

# Predicting spatial occurrence of beetles and pseudoscorpions in hollow oaks in southeastern Sweden

Thomas Ranius · Victor Johansson · Lenore Fahrig

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**Abstract** We modelled presence/absence per tree of beetles and pseudoscorpions living in tree hollows in relation to trunk circumference, habitat openness, and connectivity (= density of hollow oaks in the surrounding area), using data from 281 oaks. The presence/absence models were then used to predict species' occurrences in a county (11,600 km<sup>2</sup>) in southeastern Sweden. For eight of the nine species, the most parsimonious occupancy model included a positive relationship with connectivity and at least one tree characteristic. Occupancy underestimates from occurrence records—the ratio of the area of occupancy based on our predictive model to the area of occupancy based on occurrence records—varied between 3 and 83 among species when using occurrence records up to 1993, with significantly larger underestimates for smaller beetle species. Today (after extensive surveys), underestimation has decreased to 1.3–25, confirming that calculations solely based on species occurrence records greatly underestimate the area of occupancy. We suggest this should be taken into account to a greater extent and in a clearer way than today when constructing red lists. The radius of the connectivity measure that generated the best fit varied between 135 and 2,857 m among species, with longer distances for more threatened species. Consequently, preservation of the most threatened species (*Elater ferrugineus* and *Tenebrio opacus*) requires conservation efforts at larger spatial scales than required to protect *Osmoderma eremita*, which frequently has been used as an indicator and umbrella species.

**Keywords** Connectivity · *Quercus robur* · Red list · Spatial occurrence patterns · Scale · Spatial extent

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## Introduction

Red-listing aims at assessing species' extinction risks. Except for a very limited number of well-known species, red-listing is typically based on observational data, and only rarely on monitoring data of population trends or quantitative analyses of extinction risks (e.g. Hallingbäck et al. 1998; Komonen et al. 2008; Newton and Oldfield 2008). A difficult but important task is how to handle the fact that an unknown number of subpopulations are unrecorded. In Sweden, for instance, "area of occupancy", a measure used in red-listing, is obtained by multiplying the area of grid squares with recorded occurrences with an estimated factor of underestimation. This factor is defined as the inverse of the proportion of all subpopulations assumed to have been recorded. However, this is not supported by empirical evidence; we are not aware of any study in Sweden or elsewhere that has estimated the proportion of all occurrences that have been recorded under different circumstances.

Our first aim of this study was to estimate the degree of underestimation of the area of occupancy of seven beetle and two pseudoscorpion species in Sweden. We did this by investigating how per-tree occurrence of each species is related to habitat openness, trunk circumference, and connectivity (= density of hollow oaks in the surrounding area). We then estimated factors of underestimation by comparing predicted occupancy to the localities that are known in 2009 to be occupied (after extensive surveys; Jansson 2006) and were known in 1993 years ago to have been occupied (mainly based on incidental records from amateur entomologists), in an 11,600 km<sup>2</sup>-large Swedish county, where hollow trees have been surveyed. We predicted a negative relationship between species body size and underestimation on the assumption that smaller species are harder to detect.

Metapopulation theory (Johst et al. 2002) and studies of butterflies (Kotiaho et al. 2005; Maes and van Dyck 2001) suggest that less mobile species are more susceptible to habitat loss than are more mobile species. However, some theoretical and empirical studies have shown the opposite; more mobile species can be more susceptible to habitat loss due to a higher risk of dispersal mortality (reviewed in Fahrig 2007).

Our second aim was to test whether the spatial scale of effect is related to red list category across the nine species in our study. The scale of strongest effect is thought to be positively related with the movement range of the species (e.g. Schmidt et al. 2008). For this we first conducted multi-scale analyses of the effect of landscape structure (connectivity) on occurrence of each species. We then tested for a cross-species relationship between the spatial scale of effect of the landscape and red list category to determine whether species with smaller or larger scales of effect (i.e. dispersal ranges) are in higher red list categories.

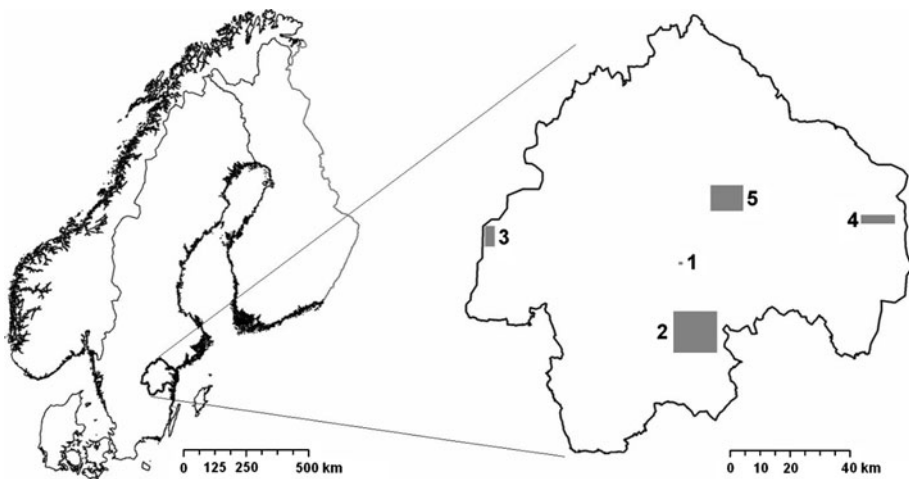
## Methods

### Collecting field data on invertebrates

Five areas were surveyed, all in the county of Östergötland, southeast Sweden (Table 1; Fig. 1). Areas with large differences in the density of hollow oaks were selected, to obtain a wide variability in connectivity among the studied trees (cf. Eigenbrod et al. 2011). Before the invertebrate surveys, we identified potentially suitable trees by visiting sites with large or hollow trees, which we found using information from previous inventories (see Ranius et al. 2010, for details). In Omberg, Kättilstad and Bjärka Säby, pedunculate

**Table 1** Characteristics of the five study areas in the county of Östergötland, southeast Sweden (Fig. 1), in which beetles and pseudoscorpions in hollow oaks were sampled

Name	Coordinates (midpoints)	Size (km <sup>2</sup> )	Hollow oaks/km <sup>2</sup>	No. sampled trees	Sample year
Bjärka Säby	58°16'N, 14°45'E	1.3	79.2	46	2000
Kättilstad	58°04'N, 15°50'E	201.0	1.0	127	1996
Omberg	58°21'N, 14°39'E	22.5	11.7	41	2007
Sankt Anna	58°24'N, 16°52'E	32.7	6.3	26	1997–1998
Skärkind	58°28'N, 16°01'E	94.7	1.5	41	2007

**Fig. 1** Study areas in the county of Östergötland, Sweden. 1. Bjärka Säby; 2. Kättilstad; 3. Omberg; 4. Sankt Anna; 5. Skärkind

oak (*Quercus robur* L.) was by far the dominant tree species among hollow trees. In Skärkind and Sankt Anna there were also other tree species—birch (*Betula verrucosa* Ehrh.), aspen (*Populus tremula* L.), linden (*Tilia chordata* Mill.), and apple (*Malus sylvestris* (L.)). However, our observations of these hollows indicated that the amount of wood mould (i.e. loose material of dead wood in the tree hollows) they contain is generally low. Ranius et al. (2010) found a strong positive relationship between wood mould and species occurrence. Given the low volume of wood mould in non-oak species we chose to restrict our sampling to larger oak hollows. There are hollow-dwelling species for which other tree species are also important, but we avoided that problem by only analysing beetle and pseudoscorpion species that have been observed predominantly in hollows in oaks (>90% of the findings made in the hemiboreal region in Sweden, according to a database provided by the Swedish Species Information Centre). We acknowledge that, to some extent, the very strong predominance for oaks in the observations may reflect that oaks have been surveyed more frequently than other species, although invertebrates have been surveyed in hollow trees of other species as well (e.g. Jansson 2006).

When estimating connectivity, we used data on the position of every hollow oak within the study landscapes and 4-km wide buffer zones around these landscapes. We combined a tree survey by the County Administration Board (Claesson and Ek 2009) with information

from our own field survey to obtain data on the positions of all oaks with hollows containing at least 2 l of wood mould. The volume of wood mould was estimated by examining the hollows. When hollows were impossible to reach, trees with entrance holes with diameters >10 cm were included. At least some of our study species have been observed also in trees with smaller entrance holes (e.g. *Osmoderma eremita*; Martin 1993), but it is not known how frequently this occurs. Trees with smaller entrance holes usually have amounts of wood mould that probably are too small for the study species, because there is a strong positive correlation between wood mould volume and size of the entrance hole (Ranius et al. 2009a). Connectivity was calculated by summing the hollow oaks with wood mould within a circle of a given radius; we calculated connectivity using radii within a range from 25 to 4,000 m. We identified the scale that generated the minimum residual deviance for the total model graphically, with an accuracy of 1 m. This has been found to be a surprisingly good connectivity measure for this study system, in comparison to more complicated connectivity measures (Ranius et al. 2010). Note we could not use connectivity measures that include species occurrence because we were using the prediction model in a landscape where we did not have species occurrence data available for most trees.

Sampling was done by taking eight litres of wood mould from a hollow in each tree (or the total volume, if less than 8 l was available). The wood mould was sieved, and spread out on a white sheet in the field. We examined the material for an hour, and then returned it to the hollow. Presence/absence of larvae (only possible to determine to species for *Osmoderma eremita* and *Elater ferrugineus*), adults (beetles and pseudoscorpions) or adult beetle body parts (elytra, pronota, or heads of beetles) was recorded. There is a strong correlation between the occurrence of adult beetle body parts and live adult beetles (Ranius and Nilsson 1997). As most of the species records are based on body parts that may remain in the trees over several years, at least for these species the result is not sensitive to the fluctuations of population sizes or weather between years. For the two pseudoscorpion species this sampling method seems to be efficient (Ranius and Wilander 2000), and a comparison of different sampling methods showed that this was the most efficient for the seven beetle species analysed (one species for which this method was not efficient was excluded from analyses; Ranius and Jansson 2002). Hollows up to 5 m from the ground were sampled. In Omberg and Skärkind, hollows at the ground level were avoided. In Kättilstad and Bjärka Säby, we sampled as many hollow oaks as possible (61 and 46% of all hollow oaks, respectively). In Omberg, Sankt Anna, and Skärkind, all trees in smaller stands were selected, while in bigger stands, trees were randomly selected (resulting in sampling of 14, 29 and 16% of all hollow oaks, respectively). For each tree, we measured two characteristics that have been found to influence the occurrence of the inhabiting species (Ranius and Wilander 2000; Ranius 2002a): habitat openness and trunk circumference. Habitat openness was the vertical projection of the foliage at a 2 m wide zone around the tree crown: >75% (0), 25–75% (1) or <25% (2). The trunk circumference was measured 1.3 m above ground. In a previous analysis, we found that height above ground of the entrance, direction of the entrance, and wood mould volume also affected species occurrence (Ranius et al. 2010), but we did not include these variables in the present study, as the aim was to predict species occurrence in a whole county, and we did not have data on these variables for every tree in the county. We found no significant correlation ( $P < 0.05$ , Pearson correlation coefficient) between any of these three variables and connectivity at scales between 25 and 4,000 m, which implies that there is little risk that observed correlations between connectivity and species occurrence are due to confounding effects of these variables.

## Fitting models predicting species occupancy

We built two sets of models; the first was aimed at conservative tests of the local and landscape variables affecting occurrence of each species, and the second was to be used in making predictions of occurrence in landscapes not included in our study. For the first set we constructed generalized linear mixed-effect models with a binomial error distribution and a logit link function for each species (Quinn and Keough 2002). Species presence/absence per tree was the dependent variable, habitat openness, trunk circumference, and connectivity were the independent fixed factors and landscape identity was a random factor. By including landscape identity in the model, we took into account that the occupancy per study landscape may be affected by some unmeasured landscape-scale characteristic(s). We used these models as conservative tests of the effects of the tree variables and connectivity on species occupancy. The tests are conservative because some of the variance actually explained by the fixed effects may in fact be attributed to the random effect for landscape identity, if the fixed effects differ among landscapes. For example, since the density of hollow oaks differs among study landscapes, connectivity is confounded to some extent with landscape identity, so part of any real effect of connectivity will be interpreted as a landscape identity effect rather than as a connectivity effect.

To make predictions to landscapes other than those where the data were collected, we therefore also fit models that did not include a random effect for landscape identity. Not only would it be impossible to include the effect of landscape identity when predicting occupancy in other landscapes but also, in making predictions to other landscapes, we wish to assume that the apparent effect of the tree variables and connectivity are actually attributable to those variables rather than to some other unmeasured variable(s) that differs among the sampled landscapes. We modelled species occupancy in relation to habitat openness, trunk circumference and connectivity using a generalized linear model with a binomial error distribution and a logit link function.

For the first set of models, landscape identity was included in the models irrespective of how it affected AIC, while the variables at the tree level were included only if they decreased the AIC value. The latter was also true for the second set of models in which landscape identity was not included. The AIC value was calculated as  $-2\log\text{-likelihood} + 2k$ , where  $k$  is the number of parameters in the logistic regression model plus one for the radius of the connectivity measure, as that was also estimated when fitting the model. For both sets of models, we calculated the explained deviance (% the proportion of variability in a data set that is accounted for by the statistical model, which means it is an analogue to  $R^2$ ) and for the first set of models also  $P$  values (from log likelihoods) since here we were interested in testing hypotheses.

## Predicting species occupancy in a whole county

We used the predictive models (above) to predict species occupancy in the county of Östergötland, which is about 11,600 km<sup>2</sup>. To predict occupancy of our study species, we used tree survey data from the County Administration Board (Claesson and Ek 2009). Using aerial photos, they have identified all sites where large trees might be present. These sites were surveyed on ground, and trees that are large or hollow were individually mapped. The County Administration Board had classified all presumed trees in terms of the tree's developmental stage, based on the size of their entrance holes. We tested their classification using the trees at our five study sites (see above). When we compared our field data with their data, we found that many of the trees they had classified as being in the

earliest hollow stage (entrance hole <10 cm) actually did not have any cavities, just shallow injuries. Furthermore, Sverdrup-Thygeson et al. (2010) found that the number of oak species was lower in trees in the earliest hollow stage, using the same classification as the County Administration Board. When we removed the trees in this class (42% of all hollow oaks), remaining trees in the County Administration Board data set was reasonably similar to the set of trees that we had estimated to have enough wood mould to constitute habitat for the study species; the difference was less than 35% for each of the five areas. Thus, when we used tree data from the County Administration Board we included only trees belonging to categories with at least one entrance hole >10 cm. We also included only oaks (*Quercus robur* and *Q. petraea* (Matt.) Liebl.), which constituted about 30% of all trees in these categories, because the study species have rarely been observed in other tree species. Trunk circumference, habitat openness, and connectivity (see above) were used in the statistical models as predictors of the probability of occurrence for each study species in each of the 9,835 trees. Since the height of the entrance hole was not estimated for these trees, we could not use that variable as a predictor. This means that we assumed that the probability of occurrence was the same in trees with hollows up to 5 m from the ground as in trees with hollows higher up. We have found that height has an effect on several of our study species (positive effect on the occupancy of four species, negative on one, in hollows 0–5 m from the ground; Ranius et al. 2010), and consequently this may result in some underestimation (or for one species overestimation) of the probability of occurrence. We overlaid a grid with a mesh size of 2 km × 2 km over the county of Östergötland, and summed the probabilities of occurrence for all the trees in each cell using GIS, to get the predicted number of occupied trees in each cell. We used 2 km × 2 km squares because this is the approach used in the red-listing process in Sweden (Gärdenfors 2009). The predictions were validated by comparison with known occurrences of the species. We assumed that when the predicted number was lower than a certain cut-off, the species was absent from the square, but when higher than this cut-off, the species was present. We compared the fit when using 1, 2, and 4 occupied trees as cut-off values, and used 1 as the cut-off in subsequent analyses, because it generated the best fit with field data for most of the species (see Results). Using this cut-off we predicted area of occupancy, recognizing that occupancy does not necessarily imply that the species is occurring in viable populations.

For each species, we calculated the factors of underestimation for 1993 and 2009 as the quotient between the predicted number of occupied squares and the number of squares with records known in 1993 and 2009. Old oaks constitute a long-lived and stable habitat, and therefore the change in habitat availability has been relatively small from 1993 to now. The species records come from a database managed by the Swedish Species Information Centre, and are the same data as used in the Swedish red-listing process. We excluded species data originating from the present study, to avoid dependence of data sets. The data base contains records from surveys, museums, and private collections. Up to 1993 there were no records made by any professional nature conservationists, and consequently almost all data were collected in a non-systematic way. However, even this dataset is quite extensive (Table 2) because entomologists have been interested for a long time in the beetle fauna in ancient trees (e.g. Jansson 1930); less attention has been paid to pseudoscorpions (see however Lohmander 1944). After 1993, systematic surveys of hollow oaks have been conducted using traps at about 100 sites, mainly in areas of conservation interest (Jansson 2006). In addition, at least ten amateurs have made significant records (Jansson 2006). One of the study species, *Osmoderma eremita*, has been surveyed with traps at

**Table 2** Observed and predicted occupancy per 2 km × 2 km squares in the county of Östergötland, Sweden

Species	Red list	Records 1993	Records 2009	Occ. 1993 (%)	Occ. 2009 (%)	Occ. pred. (%)	U-est. 1993	U-est. 2009
<i>Allochernes wideri</i> (P)	LC	10	47	0.2	0.8	19.6	82.6	24.5
<i>Ampedus hjorti</i> (B)	LC	54	192	0.5	2.0	13.7	28.9	7.0
<i>Allecula morio</i> (B)	NT	42	261	0.7	2.4	17.3	24.3	7.1
<i>Ampedus cardinalis</i> (B)	NT	49	203	0.7	1.8	11.4	17.5	6.2
<i>Larca lata</i> (P)	NT	4	93	0.1	1.5	2.0	16.8	1.3
<i>Osmoderma eremita</i> (B)	NT	158	828	1.3	4.7	15.8	12.1	3.4
<i>Prokraerus tibialis</i> (B)	NT	59	196	0.4	1.9	15.9	35.8	8.5
<i>Elater ferrugineus</i> (B)	VU	44	132	0.4	0.6	1.4	3.3	2.4
<i>Tenebrio opacus</i> (B)	VU	53	112	0.3	0.7	4.3	13.2	6.3

Beetle (B) and pseudoscorpion (P) species of study; Total number of squares: 3,378

*Red list* red list categories in Sweden (*VU* vulnerable, *NT* near threatened, *LC* least concern; Gärdenfors 2010), *Records 1993* number of records in 1993 or earlier, *Records 2009* number of records in 2009 or earlier, *Occ. 1993* proportion of squares with records in 1993 or earlier, *Occ. 2009* proportion of squares with records in 2009 or earlier, *Occ. pred.* proportion of occupied squares according to the predictive model, *U-est. 1993* factor of underestimation (= number of predicted occurrences/known occurrences) of the number of occupied squares, if only records in 1993 or earlier are considered, *U-est. 2009* factor of underestimation of the number of occupied squares, if records up to 2009 are considered

about 150 sites (Antonsson et al. 2003). This makes Östergötland one of the most well-investigated counties in Sweden (Jansson 2006).

For body size of the species we used the mean values for adults given by Henriksen (1913), Hansen (1925, 1945), and Gärdenfors and Wilander (1992). Generalized linear modelling was conducted using R 2.9.0 (R Development Core Team 2009) and other analyses were conducted in SPSS 16.0.

## Results

For six of nine species, there was a statistically significant positive relationship with trunk circumference, and for two species there was a positive relationship with habitat openness (Table 3; Fig. 2). For eight of nine species, there was a statistically significant positive relationship with connectivity. The radius of the connectivity measure that generated the best fit with the data varied between 135 and 2,857 m among species (Table 3). The more endangered a species is according to the red list, the better its occurrence pattern was explained by its statistical model, i.e., the bigger proportion of the deviance was explained by the model ( $P = 0.005$ , ordinal regression). Furthermore, more endangered species tended to have a larger radius of the connectivity measure that generated the best fit to the field data ( $P = 0.026$ , ordinal regression, Table 3).

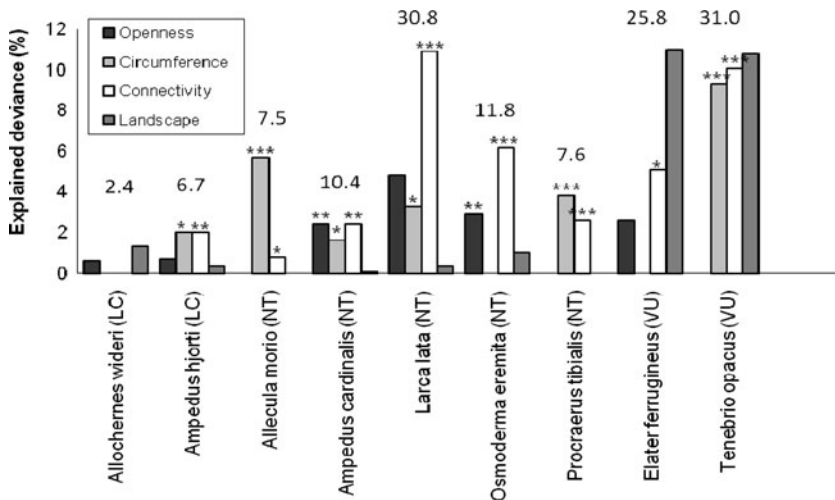
More endangered species had smaller predicted areas of occupancy ( $P = 0.017$ , ordinal regression, Table 2). For all species, there was a strong positive relationship between predicted occurrence for each square and whether the species had been recorded there or not (Table 4; Fig. 3). For most species, the relationship between prediction and field data was stronger when one occupied tree was used as a cut-off, rather than when a higher cut-off level was used (Table 4). Therefore we used one occupied tree as a cut-off in all further

**Table 3** Study species, red list categories in Sweden, occupancy per tree (Occ.), and for the most parsimonious (lowest AIC value) multiple logistic regression model of species' presence/absence per tree: intercept, coefficients, radius of the connectivity measure (Radius) and explained deviance (Exp. dev.)

Species	Red list	Occ. (%)	Intercept	Openness	Circum	Connectivity	Radius	Exp. dev. (%)
<i>Allocheres wideri</i> (P)	LC	31	-1.07	0.286			135 <sup>a</sup>	1.2
<i>Ampedus hjorti</i> (B)	LC	31	-2.39		0.00265	0.0340	384	5.4
<i>Allecula morio</i> (B)	NT	37	-2.72		0.00503	0.0100	919	12.4
<i>Ampedus cardinalis</i> (B)	NT	25	-3.52	0.793	0.00271	0.0404	329	10.3
<i>Larca lata</i> (P)	NT	7	-8.13	0.725	0.00549	0.0211	2857	30.5
<i>Osmoderma eremita</i> (B)	NT	37	-1.96	0.685		0.0740	192	10.9
<i>Procræus tibialis</i> (B)	NT	35	-2.68		0.00429	0.0132	911	7.6
<i>Elater ferrugineus</i> (B)	VU	6	-5.23	0.278		0.0323	1104	21.9
<i>Tenebrio opacus</i> (B)	VU	15	-6.86		0.00918	0.0141	2760	23.8

Data from 281 hollow oaks in southeastern Sweden (Fig. 1)

<sup>a</sup> In the most parsimonious model for *A. wideri* the connectivity variable was excluded. When included, the relationship was positive



**Fig. 2** The increase in explained deviance (%) of logistic regression models when adding different independent variables to the most parsimonious model but with this variable absent. Species presence/absence per tree is the dependent variable, habitat openness, trunk circumference, and connectivity (number of surrounding trees) are the independent fixed factors, and landscape identity is a random factor. All relationships were positive. If inclusion of the variable did not lower the AIC value, the explained deviance was reported as 0. For variables at the tree level, significance levels are given as \* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ . The total explained deviance for the models are given as figures above the bars. VU vulnerable, NT near threatened, LC least concern

analyses. A comparison between calculations based on our predictive models and species records up to the present suggested that the factors of underestimation were between 1.3 and 25. In 1993, before any systematic inventories had been conducted, the calculated factors of underestimation were between 3 and 83. When only considering beetles, smaller species generally had larger occupancy underestimates than larger species ( $P = 0.011$ ,



**Table 4** Relationships between predicted occurrence per 2 km × 2 km square and occurrence records up to 2009 for each species

Species	Red list	Limit = 1 Explained deviance (%)	Prop. occupied squares with occurrence predicted (%)	Prop. absent squares with absence predicted (%)	Limit = 2 Explained deviance (%)	Limit = 4 Explained deviance (%)
<i>Allochernes wideri</i> (P)	LC	17.4	85.2	81.0	22.4	<b>23.0</b>
<i>Ampedus hjorti</i> (B)	LC	20.8	75.8	87.6	<b>22.1</b>	16.6
<i>Allecula morio</i> (B)	NT	21.1	80.5	84.3	<b>24.5</b>	19.6
<i>Ampedus cardinalis</i> (B)	NT	<b>20.2</b>	71.0	89.7	17.5	11.5
<i>Larca lata</i> (P)	NT	<b>11.8</b>	30.0	98.4	7.8	3.5
<i>Osmoderma eremita</i> (B)	NT	<b>18.8</b>	69.4	86.8	16.2	12.1
<i>Procraterus tibialis</i> (B)	NT	24.7	85.7	85.5	17.5	<b>25.5</b>
<i>Elater ferrugineus</i> (B)	VU	<b>34.8</b>	63.2	99.0	26.0	14.0
<i>Tenebrio opacus</i> (B)	VU	<b>33.4</b>	78.3	96.2	31.5	20.9

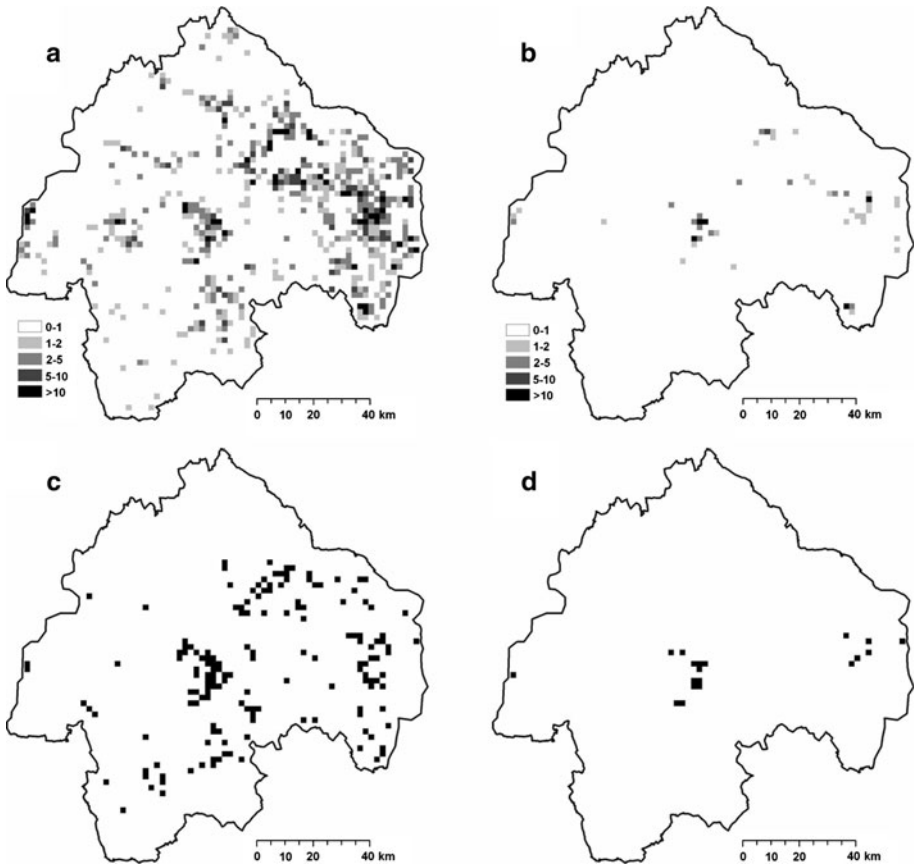
All relationships were positive and all were significant at  $P < 0.001$ . “Limit = 1”: the species is considered “present” in a square if it is predicted to be present in at least one tree. For “Limit = 2” and “Limit = 4” the cut-off level for when a species is considered “present” in a square is two or four trees, respectively. Explained deviance from generalized linear model with binomial distribution and logit link function (dependent variable: presence/absence in records, independent variable: predicted presence/absence). For each species, the highest value of the explained deviance is in bold

mixed-effect model, with year as random effect), but this relationship was not significant when the two pseudoscorpion species were also included ( $P = 0.13$ ; Fig. 4).

## Discussion

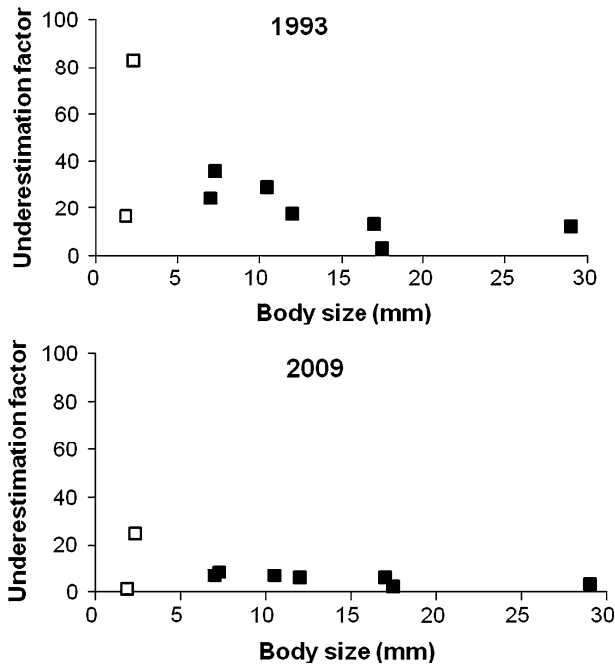
Occurrence of invertebrates in hollow oaks is affected both by tree characteristics and connectivity (Fig. 2). Similar results have been obtained for tree-living bryophytes and lichens (e.g. Snäll et al. 2003; Löbel et al. 2006). The spatial scale of effect of habitat varied widely among species, but was of the same magnitude in this study in comparison to previous studies of saproxylic beetles (Holland et al. 2005; Schroeder et al. 2006; Franc et al. 2007).

The spatial scale of effect of connectivity on occupancy is thought to be positively related to the movement range of species (e.g. Schmidt et al. 2008). While this may seem inconsistent with the fact that the species with the largest spatial scale of effect was the pseudoscorpion *Larca lata*, which lacks the ability to fly, it is likely that this species travels long distances by phoresy (= hitch-hiking with flying animals; Poinar et al. 1998). This is consistent with the observed low genetic differentiation among local populations of this species, indicating that migration between them is frequent (Ranius and Douwes 2003). It has been argued that threatened invertebrates in hollow trees require conservation efforts very near or within occupied sites, because the dispersal range is low (Hedin et al. 2008). For one of the study beetles, *Osmoderma eremita*, a limited dispersal range has indeed been demonstrated by capture-recapture and telemetric studies (Hedin et al. 2008). However, we found other beetles associated with hollow trees, that are rarer and more threatened than *O. eremita* (*Elater ferrugineus*, *Tenebrio opacus*; Table 2), whose occupancies were related to connectivity at much larger spatial scales (Table 3). This indicates that, among our study species, the most threatened species actually disperse farther than



**Fig. 3** Two examples of species' occurrences in the county of Östergötland, Sweden. **a** predicted for *Osmoderma eremita* Scopoli; **b** predicted for *Elater ferrugineus* L.; **c** observed up to 2009 for *O. eremita*; **d** observed up to 2009 for *E. ferrugineus*. The grey-scale represents the predicted number of occupied oaks per square

less threatened species such as *O. eremita*. This is consistent with Thomas (2000), who found that the distributions of butterfly species with an intermediate mobility had decreased more than the distributions of both more mobile and more sedentary species. The reason why *E. ferrugineus* and *T. opacus* are more threatened than *O. eremita* may be that dispersal from oak woods and pastures is a poor strategy in today's fragmented landscapes, as it increases the risk for emigrants to die in the matrix, thus placing species with larger dispersal ranges at greater risk. However, the rarity of *E. ferrugineus* and *T. opacus* may also be due to other factors than migration mortality. For instance, it may be that these species tend to occur in smaller and more fluctuating populations (*E. ferrugineus*: Larsson and Svensson 2011), and for that reason need a larger network of hollow trees to get enough colonisations to compensate local extinctions (cf. Drechsler and Wissel 1998). We also note that since *Elater ferrugineus* is a predator, and larvae of *Osmoderma eremita* are one of its prey (Schaffrath 2003), our result is consistent with the idea that the experienced spatial scale is larger for organisms at higher trophic levels (Holt 1996).



**Fig. 4** Relationship between adult body size of beetles (*filled*) and pseudoscorpions (*open squares*) and the factor of underestimation (the ratio of the area of occupancy based on predictive modelling to the area of occupancy based on occurrence records) if records are included (i) from 1993 and earlier, or (ii) from 2009 and earlier

To illustrate the differences among species in terms of the density of hollow oaks needed for a certain occupancy, we estimated for three species the density of hollow oaks required to obtain a probability of presence of at least 50% in a suitable tree (here defined as a hollow oak with a diameter of 1.2 m, and the highest degree of habitat openness). For *O. eremita*, 69 hollow oaks/km<sup>2</sup> are required within a radius of 192 m, for *E. ferrugineus*, 38 hollow oaks/km<sup>2</sup> are required within a radius of 1,104 m, and for *T. opacus*, 10 hollow oaks/km<sup>2</sup> are required within a radius of 2,760 m. To obtain a continuous supply of hollow trees, younger trees are also required. A previous estimation has suggested that in an oak population with a stable age structure and only natural tree mortality (i.e. the highest density of hollow oaks possible to maintain in the long run, which we call “optimal oak pasture”), 7% of the trees have hollows with wood mould (Jonsson and Ranius 2009), and the area needed for each oak is about 0.02 ha (cf. Ranius et al. 2009b). Consequently, for *O. eremita*, optimal oak pasture has to cover 20% of the area within 192 m, which means an area with optimal oak pasture of 2.3 ha. For *E. ferrugineus* and *T. opacus*, the corresponding values are 11% (42 ha within 1,104 m) and 3% (69 ha within 2,760 m), respectively. In Europe, regions with such high densities of hollow trees are rare today, but such densities were probably rather common in the old-growth broadleaved forests that originally covered wide regions in Europe. Thus, these hollow oak-dwelling species, which today are regarded as rarities, may have been common in virgin forests of Europe.

For all species, there was a strongly significant relationship between predicted and observed occurrences (Table 4). The explained deviance was relatively low mainly because the observed occupancy was much lower than predicted (i.e. the underestimation

was high). For all species except *L. lata*, at least 63% of the occurrences were observed in squares for which occupancy was predicted, while in squares with no observed occurrences, absence was predicted in at least 81% of the sites (Table 4). Thus, the recorded observations (all observations known except those used to fit our prediction model) validated the prediction model for all species, except *Larca lata*. The poor fit for *L. lata* may be because the predictive model underestimates its occupancy due to false absences in our data.

When knowledge about area of occupancy was based mainly on incidental records (up to 1993), the underestimation (total area of occupancy/known area of occupancy) was between 3 and 83. For our study species, extensive and systematic surveys have decreased the underestimations to levels between 1.3 and 25. However, the lowest underestimation factor was for *Larca lata*, whose occurrence was predicted for only a minority of all squares where it actually occurred (*Larca lata*, Table 4). With *Larca lata* excluded, the lowest factor of underestimation was 2.4. All our underestimation factors represent minimum values, as the underlying assumptions that these estimates rely on (i) the species never use any other habitat than hollow oaks with entrances >10 cm, (ii) there are no false absences in our invertebrate sampling, (iii) the probability of occurrence is equal in trees with hollows up to 5 m from the ground as in trees with hollows higher up, and (iv) all hollow oaks were found in the tree survey are unlikely to be met in all cases. Among beetles, the underestimation was larger for the smaller species (Fig. 4). An explanation for this is that among these species, mean body size is probably positively correlated both with the probability of finding specimens in the field and their identifiability (T. Ranius, pers obs). Similar relationships were suggested in an analysis of polypore fungi data, which found that identifiability and longevity of fruit-bodies were the major factors affecting the number of records of different species (Löhmus 2009).

## Implications

In the Swedish red list the assumed factors of underestimation vary from 1 to 100, which are consistent with the magnitude of underestimation obtained in the present study. However, the Swedish red list does not publish the factors of underestimation used for individual species (Gärdenfors 2010). In other cases, for instance IUCN's European red list of saproxylic beetles, the potential underestimation of area of occupancy is not even considered (Nieto and Alexander 2010). The present study shows that calculations solely based on species records severely underestimate the area of occupancy. We suggest this should be taken into account to a greater extent and in a clearer way than today when constructing red lists. The generally high levels of underestimation imply that it is difficult to solve the problem of poor knowledge about threatened species simply by collecting more data on species records. Instead, a more fruitful approach is to model the habitat requirements of species based on intensive sampling in a restricted area, collect data on habitat availability, and use the obtained data to predict the current area of occupancy.

*Osmoderma eremita* has frequently been used as an indicator and model species representing a whole community of invertebrates associated with hollow trees (Ranius 2002b). This study shows that some species that are more threatened respond to habitat connectivity at a larger spatial scale than *O. eremita*. This suggests that to preserve all threatened species, conservation efforts will have to be conducted at larger spatial scales than the scale required to preserve *O. eremita*.

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