	8	5		x	x
Anaspis rufilabris	Scraptiidae	48	7		x	
Anaspis schilskyana	Scraptiidae	180	9			
Anaspis sp.	Scraptiidae	7	4			
Anaspis thoracica	Scraptiidae	26	5		x	
Anisotoma glabra	Leiodidae	1	1			x
Anisotoma humeralis	Leiodidae	4	3		x	
Anobium nitidum	Anobiidae	1	1		x	
Anobium thomsoni	Anobiidae	1	1			p
Anoplodera maculicornis	Cerambycidae	5	3		x	x
Anoplodera rubra	Cerambycidae	1	1		x	p
Anoplodera sanguinolenta	Cerambycidae	1	1			
Anoplodera sexguttata	Cerambycidae	2	2	NT	x	
Aphidecta obliterata	Coccinellidae	70	9		x	x
Aplocnemus nigricornis	Melyridae	2	2		x	x
Atomaria morio	Cryptophagidae	1	1		x	
Attagenus pellio	Dermestidae	1	1		x	
Bibloporus bicolor	Pselaphidae	1	1		x	x

Table 8 continued

Latin	Family	Total	No. of areas	RL category	Oak	Spruce
Bolitophagus reticulatus	Tenebrionidae	1	1			
Calambus bipustulatus	Elateridae	5	3	NT	x	
Callidium coriaceum	Cerambycidae	1	1			p
Calosoma inquisitor	Carabidae	1	1			
Cartodere constricta	Latridiidae	2	2		x	x
Cerylon fagi	Ceryloniidae	2	2		x	
Cerylon ferrugineum	Ceryloniidae	14	6		x	x
Cerylon histeroides	Ceryloniidae	5	4		x	x
Chrysanthia sp.	Oedemeridae	1	1			
Cis bidentatus	Ciidae	1	1		x	x
Cis castaneus	Ciidae	2	1	NT	x	
Cis punctulatus	Ciidae	1	1			x
Clytus arietis	Cerambycidae	2	2		p	
Colydium elongatum	Colydiidae	1	1	EN		x
Conopalpus testaceus	Melandyridae	5	2		x	
Corticaria abietorum	Latridiidae	2	2		x	p
Corticaria foveola	Latridiidae	1	1			x
Corticaria longicollis	Latridiidae	2	2		x	p
Corticaria rubripes	Latridiidae	3	2		x	p
Cortodera femorata	Cerambycidae	3	2			x
Cryphalus abietis	Curculionidae	7	6			p
Cryptarcha strigata	Nitidulidae	4	3		x	
Cryptarcha undata	Nitidulidae	1	1		x	
Cryptophagus badius	Cryptophagidae	1	1		x	
Cryptophagus confusus	Cryptophagidae	2	2		x	
Cryptophagus dentatus	Cryptophagidae	34	5		x	
Cryptophagus dorsalis	Cryptophagidae	7	4			
Cryptophagus lapponicus	Cryptophagidae	1	1			
Cryptophagus longitarsis	Cryptophagidae	1	1			
Cryptophagus micaceus	Cryptophagidae	60	6			
Cryptophagus scanicus	Cryptophagidae	191	7		x	
Cryptophagus sp.	Cryptophagidae	1	1			
Cryptophagus subdepressus	Cryptophagidae	7	4			
Crypturgus subcribrosus	Curculionidae	2	2			p
Ctesias serra	Dermestidae	19	6		x	
Dacne bipustulata	Erotylidae	1	1		x	
Dasytes aerosus	Melyridae	2	1		x	
Dasytes cyaneus	Melyridae	33	6		x	
Dasytes niger	Melyridae	2	2		x	
Dasytes plumbeus	Melyridae	98	7		x	
Dendroctonus micans	Curculionidae	2	2			p
Denticollis linearis	Elateridae	3	3		x	x
Dexiogya corticina	Staphylinidae	3	3		x	x

Table 8 continued

Latin	Family	Total	No. of areas	RL category	Oak	Spruce
Diaperis boleti	Tenebrionidae	31	8		x	
Dorcatoma chrysomelina	Anobiidae	34	1		p	
Dorcatoma dresdensis	Anobiidae	4	3		x	p
Dorcatoma flavicornis	Anobiidae	1	1		p	
Dromius agilis	Carabidae	88	9		x	p
Dromius quadrimaculatus	Carabidae	1	1		p	
Dryocoetes autographus	Curculionidae	4	3			p
Dryocoetes villosus	Curculionidae	4	2		p	
Dryophilus pusillus	Anobiidae	1	1			p
Eledona agricola	Tenebrionidae	1	1		p	
Enedreytes sepicola	Anthribidae	1	1	NT	x	
Enicmus rugosus	Latridiidae	39	8		x	x
Enicmus testaceus	Latridiidae	45	7		x	
Ennearthron cornutum	Ciidae	6	3		x	x
Epuraea adumbrata	Nitidulidae	2	1			
Epuraea guttata	Nitidulidae	2	1		x	
Epuraea muehli	Nitidulidae	1	1			x
Ernobius abietinus	Anobiidae	4	4			p
Ernobius abietis	Anobiidae	2	1			x
Ernobius angusticollis	Anobiidae	1	1			x
Ernobius nigrinus	Anobiidae	1	1			x
Ernobius pini	Anobiidae	2	1			
Ernobius sp.	Anobiidae	1	1			
Euplectus fauveli	Staphylinidae	2	2		x	
Euplectus karsteni	Staphylinidae	1	1		x	x
Euplectus piceus	Staphylinidae	1	1		x	
Euplectus punctatus	Staphylinidae	2	2		x	
Exochomus 4-pustulatus	Coccinellidae	1	1			
Gabrius splendidulus	Staphylinidae	1	1		x	x
Glischrochilus hortensis	Nitidulidae	1	1		x	
Gnathoncus buyssoni	Histeridae	15	6			
Gnathoncus nannetensis	Histeridae	2	2		x	
Grammoptera ustulata	Cerambycidae	7	1		x	
Grynocharis oblonga	Trogossitidae	3	2		x	x
Hallomenus binotatus	Melandryidae	1	1		x	x
Hapalaraea floralis	Staphylinidae	1	1			
Hapalaraea gracilicornis	Staphylinidae	15	5			
Hapalaraea ioptera	Staphylinidae	18	3			
Hapalaraea linearis	Staphylinidae	1	1			
Hapalaraea pygmaea	Staphylinidae	1	1			
Haploglossa villosula	Staphylinidae	296	9		x	
Hedobia imperialis	Anobiidae	3	2		x	
Hylastes brunneus	Curculionidae	1	1			x

Table 8 continued

Latin	Family	Total	No. of areas	RL category	Oak	Spruce
Hylastes cunicularius	Curculionidae	24	8			p
Hylis cariniceps	Eucnemidae	2	2			p
Hylobius abietis	Curculionidae	2	2		x	x
Hylurgops palliatus	Curculionidae	1	1			x
Hypoganus inunctus	Elateridae	9	3		x	
Ipidia quadriplagiata	Nitidulidae	1	1		x	p
Ips typographus	Curculionidae	1	1			p
Latridius hirtus	Latridiidae	5	2		x	x
Leiopus nebulosus	Cerambycidae	20	8		p	
Leptura maculata	Cerambycidae	1	1		p	x
Leptura melanura	Cerambycidae	21	7		x	x
Leptusa fumida	Staphylinidae	10	5		x	
Leptusa pulchella	Staphylinidae	7	5		x	x
Leptusa ruficollis	Staphylinidae	43	7			
Lymexylon navale	Lymexylidae	2	2	NT	p	
Magdalis armigera	Curculionidae	1	1	NT		
Magdalis duplicata	Curculionidae	1	1			x
Magdalis ruficornisi	Curculionidae	1	1			
Malthinus facialis	Cantharidae	1	1	NT		
Malthinus flaveolus	Cantharidae	1	1		x	
Malthinus frontalis	Cantharidae	2	2			
Malthodes brevicollis	Cantharidae	2	2			
Malthodes fuscus	Cantharidae	3	3			
Malthodes guttiferi	Cantharidae	1	1			
Malthodes marginatus	Cantharidae	6	3			
Malthodes mysticus	Cantharidae	1	1			
Malthodes sp.	Cantharidae	44	9			
Malthodes spathifer	Cantharidae	12	5		x	
Melanotus castanipes	Elateridae	28	7			
Melanotus erythropus	Elateridae	8	2		x	x
Melasis buprestoides	Eucnemidae	1	1		x	
Microrhagus lepidus	Eucnemidae	1	1	NT		
Molorchus minor	Cerambycidae	2	2			x
Mycetochara axillaris	Tenebrionidae	1	1			
Mycetochara flavipes	Tenebrionidae	2	1		x	
Mycetochara linearis	Tenebrionidae	19	3		x	
Mycetophagus multipunctatus	Mycetophagidae	1	1		x	
Mycetophagus piceus	Mycetophagidae	2	2		p	
Mycetophagus populi	Mycetophagidae	1	1			
Nemadus colonoides	Leiodidae	1	1		p	
Notolaemus unifasciatus	Laemophloeidae	1	1	VU	p	
Obrium brunneum	Cerambycidae	2	2	NT		p
Orchesia fasciata	Melandryidae	5	4	NT	x	p

Table 8 continued

Latin	Family	Total	No. of areas	RL category	Oak	Spruce
Orchesia michans	Melandryidae	1	1			
Orchesia minor	Melandryidae	1	1	NT	x	x
Orchesia undulata	Melandryidae	31	6		x	
Orthocis alni	Ciidae	16	8		x	x
Orthocis festivus	Ciidae	1	1		x	
Oxymirus cursor	Cerambycidae	1	1		x	p
Oxypoda lucens	Staphylinidae	27	3		x	
Palorus depressus	Tenebrionidae	1	1		x	
Paromalus flavicornis	Histeridae	2	1		x	x
Phloeopora angustiformis	Staphylinidae	6	3		x	x
Phloeopora testacea	Staphylinidae	22	8		x	p
Phloeotribus spinolosus	Curculionidae	1	1			
Phloeotribus spinulosus	Curculionidae	34	5			p
Phloiotrya rufipes	Melandryidae	4	2	NT	x	
Phymatodes testaceus	Cerambycidae	7	2		p	
Pityogenes bidentatus	Curculionidae	3	2			
Pityogenes chalcographus	Curculionidae	16	6			p
Pityogenes trepanatus	Curculionidae	31	5			
Pityophthorus glabratus	Curculionidae	1	1			
Pityophthorus micrographus	Curculionidae	4	3			p
Platystomus albinus	Anthribidae	2	1		x	
Plegaderus caesus	Histeridae	1	1		x	
Plegaderus vulneratus	Histeridae	1	1			p
Pogonocherus fasciculatus	Cerambycidae	4	3			
Polygraphus poligraphus	Curculionidae	4	4			p
Prionocyphon serricornis	Helodidae	2	1		x	
Prionychus ater	Tenebrionidae	2	1		x	
Pseudocistela ceramboides	Tenebrionidae	8	1		x	
Ptinus rufipes	Ptinidae	5	3		p	
Ptinus rupifes	Ptinidae	3	2			
Ptinus subpilosus	Ptinidae	371	9		p	x
Rhagium mordax	Cerambycidae	4	3		x	x
Rhagium sycophanta	Cerambycidae	1	1	NT	p	
Rhizophagus bipustulatus	Rhizophagidae	10	6		p	x
Rhizophagus dispar	Rhizophagidae	3	2		x	x
Rhizophagus ferrugineus	Rhizophagidae	1	1			x
Rhyncolus ater	Curculionidae	15	4			x
Rhyncolus sculpturatus	Curculionidae	1	1		x	x
Salpingus planirostris	Salpingidae	11	5		x	
Salpingus ruficollis	Salpingidae	37	9		x	x
Saperda scalaris	Cerambycidae	2	2		x	
Scaphisoma agaricinum	Scaphidiidae	3	3		x	x
Schizotus pectinicornis	Pyrochroidae	3	3		x	x

Table 8 continued

Latin	Family	Total	No. of areas	RL category	Oak	Spruce
Scolytus intricatus	Curculionidae	17	5		p	
Scydmaenus hellwigi	Scydmaenidae	1	1		p	
Serropalpus barbatus	Melandryidae	1	1			x
Silvanoprus fagi	Silvanidae	1	1			x
Soronia grisea	Nitidulidae	5	4		x	
Stenichnus godarti	Scydmaenidae	1	1		p	
Stichoglossa sp.	Staphylinidae	2	2			
Tetropium castaneum	Cerambycidae	1	1			p
Tetropium fuscum	Cerambycidae	2	1			p
Thanasimus femoralis	Cleridae	1	1			x
Thanasimus formicarius	Cleridae	6	4		x	p
Thymalus limbatus	Trogossitidae	8	3		x	
Tomicus piniperda	Curculionidae	1	1			x
Trichius fasciatus	Scarabaeidae	1	1		x	
Trichoceble memnonia	Melyridae	2	1		x	
Triplax rupifes	Erotylidae	1	1			
Trox scaber	Trogidae	3	2		x	
Trypodendron domesticum	Curculionidae	1	1		x	
Trypodendron lineatum	Curculionidae	2	2			x
Xestobium rufovillosum	Anobiidae	38	3		p	
Xyleborus monographus	Curculionidae	10	2	NT	p	
Zilora ferruginea	Melandryidae	1	1	NT		x
Zyras cognatus	Staphylinidae	4	1		x	
Unknown sp., prob. saproxylic	Unknown	1	1			

Host tree association (Oak and Spruce) is according to (Dahlberg and Stokland 2004) and red-list (Andersson (formerly Baranowski)) category is according to (Gärdenfors 2005). "*x*" and "*p*" refers to host tree association, where the latter stands for preference

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