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ORIGINAL PAPER

Hollow oaks and beetle conservation: the significance of the surroundings

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Abstract In this study we investigated hollow oaks (*Quercus robur*, *Q. petrea*) situated in open landscapes and in forests in Norway in northern Europe, and compared their importance for rare and threatened beetles (Coleoptera). Old, hollow oak trees, both in parks and in forests, were extremely rich in red-listed beetles, and hosted a high proportion of threatened species. The proportion of oak associated species and the mean number of red-listed beetle species per tree was similar in the two site types, but rarefaction showed that for a certain number of individuals, oaks in forests had more threatened and near-threatened species than oaks in parks. The species composition also differed between site types: Park oaks had a higher proportion of species associated with hollows and animal nests, whereas in forests, there was a higher proportion of species depending on dead oak wood in general. Four factors were significant in explaining the richness of red-listed beetles in our study: Tree circumference, cavity decay stage, proportion of oak in the surroundings, and coarse woody debris (CWD) in the surroundings. Forest oaks were smaller, but they still trapped a species richness comparable to that of the larger park oaks—probably a result of high amounts of CWD in the surroundings. We show that oaks in open landscapes and oaks in forest have only partly overlapping beetle assemblages and, thus, cannot be substituted in conservation. Planning for conservation of red-listed beetles associated with this key habitat demands a large scale perspective, both in space and time, as the surroundings have important effects on associated threatened and near threatened species.

Keywords Coleoptera · Beetles · Diversity · Red-listed species · Oak · Quercus · Cavity · Surroundings · Forest · Park

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Introduction

Oaks (*Quercus robur* and *Q. petrea*) in northern Europe can reach a great age. As a tree ages, complex structures serving as microhabitats for several organisms develop. Coarse bark structures, with deep fissures that create gradients in sun and rain exposure are characteristic features. Dead branches of varying sizes are common in the canopy of old oaks, and hollows are created inside the trunk. The hollows expand and are slowly filled with wood mould—a nutrient-rich mixture of decayed wood and fungi, remnants of nests and droppings from birds, bats and insects as well as other detritus. Together these characteristics contribute to the oak's unique importance as habitat for many organisms, among them several species of insects, pseudoscorpions, lichens and fungi (Antonsson and Jansson 2001; Ranius 2002b; Buse et al. 2007, 2008).

One particular taxonomic group including a large number of oak associated species in Northern Europe is the beetles (Coleoptera). Previous studies have confirmed that hollow oaks are important habitats for a wide range of rare beetle species in Europe (Ranius and Jansson 2000; Ranius 2002a; Buse et al. 2007). As the number of large, old oaks is dwindling, the beetles associated with this type of substrate have become increasingly rare over the past few hundred years (Read et al. 2003), and many oak associated beetles are listed on national Red Lists as threatened or endangered (e.g. Gärdenfors 2005; Kålås et al. 2006).

Several environmental factors affect the species richness and species composition of beetles in old oaks, such as tree girth, canopy cover, forest regrowth, the entrance hole's height above ground, the direction of the opening and the stand size (Ranius and Jansson 2000; Ranius 2002a).

Old, hollow oaks may be found in different environments; in parks, in the agricultural landscape or in forest of different degree of human impact. Most studies of hollow oaks have focused on oaks in landscapes much influenced by human use, like oaks along avenues (Buse et al. 2007; Oleksa et al. 2007), in parks and in agricultural landscape (Ranius and Jansson 2000; Ranius 2002a; Read et al. 2003; Jansson et al. 2009). However, hardly any studies have investigated the beetle fauna in oaks in forests (but see Ohsawa 2007), and to our knowledge, there are no comparative studies of the beetle fauna in park oaks versus forest oaks.

An important conservation issue is whether differences in surrounding habitat influence the species richness and the composition of threatened species in hollow oaks. In some areas in Norway, oaks in managed landscapes face more imminent threats than forest oaks, as these oaks might occur as solitary trees or small groups of trees without any formal protection, in areas where the pressure from urban development is high. In other regions or countries, the situation may be the opposite. As the relative importance of these threats may differ, it is important to gain knowledge of the unique values of both forest oaks and scattered hollow oaks outside forests.

Our aim in the present paper is to evaluate how the "setting" around a hollow oak influences its conservation value measured by threatened and near-threatened beetles, focusing on possible differences between hollow oaks in forests and hollow oaks in open landscapes (including both parks and agricultural landscapes).

As our aim is applied, we focus on threatened and near threatened species. Lists of such species naturally differ between countries, although some species are threatened across borders e.g. within Europe. Even though the species in question might differ, a comparison of species in risk of extinction between different site types is relevant in a general conservation context.

In this paper, we ask whether species richness of threatened and near-threatened beetle species in hollow oaks of parks differs from those in forests. Further, we compare the species composition of threatened and near-threatened beetles in the two site types, and investigate possible systematic patterns of beetle distribution in different microhabitats that can be related to the park or forest surroundings.

Methods

Beetles were collected at selected sites with old and hollow oaks in southern Norway. In order to cover as much as possible of the total range of oaks in Norway, only a few municipalities in each of the biogeographically relevant counties were searched for potential sites. Search areas were selected on the basis of forest inventories from the forestry sector and the municipalities. Eleven sites with at least five old and hollow oak trees close to each other (<250 m) were selected and sampled in 2004, 2005 or 2006 (Fig. 1). The sites were characterised as either forest: hollow oaks surrounded by other trees, shrubs etc. in a more or less natural forest (eight sites) or open landscape, where the oaks were situated in park or in agricultural landscape; for simplicity we use the term "park" in this paper (three sites). The altitude of the sites varied between 5 and 400 m above sea level.

At each site, five hollow oak trees were selected by randomly picking one hollow oak tree with a minimum circumference of 94 cm at breast height (equalling 30 cm DBH), and

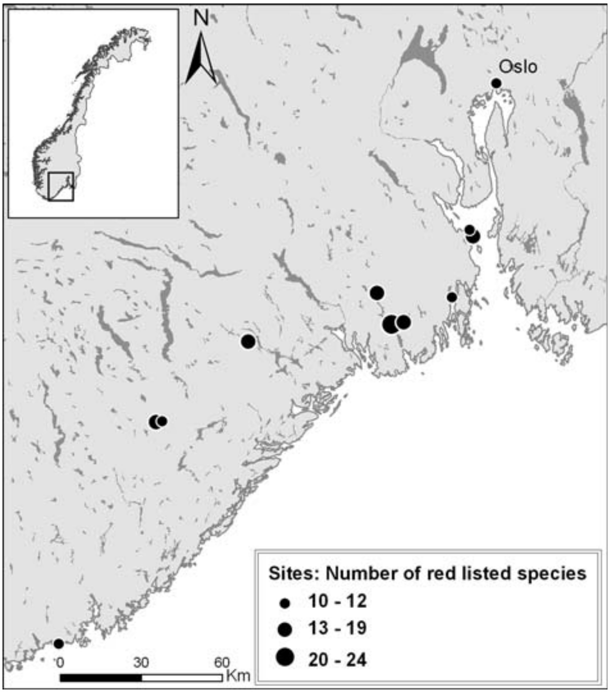

Fig. 1 The location of the study sites, each with five hollow oaks sampled by two flight interception traps each. The size of the *circles* reflects the total number of red-listed species trapped per site

then including the four hollow oaks (also >30 cm DBH) closest to it. Within each site, the distance between the trees varied from 6 to 250 m. Exact location for each tree was recorded using GPS. In addition, a number of tree- and site-specific environmental variables were recorded (Table 1). The variables relating to the surroundings were measured on the scale of approximately 5–10 ha. Cavity decay is a difficult variable to measure, as many cavities were inaccessible. Therefore, we chose to use a categorisation based on a large inventory of hollow trees in Sweden (Antonsson and Jansson 2001).

Each oak tree was sampled for beetles using two flight interception traps (window traps) measuring 20 by 40 cm. Many of the trees did not have accessible cavities, therefore pitfall trapping was judged unsuitable. One window trap was attached in front of the opening of the tree hollow (average 2–3 m above ground) and the second was hanging from branches in the canopy (average 4–5 m above ground). The preserving agent used in the traps was 70% ethylene glycol, 30% water and a few drops of detergent to break surface tension. The traps were operating from late May and emptied monthly until early August, which means that there is a chance of missing some early or late species.

Beetles were identified to species level and categorised as (1) not oak associated, (2) oak associated; defined as occurring on oak but possibly also on other tree species (including oak specialists), or (3) oak specialist; defined as primarily occurring on oak. The categorisation was based on the species information in the Norwegian Red List Database (Norwegian Biodiversity Information Centre 2006), and applies primarily to North European/Scandinavian conditions. Several species may have other/wider habitat demands in Central or Southern Europe. All oak associated species were further categorised in one of five groups based on oak microhabitat preferences, also based on the Norwegian Red List Database (Table 2): (1) associated with oak hollows, including nests (birds, ants etc.) in hollows, (2) associated with dead wood of oak, including branches or fungal sporocarps (not including species preferring hollows), (3) associated with running sap or living under bark of oak. As we wanted to focus the analysis and the management advice on the species most in need of protection, we started our work by identifying beetle species that are listed as threatened or near threatened in Norway (Kålås et al. 2006), and only saproxylic, threatened or near threatened beetles are included in the analyses in this paper.

Statistics

In order to compare the environmental variables and the proportion of species with different characteristics (threatened versus non-threatened, microhabitat associations) between park and forest sites, we used a Pearson's chi-squared test of independence to assess whether the paired observations in the contingency table were independent of each other. To alleviate the problem of low expected cell counts in some comparisons, the *P*-values were computed using a Monte Carlo permutation test (Hope 1968) with 2,000 replicates.

We compared species richness per tree in parks with species richness per tree in forest, as the sampling effort per tree was the same regardless of site type. At a site level, on the other hand, sampling effort differed between park and forest sites. Therefore, a direct comparison of species numbers pooled per site type was not appropriate. Instead, we used sample-based rarefaction to compare the dataset from parks with that from forests. Rarefaction represents the means of repeated re-sampling of all pooled samples within the site type, i.e. the statistical expectation for the corresponding accumulation curves. We compared both species density (*x*-axis scaled to samples) and species richness (by re-scaling

Table 1 The environmental variables measured in the study

Variable name	Measurement object	Measurement unit/levels	Measurement method	Parks ($N = 15$)	Forest ($N = 40$)	Test of park versus forest[a]
Landscape	Tree surroundings	Park, forest	Visual estimation	–	–	–
Circumference	Tree	M	Measuring tape, breast height	Mean = 366 cm, s.e. 0.26	Mean = 231 cm, s.e. = 0.16	*t*-test statistic = 3.64, df = 18.83, $P = 0.0018$*
CWD in surroundings	Tree surroundings	High levels, low levels	Visual estimation	High: 0 Low: 15	High: 30 Low: 10	$\chi^2 = 24.75$, $P = 0.0005$*
Cavity decay stage	Tree	1–2, 3, 4, 5[b]	Visual estimation	1–2: 4 3: 2 4: 6 5: 3	1–2: 14 3: 10 4: 11 5: 5	$\chi^2 = 1.89$, n.s.
Vitality	Tree	Healthy, reduced, dying	Visual estimation	Healthy: 1 Reduced: 8 Dying: 6	Healthy: 6 Reduced: 16 Dying: 18	$\chi^2 = 1.10$, n.s.
Crown cover	Tree surroundings	Closed, semi-open, open	Visual estimation	Closed: 0 Semi-open: 7 Open: 8	Closed: 12 Semi-open: 27 Open: 1	$\chi^2 = 22.49$, $P = 0.0005$*
Oak in surroundings	Tree surroundings	Basal area of oak (*Quercus* sp.) <20, 20–40, >50%	Visual estimation	<20%: 0 20–40%: 5 >50%: 10	<20%: 25 20–40%: 15 >50%: 0	$\chi^2 = 36.09$, $P = 0.0005$*

The names of the variables, the objects, unit and method of measurement are given. The means or proportions for parks and forests, as well as the result of a statistical test testing for differences between the two site types are shown. Significant differences are marked with an asterisk (*)

[a] Circumference is tested with a *t*-test assuming unequal variance, while the remaining variables are tested using Pearson's chi-squared test with Monte Carlo simulations (2,000 replicates)

[b] Following definition in Antonsson and Jansson (2001). In the regression models, we used an indicator variable for stage 3

Table 2 List of beetle species sampled in the study, including their family, status on the Norwegian Red List (Kålås et al. 2006), association with oak substrate including microhabitat preferences and the number of individuals sampled in oaks in park and forest site types

Species	Family	Red List	Oak assoc.	Micro-habitat	Indiv. in park oaks	Indiv. in forest oaks
Paromalus flavicornis	Histeridae	NT	A	Sap or bark	1	1
Ptenidium turgidum	Ptiliidae	NT	A	Hollows or nests	0	3
Pteryx splendens	Ptiliidae	NT	S	Sap or bark	0	3
Ptenidium gressneri	Ptiliidae	EN	A	Hollows or nests	0	1
Ptinella aptera	Ptiliidae	NT	A	Hollows or nests	1	0
Nemadus colonoides	Leiodidae	VU	S	Hollows or nests	0	5
Scaphidium quadrimaculatum	Scaphidiidae	NT	A	Dead wood general	0	1
Microscydmus nanus	Scydmaenidae	NT	A	Dead wood general	0	5
Euthiconus conicicollis	Scydmaenidae	EN	S	Hollows or nests	0	3
Nevraphes plicicollis	Scydmaenidae	VU	A	Hollows or nests	0	2
Scydmoraphes minutus	Scydmaenidae	NT	S	Hollows or nests	0	2
Microscydmus minimus	Scydmaenidae	NT	–	–	0	1
Scydmaenus hellwigii	Scydmaenidae	NT	A	Hollows or nests	0	1
Haploglossa gentilis	Staphylinidae	NT	A	Hollows or nests	0	21
Quedius brevicornis	Staphylinidae	VU	S	Hollows or nests	2	7
Hapalaraea pygmaea	Staphylinidae	NT	S	Hollows or nests	1	6
Haploglossa marginalis	Staphylinidae	NT	A	Hollows or nests	3	2
Euryusa sinuata	Staphylinidae	EN	S	Hollows or nests	1	0
Lordithon pulchellus	Staphylinidae	DD	A	Dead wood general	0	1
Thamiaraea hospita	Staphylinidae	NT	A	Sap or bark	0	1
Thiasophila inquilina	Staphylinidae	EN	A	Hollows or nests	1	0
Trichonyx sulcicollis	Staphylinidae	EN	A	Hollows or nests	0	1
Protaetia marmorata	Scarabaeidae	VU	S	Hollows or nests	1	0
Prionocyphon serricornis	Scirtidae	VU	A	Hollows or nests	1	59
Eucnemis capucina	Eucnemidae	EN	–	–	0	3
Hylis foveicollis	Eucnemidae	VU	–	–	0	1
Melasis buprestoides	Eucnemidae	NT	A	Dead wood general	0	1
Ampedus hjorti	Elateridae	EN	S	Hollows or nests	2	12
Calambus bipustulatus	Elateridae	EN	S	Dead wood general	1	1
Ampedus cinnabarinus	Elateridae	NT	A	Dead wood general	0	1
Crepidophorus mutilatus	Elateridae	EN	A	Hollows or nests	1	0
Procraerus tibialis	Elateridae	CR	S	Hollows or nests	1	0
Elater ferrugineus	Elateridae	"CR"[a]	S	Hollows or nests	0	5
Malthinus seriepunctatus	Cantharidae	VU	S	Dead wood general	0	2
Ctesias serra	Dermestidae	NT	A	Sap or bark	44	13
Gastrallus immarginatus	Anobiidae	EN	S	Sap or bark	0	33
Ptinus dubius	Anobiidae	DD	–	–	0	1
Lymexylon navale	Lymexylidae	CR	S	Dead wood general	0	2
Grynocharis oblonga	Trogossitidae	VU	A	Dead wood general	0	1
Hypebaeus flavipes	Melyridae	CR	S	Dead wood general	0	1

Table 2 continued

Species	Family	Red List	Oak assoc.	Micro-habitat	Indiv. in park oaks	Indiv. in forest oaks
Cryptarcha strigata	Nitidulidae	NT	S	Sap or bark	26	58
Cryptarcha undata	Nitidulidae	NT	S	Sap or bark	23	23
Epuraea guttata	Nitidulidae	NT	S	Sap or bark	3	2
Glischrochilus quadriguttatus	Nitidulidae	NT	A	Sap or bark	0	4
Meligethes corvinus	Nitidulidae	NT	–	–	1	0
Cryptolestes corticinus	Laemophloeidae	VU	A	Sap or bark	1	3
Cryptophagus subdepressus	Cryptophagidae	NT	–	–	0	4
Cryptophagus labilis	Cryptophagidae	VU	A	Dead wood general	1	1
Leiestes seminigra	Endomychidae	NT	–	–	0	1
Enicmus planipennis	Corticariidae	NT	–	–	2	0
Aridius norvegicus	Corticariidae	DD	A	Sap or bark	1	0
Mycetophagus piceus	Mycetophagidae	VU	A	Dead wood general	0	22
Mycetophagus fulvicollis	Mycetophagidae	NT		–	0	4
Mycetophagus populi	Mycetophagidae	VU	A	Dead wood general	1	3
Triphyllus bicolor	Mycetophagidae	EN	A	Dead wood general	0	1
Cis dentatus	Ciidae	NT	–	–	0	1
Cis micans	Ciidae	NT	A	Dead wood general	1	0
Conopalpus testaceus	Melandryidae	NT	A	Dead wood general	0	12
Phloiotrya rufipes	Melandryidae	VU	A	Dead wood general	0	4
Orchesia fasciata	Melandryidae	NT	A	Dead wood general	0	1
Orchesia luteipalpis	Melandryidae	VU	–	–	0	1
Ripidius quadriceps	Rhipiphoridae	"DD"[a]	A	Hollows or nests	1	0
Mycetochara linearis	Tenebrionidae	NT	A	Dead wood general	16	27
Prionychus ater	Tenebrionidae	NT	A	Hollows or nests	8	3
Mycetochara humeralis	Tenebrionidae	EN	A	Hollows or nests	6	0
Eledona agricola	Tenebrionidae	VU	S	Dead wood general	0	3
Ischnomera caerulea	Oedemeridae	VU	A	Hollows or nests	0	1
Lissodema cursor	Salpingidae	NT	A	Sap or bark	3	0
Euglenes oculatus	Aderidae	NT	S	Hollows or nests	991	360
Scraptia fuscula	Scraptiidae	NT	S	Hollows or nests	63	1
Magdalis cerasi	Curculionidae	DD	A	Dead wood general	1	0
Phloeophagus lignarius	Curculionidae	VU	A	Hollows or nests	0	1
Phloeophagus turbatus	Curculionidae	VU	A	Hollows or nests	0	1
Sum individuals					1,210	745

[a] Assumed Red List category of species found new to Norway after the latest revision of the Norwegian Red List (2006) when evaluated by the same IUCN criteria

Oak association: "*S*" oak specialist, defined as primarily occurring on oak in Scandinavia, "*A*" oak associated, defined as occurring on oak but possibly also on other tree species in Scandinavia (the group includes "S"), and "–" not oak associated. Based on information in Norwegian Biodiversity Information Centre (2006) the *x*-axis to individuals) (Gotelli and Colwell 2001), and both including and excluding one very abundant species.

In order to investigate whether the observed number of unique species in each site type was higher than expected by chance alone, we ran a bootstrapping test. The total sample was divided into two groups of three versus eight sites and the number of unique species in each group was counted in 1,000 runs. The observed values of unique species in each site type were then compared with the estimated number of unique species from the bootstrapping.

We searched for the best model explaining the richness of oak associated species and the richness of oak specialist species, based on the assumption that the data followed a Poisson distribution. We performed a backward stepwise selection process in which different models were compared on the basis of AIC score, aiming to find the model that best explains the data with a minimum of free parameters. We started with the full model including all the variables in the study: Response variable ~ Circumference + CWD in surroundings + Landscape + Vitality + Cavity decay stage + Crown cover + Oak in surroundings.

Initial analyses suggested that species richness was highest at an intermediate cavity decay stage (stage 3) (Antonsson and Jansson 2001). In the regression models we therefore used an indicator variable for this stage.

All statistical analysis was performed in the software R, version 2.6.1 (R Development Core Team 2007).

Results

We sampled 1,955 beetles belonging to 73 red-listed species. One red-listed species was phytophagous and therefore excluded from the analyses, the remaining red-listed species were all saproxylic. A total of 62 species were oak associated (Table 2). This accounts for more than half of all beetles on the Norwegian Red List associated with oaks (Kålås et al. 2006). Further, 23 of the 62 species were oak specialists (Table 2).

A large proportion of the species were represented by only one individual (44%). Especially among the species not associated with oak, there were a high proportion of singletons (64%, compared to only 17% singletons among the oak specialist species). On the other hand, a few of the red-listed species were extremely abundant, e.g. *Euglenes oculatus* (Aderidae) with as much as 1,351 individuals.

Environmental variables

Some of the environmental variables showed significant differences between oaks in parks and oaks in forests. The circumference was higher in park oaks, and more of the park trees occurred in open or semi-open settings, while more of the forest oaks were located in semi-open or closed forest (Table 1). The forest oaks was surrounded by a more mixed tree species composition and therefore with less oak, but with more dead wood (Table 1).

Species assemblages

Parks and forests shared only 18 of the 72 red-listed species. The observed values of 13 unique species in parks and 40 unique species in forests were significantly higher than the means from the bootstrapping results (simulated groups of 3 sites: Mean = 10.5, 95%

CI = 10.4-10.7, $P_{t\text{-test}} < 0.0001$, simulated groups of eight sites: Mean = 37.7, 95% CI = 37.5-37.9, $P_{t\text{-test}} < 0.0001$).

In addition to the 13 unique species in parks, four species that occurred with more than five individuals in the total sample, were significantly more common in parks than in forests, even though parks were undersampled: *Ctesias serra*, *Euglenes oculatus*, *Scraptia fuscula*, and *Prionychus ater* (Table 2).

Species richness and proportions of ecological groups

In total, we sampled 28 beetle species (1,210 individuals, or 219 individuals when *E. oculatus* was excluded) in park oaks and 62 species (744 individuals, or 384 individuals when *E. oculatus* was excluded) in forest oaks. The mean number of red-listed beetle species *per tree* was similar for oaks in parks (mean = 4.7, s.e. = 2.4) and oaks in forest (mean = 4.1, s.e. = 2.7, *t*-test n.s.). The proportion of oak associated species per tree (parks: 88%; forests: 90%) and oak specialist species per tree (parks: 44%; forests: 39%) was also similar.

Rarefaction showed that for a certain number of individuals, oaks in forests had more red-listed species than oaks in parks (Fig. 2a). When considering a certain number of samples (i.e. trees), park and forest oaks were not significantly different in terms of species numbers (Fig. 2b). When the outlier *E. oculatus* was excluded, the difference was less clear (Fig. 2c, d), but the mean species richness in forest oaks was still above the confidence interval of the park oaks for samples with more than ca 75 individuals (Fig. 2c). This results remained similar if non-oak associated species were removed (not shown).

The proportion of threatened species (categories CR, EN, VU) was high in both parks and forests (41 and 47%, respectively), and not significantly different between the two site types (Pearson chi-squared test, $\chi^2 = 0.1639$, df = 1, $P = 0.69$).

The relative proportion of species preferring different microhabitats within oaks differed between park and forest oaks (Table 3). The proportions of microhabitat groups differed significantly among species sampled only in parks, only in forests, or in both types of landscape (Pearson's chi-squared test with simulated *P*-value (2,000 replicates): $\chi^2 = 12.279$, *P*-value = 0.048). Park oaks had a higher proportion of species associated with hollows and animal nests. Among the species sampled only in forests, there was a higher proportion of species not associated with oaks, but also a higher proportion of species dependent on dead oak wood in general. Among the species not associated with oaks, none occurred in both site types.

Modelling species richness

The best model resulting from the stepwise model selection for richness of oak associated species included the variables Circumference, Cavity decay stage, Oak in surroundings and CWD in surroundings (Table 4). The model selection process for oak specialist species resulted in a model with the same variables, but with higher significance levels (Table 4). The effect on species richness of abundant dead wood in the surroundings is comparable to a large increase in tree circumference (Fig. 3a) or a large increase in Oak in surroundings (Fig. 3b).

Discussion

The aim of our study was to compare hollow oaks in parks and forests, to evaluate the effect of the surroundings on species richness and species composition of red-listed,

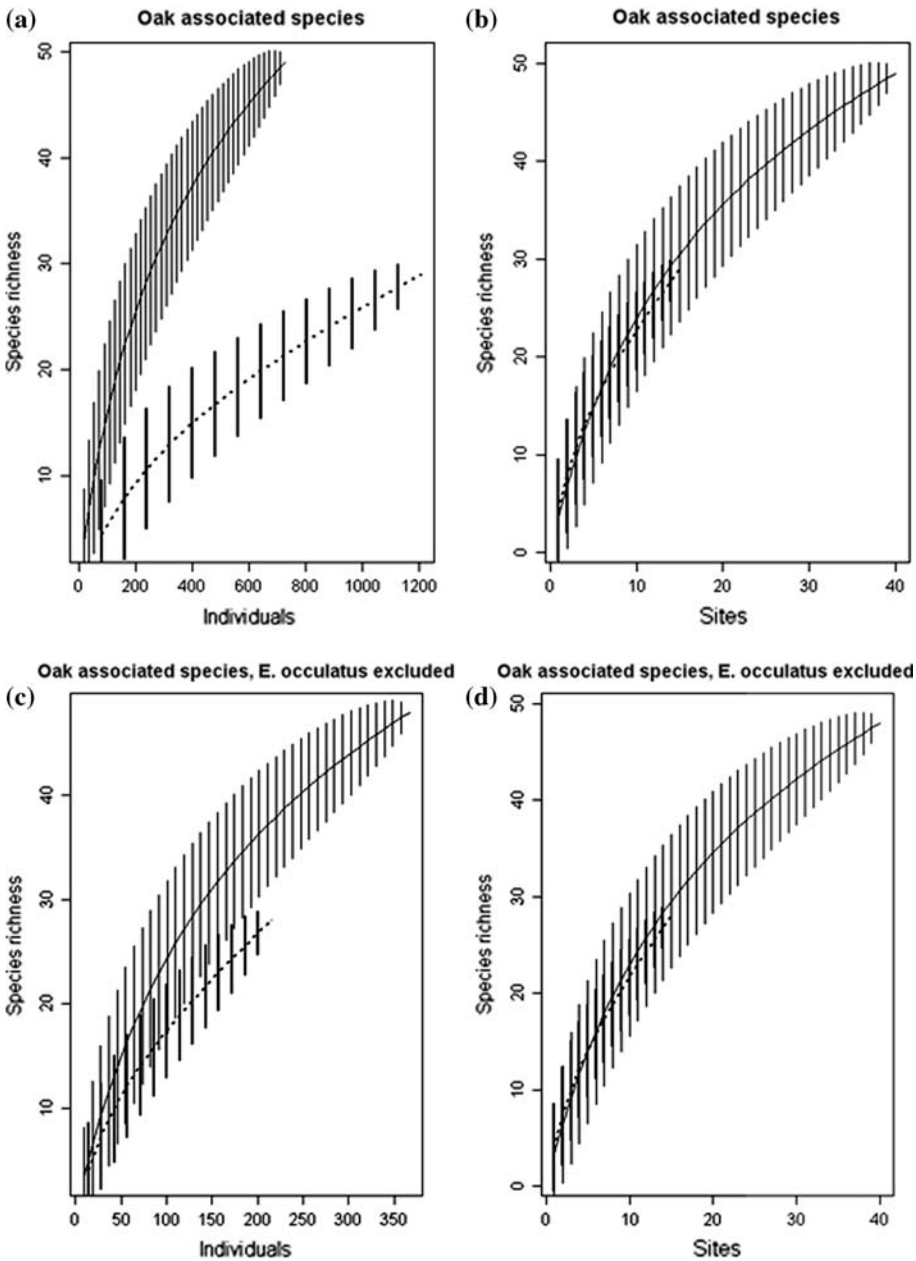

Fig. 2 Rarefaction curves for park oaks (*dotted line*) and forest oaks (*regular line*). The number of species is standardized either by number of samples (**a**, **c**) or by the number of individuals (**b**, **d**), and run either with all species (**a**, **b**) or with one outlier (*Euglenes oculatus*, 69% of all individuals) excluded (**c**, **d**). Confidence intervals are shown as *vertical lines*

saproxylic beetles. Our results show that old, hollow oak trees, both in parks and forests, are extremely rich in red-listed beetles. Although their species composition is different, trees in both site types host a high proportion of threatened species. Four factors are

Table 3 The distribution of beetles belonging to different microhabitat groups, in park oaks and forest oaks respectively

Microhabitat	Species, park oaks	Species, forest oaks	Prop., park oaks (%)	Prop., forest oaks (%)
Not ass. with oak	2	9	6	15
Hollows or nests	16	21	50	36
Dead wood general	6	19	19	32
Sap or bark	8	10	25	17
Sum	32	59	100	100

Species number and proportions are shown

Table 4 Results of stepwise regression modeling

Parameter	Estimate	Standard error	*t*-value	*P*-value
Response variable: Number of red-listed *oak associated* species[a]				
Intercept	0.372	1.091	0.341	0.735
Circumference	0.841	0.325	2.585	0.013*
CWD in surroundings: high	1.814	0.734	2.472	0.017*
Cavity decay stage: 3	1.812	0.732	2.475	0.017*
Oak in surroundings: 20–40%	−1.212	0.712	−1.702	0.095
Oak in surroundings: >50%	1.779	1.120	1.589	0.119
Response variable: Number of red-listed *oak specialist* species[b]				
Intercept	−0.224	0.607	−0.369	0.714
Circumference	0.518	0.181	2.861	0.006*
CWD in surroundings: high	1.332	0.408	3.263	0.002*
Cavity decay stage: 3	1.022	0.407	2.510	0.015*
Oak in surroundings: 20–40%	−1.332	0.396	−3.365	0.002*
Oak in surroundings: >50%	1.148	0.623	1.843	0.071

Significant parameters are marked with an asterisk (*)

[a] Full model: AIC = 254.44. Final model: AIC = 248.71

[b] Full model: AIC = 189.73. Final model: AIC = 184.22

significant in explaining richness of red-listed beetles in our study, namely Circumference, Cavity decay stage, Oak in surroundings and CWD in surroundings.

Tree size

Several earlier studies have found that tree size is an important factor explaining species richness of saproxylic beetles in general (Martikainen et al. 1999; Grove 2002), as well as the occurrence of several red-listed species inhabiting oak hollows (Ranius 2002a, b).

The positive effect of diameter on species richness can be explained by general ecological theory, with big habitat patches (=big trees) maintaining more species (island biogeography) and more viable populations (metapopulation ecology) in comparison to small habitat patches. There is probably a correlation between tree size and the amount of wood mould, but relevant studies on this correlation is lacking as wood mould is difficult to

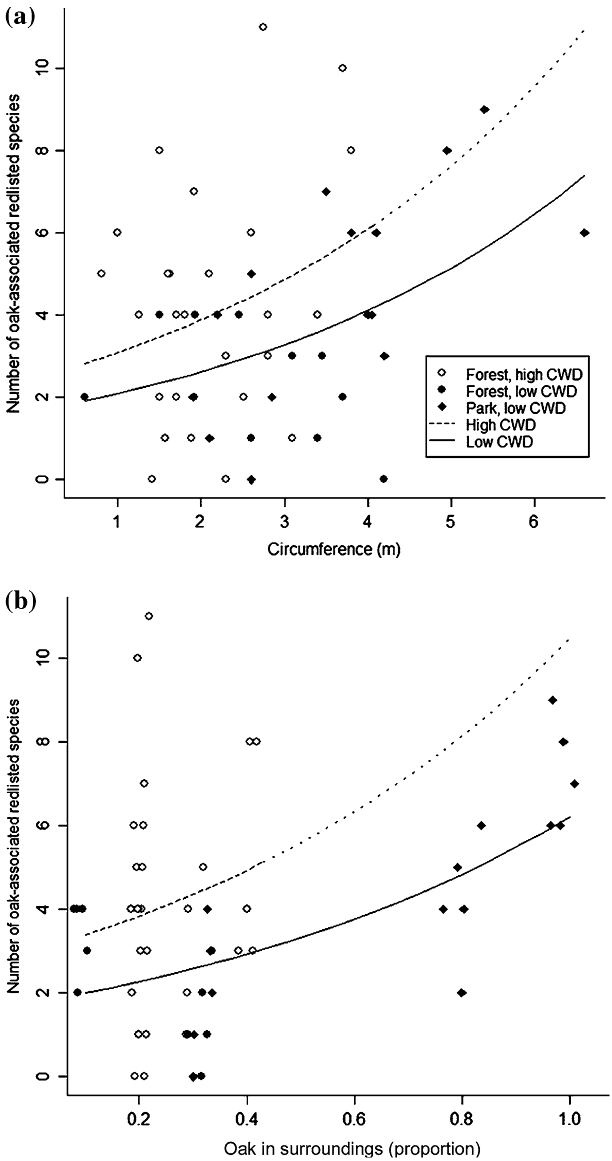

Fig. 3 The effect of oak and site type characteristics on species richness. The regression lines show the predicted species richness of oak associated beetles from the predictors "CWD in surroundings" and either **a** "Circumference" or **b** "Oak in surroundings" (generalized linear models assuming quasipoisson distribution). The legend in **a** applies to both panels. Extrapolation of the curves above the observed circumference for forest oaks (**a**) and above the proportion of oak in the forest surroundings (**b**) is indicated by *dotted lines*

measure. In addition, large oaks may provide a more stable microclimate, e.g. in the wood mould inside hollows (Ranius and Jansson 2000) or unique habitat characteristics, for instance the development of deep bark crevices (Buse et al. 2007) or large cavity openings.

Cavity decay stage

In our study, trees with hollows in medium decay stages hosted a higher richness of saproxylic beetles than trees hollows with less or more decay. This may be seen as an optimum during a succession process. When hollows start developing, they contain a small amount of wood mould, which is an important element for many of the cavity-dwelling insects. As the years go by, the opening and the hollow increases in size and at the same time decayed wood, frass and remnants of animal nests accumulate. Beetle populations establishing in hollow trees can stay for tens if not hundreds of years (Ranius and Hedin 2001), and it is thus to be expected that species richness also increase with age and decay stage, at least up to a certain point. In later stages, the opening of a tree cavity will often be so large that rain enters the interior, which has proven detrimental for certain beetles (Ranius 2002a). Also, if the decay and the opening extend all the way down to the ground, contact with the soil will start changing the unique characteristics of the wood mould. Gradually, more common ground fauna like ground beetles and small rodents will dominate the interior. When openings allow bigger animals, and humans, to enter inside, they can reduce the value of hollow trees for saproxylic fauna by disturbing and compressing the wood mould.

Importance of the surroundings

The oaks in the parks and forests in our study were clearly different when it comes to size and sun exposure: Park oaks were both bigger and had less canopy cover. Based on earlier studies like Ranius and Jansson (2000) one would therefore expect richness of red-listed beetles to be higher in the park oaks, but this is not the case in our study. Rather, species richness of red-listed beetles in forest oaks was similar or even higher than in park oaks (Fig. 2). When considering species richness by samples, the park oaks did not differ from the forest oaks, but if we compared richness by individuals, forest oaks were more species rich. This means that the catches from forest oaks were more heterogeneous than the park oaks. This can be due to the fact that forest oaks are situated in more diverse surroundings, with more different tree species and probably more variation in microclimate at a smaller scale than the rather homogeneous parks surrounded by grassy areas with a sparse, oak dominated tree cover. The results for the third significant factor in our model, Oak in surroundings, support this notion. Oak in surroundings had higher scores in parks than in forests, but this is a relative and not an absolute variable (measuring the proportion of oaks among the surrounding trees). As parks are more open than forests (Table 1), this means that our park oaks are surrounded by fewer trees of which a higher proportion is oak.

Yet another factor related to the surroundings can contribute to an explanation of the high species richness in forest oaks, namely the amount of dead wood in the surroundings. Forest oaks had significantly higher levels of dead wood in the surroundings than park oaks (Table 1). The importance of dead wood in the surroundings has proven influential in other studies of saproxylic beetles (Økland et al. 1996; Franc et al. 2007).

Figure 3a illustrates how high levels of CWD add to the value of both small and large hollow oaks, represented by species richness of red-listed beetles. Thus, it seems like high amounts of CWD in the surroundings to a certain degree "compensate" for the negative effect on species richness of smaller diameters and less sun exposure in forest oaks.

Similar species richness, but different species

Although species richness is similar in oaks in parks and oaks in forests, different species are present in the two site types. Oaks in parks and forests, respectively, probably represent resources important to different species of beetles. This is reflected by the results that forest oaks had more species depending on dead oak wood in general, while species specialising on wood mould and animal nests find better conditions in the larger oaks in the parks.

Previous studies on oak communities have showed that the beta diversity (diversity between oak trees) is high (Engen et al. 2008). Still, the difference in species composition between park and forest oaks is not only due to the general heterogeneity in the total sample. Rather, it seems to be a relationship between the site type and the species overrepresented in that site type, as the number of unique species in both park and forest oaks is significantly higher than what can be explained by chance alone. Among the four species overrepresented in park oaks *Euglenes oculatus*, *Scraptia fuscula*, *Prionychus ater* and *Ctesias serra*, the first three are associated with wood mould. The larger diameter in the park oaks probably correlates with more wood mould, and could, thus, explain this pattern.

Conclusions and conservation implications

The results of our study emphasize the importance of conserving old, hollow oaks, as they harbour a large proportion of the red-listed, saproxylic beetles in Norway. Although the number of red-listed beetles per tree is similar in parks and forests, the beta diversity between park oaks seem to be lower than between forest oaks, probably because of more diverse surroundings in the forests.

This study gives a limited view of the whole saproxylic beetle assemblage inhabiting oaks, as we focus on red-listed beetles. Still, as these species are the ones with the highest risk of extinction, we think that it is important to direct the management towards these species. Although the exact species being red-listed differ between countries, we think the results are more generally applicable in that they pinpoint some environmental factors that limit demanding beetle species in this type of substrate.

It is clear that oaks in park habitat and oaks in forests have unique beetle assemblages when it comes to the threatened and near-threatened species and thus cannot substitute each other. The importance of hollow oaks for biodiversity must be communicated to landscape architects and park managers, and alternatives to cutting down trees with hollows and dead branches should be promoted. As sun exposure is important for many of the red-listed beetles, some management actions like removal of regrowth will be needed in many park localities.

Concerning the forest oaks, we know less of the natural dynamics and the need for management. In central parts of Europe, the degree of openness in the pre-historic forest landscape is debated (Vera 2000; Birks 2005; Mitchell 2005), but as pointed out by Ranius (2002b): If the wood-pasture hypothesis by Vera is valid, it is reasonable to assume that saproxylic beetles have adapted to the semi-open, sun exposed conditions in these primeval forests. A precautionary approach would then imply that at least some of the remnants of oak forest in Central Europe should be kept in a semi-open stage, either by grazing animals (Buse et al. 2007) or by human management. In Norway, this debate may not affect the management of forest oaks as much as in central parts of Europe, as many of the remaining forest sites with hollow oaks are in rugged terrain where tree growth is sparse and a naturally sun exposed environment forms.

On a single tree scale, large diameter and medium decay stage provide good conditions for red-listed beetles. We further show that the qualities of the area surrounding the hollow oaks matter to the red-listed beetles present, both when it comes to proportions of oak and amount of CWD in the surroundings. This means that hollow trees should not be regarded as independent units that will continue to host a large array of rare and endangered species regardless of the management of the surroundings. Planning for continued conservation of these oak associated species demands a large scale perspective, both in space and time. The amount of existing substrate in terms of hollow oaks and dead oak wood, in general, as well as the recruitment of new hollow oaks, must be taken into account when planning for the future of red-listed oak beetles.

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