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Factors and scales potentially important for saproxylic beetles in temperate mixed oak forest

Niklas Franc^{a,*}, Frank Götmark^a, Bjørn Økland^b, Björn Nordén^c, Heidi Paltto^c

^aDepartment of Zoology, Göteborg University, Box 463, SE-405 30 Göteborg, Sweden

^bNorwegian Forest and Landscape Institute, Box 115, 1431 Ås, Norway

^cBotanical Institute, Göteborg University, Box 463, SE-405 30 Göteborg, Sweden

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ABSTRACT

The influence of environmental factors on species richness and species composition may be manifested at different spatial levels. Exploring these relationships is important to understand at which spatial scales certain species and organism groups become sensitive to fragmentation and changes in habitat quality. At different spatial scales we evaluated the potential influence of 45 factors (multiple regression, PCA) on saproxylic oak beetles in 21 smaller broadleaved Swedish forests of conservation importance (woodland key habitats, WKH). Local amount of dead wood in forests is often assumed to be important, but two landscape variables, area of oak dominated woodland key habitats within 1 km of sites and regional amount of dead oak wood, were the main (and strong) predictors of variation in local species richness of oak beetles. The result was similar for red-listed beetles associated with oak. Species composition of the beetles was also best predicted by area of oak woodland key habitat within 1 km, with canopy closure as the second predictor. Despite suitable local quality of the woodland key habitats, the density of such habitat patches may in many areas be too low for long-term protection of saproxylic beetles associated with broadleaved temperate forests. Landscapes with many clustered woodland key habitats rich in oak should have high priority for conservation of saproxylic oak beetles.

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1. Introduction

In biogeography, species richness and composition are clearly related to latitude and altitude (Wright, 1983; Stevens, 1989; Cox and Moore, 1999; Gaston, 2000). Species richness and composition are also assumed to depend on spatio-temporal factors such as region, landscape quality and configuration, habitat continuity, and habitat or stand quality (Meffe and Carroll, 1997; Nilsson and Baranowski, 1997; Forman, 1999; Gaston and Blackburn, 2000). Some studies emphasize the importance of the surrounding landscape for local species

richness. For instance, the surrounding landscape seems to influence species richness of birds in riparian forests (Saab, 1999); bark beetles in boreal forests (Peltonen et al., 1998); saproxylic beetles in boreal forest (Økland et al., 1996); fungus gnats in temperate forest (Økland, 1996; Økland et al., 2005); herbivorous insects on thistles (Kruess, 2003); plants, insects and birds in semi-natural pastures (Söderström et al., 2001); and insects and plants in farmland (Weibull et al., 2003). Studies of single beetle species (Rukke and Midtgaard, 1998; Kehler and Bondrup-Nielsen, 1999) and of a moth species (Gripenberg and Roslin, 2005), also indicate impact of the surround-

* Corresponding author. Tel.: +46 31 773 3650; fax: +46 31 41 67 29.

E-mail addresses: niklas.franc@zool.gu.se (N. Franc), frank.gotmark@zool.gu.se (F. Götmark), bjorn.okland@skogoglandskap.no (B. Økland), bjorn.norden@systbot.gu.se (B. Nordén), heidi.paltto@botany.gu.se (H. Paltto).

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ing landscape on local abundance. All these studies analysed at least two different spatial scales and two or more variables potentially influencing species richness.

Recently, there has been focus on the local stand and its qualities seem to be important for species richness of insects (Siitonen and Martikainen, 1994; Rosenzweig, 1995; Sverdrup-Thygeson, 2001), but few insect studies have related local diversity to landscape factors and even fewer to several spatial scales (but see Peltonen et al., 1998; Økland et al., 2005). Patches of semi-natural forest of conservation concern are often small and scattered in the landscape, reducing local population sizes of taxa and impeding dispersal. Therefore, besides factors or processes at site or stand level (about 1–3 ha), variation in the surrounding landscape (in this study about 3–1200 km²), climate, and topography is likely to influence local species richness and species composition. The relative roles of the scales, and temporal factors, have rarely been investigated.

Dead wood in natural forests is a very species-rich substrate (Samuelsson et al., 1994; Speight, 1989), which is scarce in European production forests today (Nilsson et al., 2001; Siitonen, 2001; Nilsson et al., 2002; Nordén et al., 2004a; Christensen et al., 2005). Fungi and insects colonize and decompose dead trees; the saproxylic beetles represent a major part of this biodiversity, including 1257 species in Scandinavia of which several hundred are red-listed in Sweden (Dahlberg and Stokland, 2004; Gärdenfors, 2005). Several factors influencing species richness of saproxylic beetles have been identified: continuity of forest and/or substrate (Siitonen, 1994; Jonsell and Nordlander, 2002; Similä et al., 2003; Bouget and Duelli, 2004), quality/amounts of dead wood in local stands (Nilsson and Baranowski, 1997; Ranius and Jansson, 2000; Schiegg, 2000; Ranius, 2002), and composition of the surrounding landscape (Økland et al., 1996).

In this study a range of local and landscape variables of potential importance for species richness and species composition of beetles in mixed oak-dominated forest are evaluated. The study is explorative and the following general question was posed: What factors predict or are related to variation in local species richness and species composition of saproxylic beetles in oak-dominated temperate mixed forest, and at what spatial scale are the relationships strongest?

For analysis of different scales, we quantified the following major variables: dead wood, species richness of fungi (often used by saproxylic beetles (Gilbertson, 1984)), forest composition, land use, climate, and topography.

2. Methods

2.1. Study area and stands

We studied 21 semi-natural forests in the boreonemoral vegetation zone of southern Sweden (Fig. 1), a transition between boreal and nemoral or temperate forest (Ahti et al., 1968; Nilsson and Baranowski, 1997; Nilsson et al., 2001). The study sites were abandoned pasture woodlands situated 5–230 m above sea level, with mature oaks (*Quercus robur* and *Q. petraea*, oldest trees 80–200 years). At each site we used two 100 × 100 m plots about 50 m apart. The canopy in the plots was closed or almost closed with 14.1% (SD = 3.5%, $n = 21$ sites) of visible sky from ground level. The mean basal area, at breast height (1.3 m) of trees larger than 1 cm in diameter, was 25.1 m²/ha (SD = 3.8 m², $n = 21$), and the mean basal area of oak was 12.5 m²/ha (SD = 4.8, $n = 21$). Other common trees were spruce (*Picea abies*, mean basal area 11.1%), birches (*Betula verrucosa* and *B. pubescens*, 9.5%), aspen (*Populus tremula*, 6.8%), ash (*Fraxinus excelsior*, 6.2%), lime (*Tilia cordata*, 3.1%), pine (*Pinus sylvestris*, 2.5%) and maple

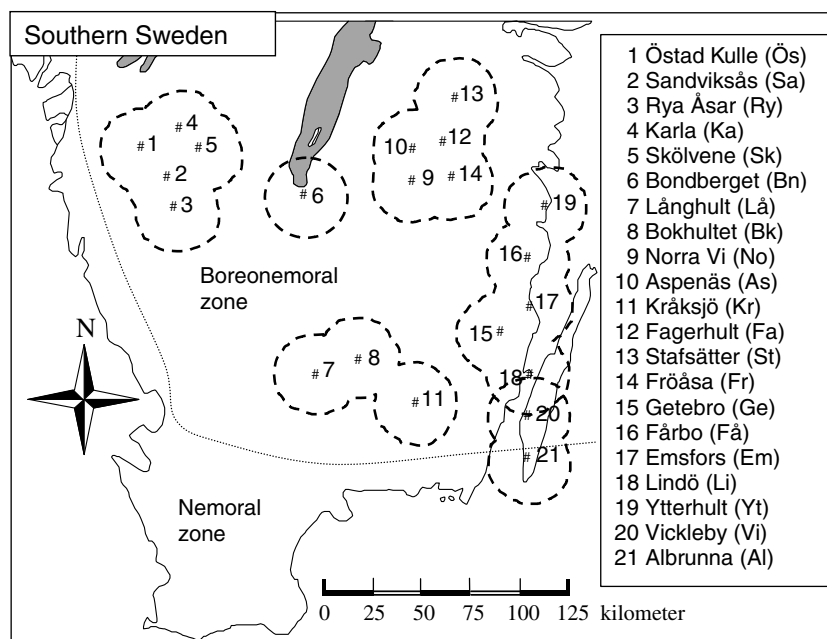


Fig. 1 – Study sites in southern Sweden. The encircled areas are large landscapes or regions, where mean values of dead wood were estimated by the National Forest Survey.

(*Acer platanoides*, 1.5%). The ground was mesic, and usually a bit stony.

The 21 stands contained on average 12.0 m³ (SD = 8.1) of coarse (>10 cm in diameter) dead wood per hectare (compared to on average about 3–4 m³ in Swedish production forest (Fridman and Walheim, 2000)) and about as much (10.5 m³/ha, SD = 5.2) fine dead wood (1–10 cm diameter) (Nordén et al., 2004a). About 80% of the dead wood volume was logs (downed) and 20% snags (standing); 40% of the snag volume and 22% of the log volume consisted of oak. In addition, the sites contained an average of 1.6 m³/ha (SD = 0.9) of dead wood attached to living trees and 1.6 m³/ha (SD = 1.1) of stumps (both types mainly oak) (Nordén et al., 2004a). A common definition of coarse dead wood (≥ 10 cm in diameter) is used instead of the ≥ 40 cm definition that was indicated to be important for saproxylic beetles in Norway (Økland et al., 1996) as dead oak ≥ 40 cm was very rare in the stands. The monthly precipitation in the study area, during May to September (sampling period), decreases from about 66 mm at the western site to about 51 mm at the eastern coastal sites, and mean temperature varies from about 13.2 °C in the west to about 14.1 °C in the east (mean values 1961–1990). In 2001 the entire area had normal precipitation and the air temperature was about 1 °C above normal.

2.2. Sampling methods and insect material

Beetles were sampled in 2001 (complementary sampling in 2002) using flight interception traps of the trunk-window type. The traps had a 20 × 30 cm transparent plastic pane attached above a 2 l white plastic vessel (Fig. 2) in which beetles were collected. Because dead oak is particularly rich in threa-

tened saproxylic beetles in Sweden (Jonsell et al., 1998), this substrate was used for the traps. In addition, a “freestanding” trap, not attached to any substrate (>3 m from tree or coarse dead wood), was used. On snags, the traps were oriented to the south. The vessels were attached as close as possible to the bark or wood on the trunks and contained 50% water, 50% ethylene glycol for preservation of beetles, soap (3 drops/l) to decrease surface tension, and a bitter agent (Bitter[®], Denatonium Benzoat, MacFarlan Smith Ltd, Edinburgh, UK – 3 drops/l) to deter vertebrates. The vessels had small holes, 2 cm below their upper edge, for drainage of excess rainwater. On snags the traps were placed 1.5–2.0 m above ground, except at two sites, where they were placed at 2.5–3.0 m height to avoid disturbance from cattle. On the logs they were attached on the south facing side of the stem (Fig. 2) at its middle part. Centre height of the log panes ranged from 30 to 50 cm above ground. To standardize conditions, only snags and logs without visible fruit-bodies of fungi were used. The freestanding trap with a 40 × 60 cm plastic pane and 5 l plastic vessel was attached to two wooden poles by steel-wire. The centre of the plastic pane was about 1.1 m above ground.

Four traps were set up in each plot (8 traps per study site): one on a snag with minimal degree of stem decay (young snag), one on a snag with moderate to advanced degree of stem decay (old snag), one on a log with variable degree of stem decay (minimal to advanced, see below), and one free-standing trap. In 28 out of 42 plots, newly dead snags could not be found. Living trees in poor conditions were then selected, carefully girdled, and used as trap substrate. In each plot, trap substrates in each group were randomly chosen, traps were set up in mid May, and emptied late in June, early August and mid September. For each site beetles from all eight traps were pooled for analysis. For logs only the first period (May–June) was used due to trap disturbances (possibly badgers). At two sites (Ytterhult and Skölvène) cattle disturbed traps in 2001. These two sites were resampled in 2002 and only that material was used in the study. At Ytterhult, traps active in both years indicated that numbers of saproxylic species and individuals were similar and comparable between years.

Young snags had mean trunk diameter at breast height of 35 cm (SD = 15 cm, $n = 42$), old snags 34 cm (SD = 19 cm, $n = 42$) and logs at their middle part 20 cm (SD = 9.8, cm $n = 42$). The diameter of young snags, old snags and logs differed significantly ($P < 0.01$, Kruskal–Wallis ANOVA), due to smaller size of logs. Stem decay was estimated in five classes (0–4): (0) ring-barked the same year; (1) wood hard, bark firmly attached to the stem, bark beetles may be present, dead <2 years; (2) wood hard, bark partly loose, dead 2–5 years; (3) wood soft, able to penetrate with knife (1–5 cm), bark more or less gone, dead >5 years; (4) knife penetrates the wood without resistance, bark loose and mostly gone (decay stage 4 was not used in this study). Stem decay differed among substrates ($p < 0.01$, means: logs = 1.7, SD = 0.9; old snags = 1.9, SD = 0.7; and young snags = 0.4, SD = 0.5), since the young snags were less decayed.

Niklas Franc identified beetles to species level, with some help from Bengt Andersson, Richard Andersson, Johnny Lindqvist, and Stig Lundberg. Nomenclature is based on Lundberg (1995) and red-list categories on Gärdenfors (2000,

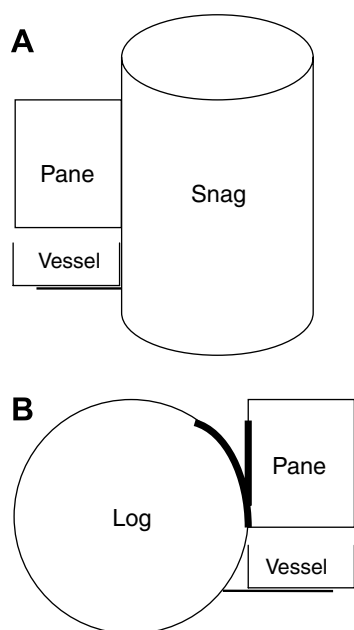


Fig. 2 – Trunk window traps of flight interception type mounted on dead oak wood of (A) snag and (B) log (shown in cross-section). The vessels were attached to 7-in. nails with duck tape. Panes on logs were supported with a bent steel band and on snags with 1.5-in. nails.

2005). Classification of saproxylic beetles and their preference (dead oak) was based on a saproxylic database (Dahlberg and Stokland, 2004), and the definition of saproxylics follows Speight (1989). Obligate and facultative saproxylic species connected to oak (from the database) were pooled, but we also tested obligate species separately. One saproxylic taxon, the genus *Acrotrichis* (family Ptilidae), was excluded due to identification problems.

2.3. Environmental variables

In total, 45 environmental variables were considered as potentially important for local species richness of saproxylic beetles (Table 1). For the site level, environmental variables were recorded within the two plots (Table 1). The fungi variables, ASCOM and BASIDIO, are based on standardized inventory of fruit-bodies of wood-inhabiting ascomycetes and basidiomycetes in 2000 and 2001 (Nordén et al., 2004b). Many saproxylic beetles are considered more or less dependent upon fungi (Gilbertson, 1984). Canopy closure was based on 16 digital photographs taken from ground level towards the sky at each site (8 photos along transects in each plot). Using the program NIH Image we converted the colour pixels to binary black-and-white pixels and calculated the mean proportion visible sky. Dead wood was quantified along transects, and basal area of living trees >1 cm dbh was inventoried in 0.6 ha at each site (see Nordén et al., 2004a).

Two levels were used for the landscape scale: 1 and 10 km radius from site (Table 1). In southern Sweden, semi-natural forests with higher biodiversity values occur as small fragments in the dominating coniferous production forest; they are currently mapped as woodland key habitats (WKH, see Gustafsson, 2002; Götmark and Thorell, 2003). On the basis of forest structure and indicator species, the majority of all Swedish WKHs have been identified (Nitare, 2000; Gustafsson, 2002; <http://www.skogsstyrelsen.se>). We obtained WKH files from forestry boards and forest companies and calculated the area of WKH in ArcView 3.2. For oak dominated WKH (WKHOD), the dominating tree was oak, and for oak rich WKH (WKHOR) oak was the second dominating tree. The WKH data were pooled with data from nature reserves obtained from County administrations. To standardise classification we used texts describing each reserve, sorting the reserve forest into similar categories as for the WKHs, and as non-WKH forest.

Land use variables from the cadastral map (scale 1:10,000), based on aerial photographs 1996–2002, were agriculture land, coniferous forest, and deciduous forest. The smallest area to be shown on maps is generally one ha, but for deciduous forest it is 8 ha, except for forest with oak, beech, ash, maple, lime and elm, where it is 4 ha (Andersson, 2002).

As complement to the rather coarse map data, data for deciduous forest were obtained from kNN. These data were based on satellite images and ground collected data (resolution of these maps was 25 × 25 m) from the Swedish NFI (National Forest Inventory) (Reese et al., 2003). To exclude clear-cuts with small deciduous trees, only forest older than 30 years was analysed. The figures were adjusted for absence of data due to clouds and rivers/lakes in forested areas.

NFI provided regional landscape densities of dead wood from the period 1998–2000; estimates for six larger landscapes (see Fig. 1). Classification into decay stage in NFI is based on the proportion of the wood volume consisting of decomposed wood: 0–9% correspond to hard wood; 10–25% to slightly decayed wood; 26–75% to decayed wood; and 76–100% to well-decayed wood (for more details about NFI, see Fridman and Walheim, 2000).

Temperature and rainfall data were from the Swedish Meteorological and Hydrological Institute (SMHI). Data for each site was compiled from the two or three (depending on distance from study site) closest observation stations. Mean values were calculated for May to September (the sampling period).

2.4. Statistical analyses

To analyse species richness of beetles in relation to predictor variables, stepwise multiple linear regression in SPSS 11.5 was used. Using many predictors in multiple regression can give rise to collinearity (Pedhazur, 1997). To identify collinearity and reduce the number of variables in the regressions, Pearson correlations were computed for all pairs of variables (Table 2). Collinearity was evaluated by the correlation coefficient and $r \geq 0.75$ was considered serious collinearity. If collinearity could be explained by biological or other obvious reasons, the variable least relevant to beetles and the ecosystem was excluded. For instance in the satellite-data, oak forest (OAKF), oak forest older than 60 year (OAKF-60) and deciduous forest (DECF) were inter-correlated (Table 2), accordingly only DECF which matched the other two best, was used in the regression analyses. For dead wood in the landscape (NFI), we included deciduous wood (DWRDEC) and oak wood (DWROAK) and excluded variables that were inter-correlated with these two (Tables 1 and 2). When correlation could not be explained, both variables were used but in separate models (see variables marked in Table 1 and below). DWROAK was strongly correlated with oak dominated woodland key habitats within 1 km (WKHOD1) and therefore these two variables were analysed in separate models. Also temperature (TEMP) and amount of living oak/ha in 1795 (OAK1795) were analysed separately in the same way. After controlling variables in this way, 31 predictors remained for inclusion in the analyses (Table 1). The historical oak data (Table 2) were from Eliasson et al. (2002), divided by land area of the counties to obtain oak densities.

In the multiple regression, the stability measure (VIF or variance inflation factor) was used to further evaluate collinearity among explanatory variables (Pedhazur, 1997). The VIF-value was normally below 2.0 and never exceeded 2.4, which are considered low values and no serious collinearity (Graham, 2003).

In spatial studies, spatial autocorrelation is important to control for (Diniz et al., 2003). Between sites there was a minimum of 14 km (mean 26 km) of heterogeneous buffer zone containing mainly coniferous forest or agriculture land. Independence of the 21 sites was evaluated with Mantel's randomisation method. Matrix one contained absolute differences in species richness of saproxylic beetles between sites, and matrix two contained geographic distance between sites.

Table 1 – Environmental variables (46) used in analyses of species richness and species composition

Variable	Explanation	Variable range	Correlations (see foot-note)
<i>Stand characteristics, measured within sites (plots)</i>			
CANOPY	% of sky visible from ground	9–23	
PH	pH from soil samples	4.4–6.9	
BA	Basal area of living trees (m ² /ha)	13–36	
BAOAK	Basal area of living oak trees (m ² /ha)	6–26	
BASPRUCE	Basal area of living spruce trees (m ² /ha)	0–15	
BABROADL	Basal area of living broadleaf trees except oak (m ² /ha)	0–17	
DWTOT	Dead wood (m ³ /ha)	13–47	
DWOAK ^a	Dead wood of oak (m ³ /ha)	3–25	DWOAKC ^a , DWOAKL DWOAKS
DWOAKC ^a	Coarse dead wood of oak (m ³ /ha; diameter >10 cm)	2–20	DWOAK ^a , DWOAKS
DWOAKL	Lying (coarse) deadwood of oak (m ³ /ha)	1–16	DWOAK ^a
DWOAKS	Standing (coarse) dead wood and attached dead wood of oak (m ³ /ha)	1–11	DWOAK ^a , DWOAKC
ASCOM	No. of wood-inhabiting ascomycete species	9–36	
BASIDIO	No. of wood-inhabiting basidiomycete species	71–135	
<i>Landscape characteristics</i>			
AGRI1 ^a	Area (ha) of fields and open land (mainly pastures) within a radius of 1 km	1–282	AGRI10, CONIF10 ^a
CONIF1	Area (ha) of coniferous forest including clearings within a radius of 1 km	0–271	CONIF10 ^a
DECID1	Area (ha) of broadleaf forest within a radius of 1 km	0–113	
AGRI10	Area (ha) of fields and open land (mainly pastures) within a radius of 10 km	2059–17,362	
CONIF10 ^a	Area (ha) of coniferous forest including clearings within a radius of 10 km	146–25,687	CONIF1, AGRI1, AGRI10
DECID10	Area (ha) of broadleaf forest within a radius of 10 km	147–2858	
WKH1 ^a	Area (ha) of WKH and reserves within a radius of 1 km	0–85	WKHOR1, WKHOR10
WKHOD1 ^b	Area (ha) of WKH and reserves of oak dominated forest within a radius of 1 km	0–33	DWROAK ^b
WKHOR1	Area (ha) of WKH and reserves containing oak within a radius of 1 km (except WKHOD1)	0–81	WKH1 ^a
WKH10	Area (ha) of WKH and reserves within a radius of 10 km	44–660	
WKHCON10	Area (ha) of WKH and reserves of coniferous forest within a radius of 10 km	0–250	
WKHMIX10	Area (ha) of WKH and reserves of mixed coniferous forest with in a radius of 10 km	0–157	
WKHDEC10	Area (ha) of WKH and reserves of broadleaf forest within a radius of 10 km	0–117	
WKHOD10	Area (ha) of WKH and reserves of oak dominated forest within a radius of 10 km	3–388	
WKHOR10	Area (ha) of WKH and reserves containing oak within a radius of 10 km (except WKHOD10)	3–330	WKH1 ^a
OAKF1 ^a	Volume (m ³) of oak forest within 1 km radius (satellite data)	960–7300	OAKF1-60 ^a DECF1, OAKF10 ^a
OAKF10 ^a	Volume (m ³) of oak forest within 10 km radius (satellite data)	12,500–286,100	OAKF10-60 ^a DECF10, OAKF1 ^a
OAKF1-60 ^a	Volume (m ³) of oak forest over 60 years of age within 1 km radius (satellite data)	80–3600	OAKF1 ^a , DECF1, OAKF10-60 ^a
OAKF10-60 ^a	Volume (m ³) of oak forest over 60 years of age within 10 km radius (satellite data)	1900–89,000	OAKF10 ^a , DECF10, OAKF1-60 ^a
DECF1	Volume (m ³) of broadleaf forest within 1 km radius (satellite data)	2300–20,400	OAKF1 ^a OAKF1-60 ^a
DECF10	Volume (m ³) of broadleaf forest within 10 km radius (satellite data)	41,100–946,000	OAKF10 ^a , OAKF10-60 ^a
<i>Regional deadwood</i>			
DWRCON ^a	Dead coniferous wood (m ³ /ha) within each region	0–4	TEMP ^b , DWRD:1 ^a DWRD:2 ^a , DWRD:3 ^a , OAK1795 ^b
DWRDEC	Dead broadleaf wood (m ³ /ha) within each region	0–2	DWRD:2 ^a DWRD:3 ^a
DWROAK ^b	Dead oak wood (m ³ /ha) within each region	0–1	WKHOD1 ^b

for oak beetle species, and for red-listed ones $p = 0.002$ and 0.001 for the two first distance classes, 33, respectively, 66 km). Spatial autocorrelation (Moran's I) on remaining residuals was also checked for after the regressions and no significant results for oak species richness were found. For red-listed species, we found a significant negative spatial autocorrelation in the first class (within 33 km radius).

Normality for species richness versus predictors was evaluated with plots in SPSS and indicated approximately normal distributions and acceptable distribution of residuals for all except seven variables that were log transformed to fit the regression models. Due to problems of multiple testing in stepwise regression (Pedhazur, 1997), which is not corrected for in SPSS models, we considered that p -values just below 0.05 could be due to chance. Regressions were run with default entry/removal level ($p = 0.05/0.1$). In the regression analyses (see below), there was a strong influence of a few explanatory variables from single landscape levels. For comparison with a traditional approach of using only stand level variables as predictors, it was asked which, if any, stand variables would be selected if the landscape variables were removed (topography and climate included).

Species composition among sites was analysed with PCA (principal component analysis) in PC-ORD version 4 (McCune and Mefford, 1999). All species data were transformed to binary occurrence, i.e. presence-absence of species. DCA (detrended correspondence analysis) was used before this analysis to evaluate the gradient length and the results (gradient length < 2.1 for all axes) indicated that the linear model of PCA was appropriate (see, e.g. ter Braak and Smilauer, 2002). Scaling was focused on inter-site distances. Stepwise multiple regression with the first and second PCA-axis as dependent variables, and our set of predictors was used to identify environmental variables related to variation in species composition (PCA ordination axes). Axis values were normally distributed; with no or little skew in residual distributions. A comparison between two separate ordination methods, PCA and NMDS (nonmetric multidimensional scaling (McCune and Mefford, 1999)) showed in this case high similarity between the axes of the ordination techniques. Rotation of the NMDS ordination to obtain best correlation with PCA was performed in the program R. Both the first and second axes of the ordinations were positively correlated (first axes $r_s = 0.54$, $p = 0.01$, $n = 21$; second axes $r_s = 0.58$, $p < 0.01$, $n = 21$). Below PCA was used, as its first axis summarizes most of the variation in the ordination, whilst NMDS gives equal weight to all axes.

3. Results

3.1. Species samples

At the 21 sites 30,690 beetle individuals distributed among 730 species were collected. Of these, 239 species (16,518 individuals) were saproxylics connected to oak (*Q. robur/petraea*), and of these 190 species (15,335 individuals) were obligate oak saproxylics. Forty-one species (436 individuals) were Swedish red-listed species according to Gärdenfors (2000) and 19 species and 35 individuals by the Redlist of 2005 (Gärdenfors, 2005). Another 136 species (3346 individuals) were saproxylic,

but not connected to oak (among these and the other non-saproxylic species in the data, there might be saproxylics connected to oak, but where knowledge is missing). The number of saproxylic species connected to oak varied between 43 and 111 per site (mean = 67, SD = 16, $n = 21$ sites) and for obligate species corresponding figures were 29–88 (mean = 53, SD = 14, $n = 21$ sites). The number of red-listed oak species (Gärdenfors, 2000, 2005) varied from 0 to 19 (mean = 5.6, SD = 4.7, $n = 21$, 2000), and 0 to 8 (mean = 1.7, SD = 2.1, $n = 21$, 2005). The number of red-listed oak species (2000) was strongly correlated with total number of oak species ($r_s = 0.75$, $p < 0.001$, $n = 21$). Martikainen and Kouki (2003), who compiled beetle studies from boreal forests (where oak did not occur), reported similar results. These studies used various techniques and substrates (but mainly window traps).

3.2. Factors predicting species richness

In the stepwise multiple regression, oak dominated WKH within 1 km radius (WKHOD1) accounted for much of the variation ($R^2 = 55\%$) in species richness of saproxylic oak beetles (Table 3) and was the only predictor selected in the model. Using only obligate saproxylic oak-species strengthened the results, giving $R^2 = 62\%$. The strong positive relationship between oak beetle species richness and WKHOD1 is shown in Fig. 3a. For red-listed oak species, WKHOD1 also accounted for much of the variation (Redlist of 2000; 64%, and Redlist 2005; 45%) and again was the only variable in the stepwise model (Table 3, Fig. 3b).

When WKHOD1 was exchanged with regional density of dead oak wood (DWROAK), it became the significant predictor for both oak and red-listed oak beetles, with comparable predictive power (Table 3, Fig. 3c,d). For oak species (both obligate and all saproxylics), a second predictor in the model, local basal area of broadleaves other than oaks (BABROADL), had a negative relation to species richness (Table 3), and for red-listed species, volume of broadleaf forest within 1 km radius (DECF1) had a negative relation to species richness.

When only local site variables were included in the regression, oak beetle species richness was primarily predicted by species richness of wood-inhabiting basidiomycetes (BASIDIO; positive correlation) and in addition height over sea (ELEVAT) and BABROADL (both negative correlation, Table 4). Obligate oak species richness was predicted by ELEVAT (negatively), BASIDIO (positively), and BABROADL (negatively). Red listed oak species 2000 were predicted by ELEVAT (negatively) and red listed 2005 by ELEVAT (negatively), ASCOM (negatively) and TEMP (positively, Table 4).

3.3. Factors predicting species composition

The PCA analysis of species composition (all oak species) tended to separate the sites in one group of seven eastern sites (with one outlier), and one for remaining sites (Fig. 4). The first and the second axis of the PCA explained 22% (13% and 8.8, respectively) of the total variation in the ordination. Axis 1 was positively related to species richness ($r_s = 0.74$, $p < 0.01$, $n = 21$), and species richness of red-listed beetles ($r_s = 0.76$, $p < 0.001$, $n = 21$). The multiple regression of the scores of PCA axis 1 (dependent variable) versus environmen-

Table 3 – Stepwise multiple regression in SPSS between the dependent variables (a) total number of saproxylic oak beetles, (b) number of obligate saproxylic oak beetles, (c) number of redlisted oak beetles (2000), (d) redlisted (2005), and environmental variables (Table 1)

Dependent	Predictors ^b	Unstandardized coefficient	SE	t	p	R ² , adjusted
<i>WKHOD1 included, DWROAK excluded</i>						
(a) Species on oak	CONSTANT	58.57	2.92			
	(1) WKHOD1	1.21	0.24	5.00	<0.001	0.55
(b) Obligate oak species	CONSTANT	45.04	2.42			
	(1) WKHOD1	1.16	0.20	5.77	<0.001	0.62
(c) Redlisted on oak 2000	CONSTANT	2.56	0.81			
	(1) WKHOD1	0.40	0.07	6.02	0.001	0.64
(d) Redlisted on oak 2005	CONSTANT	0.66	0.42			
	(1) WKHOD1	0.15	0.04	4.20	<0.001	0.45
<i>DWROAK included, WKHOD1 excluded</i>						
(a) Species on oak	CONSTANT	67.90	5.45			
	(1) DWROAK	36.11	6.95	5.20	<0.001	0.53
	(2) BABROADL	–1.29	0.49	–2.62	0.017	0.61
(b) Obligate oak species	CONSTANT	52.86	4.18			
	(1) DWROAK	35.72	5.32	6.71	<0.001	0.64
	(2) BABROADL	–0.86	0.35	–2.44	0.025	0.72
(c) Redlisted on oak 2000	CONSTANT	26.11	10.81			
	(1) DWROAK	10.92	2.04	5.36	<0.001	0.60
	(2) DECF1	–6.01	2.73	–2.20	0.041	0.67
(d) Redlisted on oak 2005	CONSTANT	2.13	0.82			
	(1) DWROAK	3.87	1.04	3.71	0.002	0.44
	(2) DECF1	–0.01	0.00	–2.18	0.043	0.53

a Entry and removal levels, 0.05 and 0.1, respectively.
b See Table 1 for information on variables.

tal variables (Table 5) showed that the first axis was best predicted by WKHOD1, and in separate model by DWROAK. The second axis was best accounted for by the site variable CANOPY (canopy cover) and in addition WKHCON10 and DECF10 (coniferous and deciduous components). However, the regression coefficient (Table 5) indicated that only CANOPY was influential.

4. Discussion

This study indicates that neither large scale factors in biogeography (e.g. climate and altitude), nor local (stand) factors are the major determinants of species richness of saproxylic oak beetles. Instead, qualities in the surrounding landscape seem to be more important for the local species richness of saproxylic beetles. High species richness of beetles was related to high nature conservation values (woodland key habitats) in the forest in the surrounding landscape, and also to density of dead oak wood in the large surrounding landscape (Fig. 1).

4.1. Species richness

Species richness of oak beetles and red-listed oak beetles in the study area increased from west to east (Fig. 5, for similar results see Dahlberg and Stokland, 2004). If the easternmost coastal sites are excluded there is no visible increase (Fig. 5).

One possible explanation for the west-east increase in species richness is less precipitation, more sunshine, and higher temperature in the east, which may be favourable for larval development in species limited by climate (Palm, 1959). Even though a role of climate cannot be excluded (and certainly not for heat and sun preferring species) climatic variables were not important in the regression models. Instead the landscape variable oak-dominated woodland key habitats (WKHOD1) accounted for much of the variation in species richness. Oak-dominated WKH contains more dead wood of oak than other forests (~6.6 m³/ha in our study plots (Nordén et al., 2004a) compared to a landscape mean of 0–0.8 m³/ha in NFI surveys). We suggest two not mutually exclusive reasons for our results. First, more oak-dominated key habitats in the landscape should lead to higher population sizes of vulnerable beetle species, reducing the risk of local extinction. Certain beetle species may not be able to colonize more isolated forests.

Second, more oak key habitats in the surroundings should imply a larger amount and diversity of oak substrates, and therefore higher species richness of beetles associated with such habitats. The high mobility of some saproxylic beetles may partly explain the strong influence of the surrounding landscape on the local species richness. Dead oak wood in the large landscape (DWROAK) was also a strong predictor of local species richness of beetles. The reasons given above for the importance of WKHOD1 are also relevant for DWROAK.

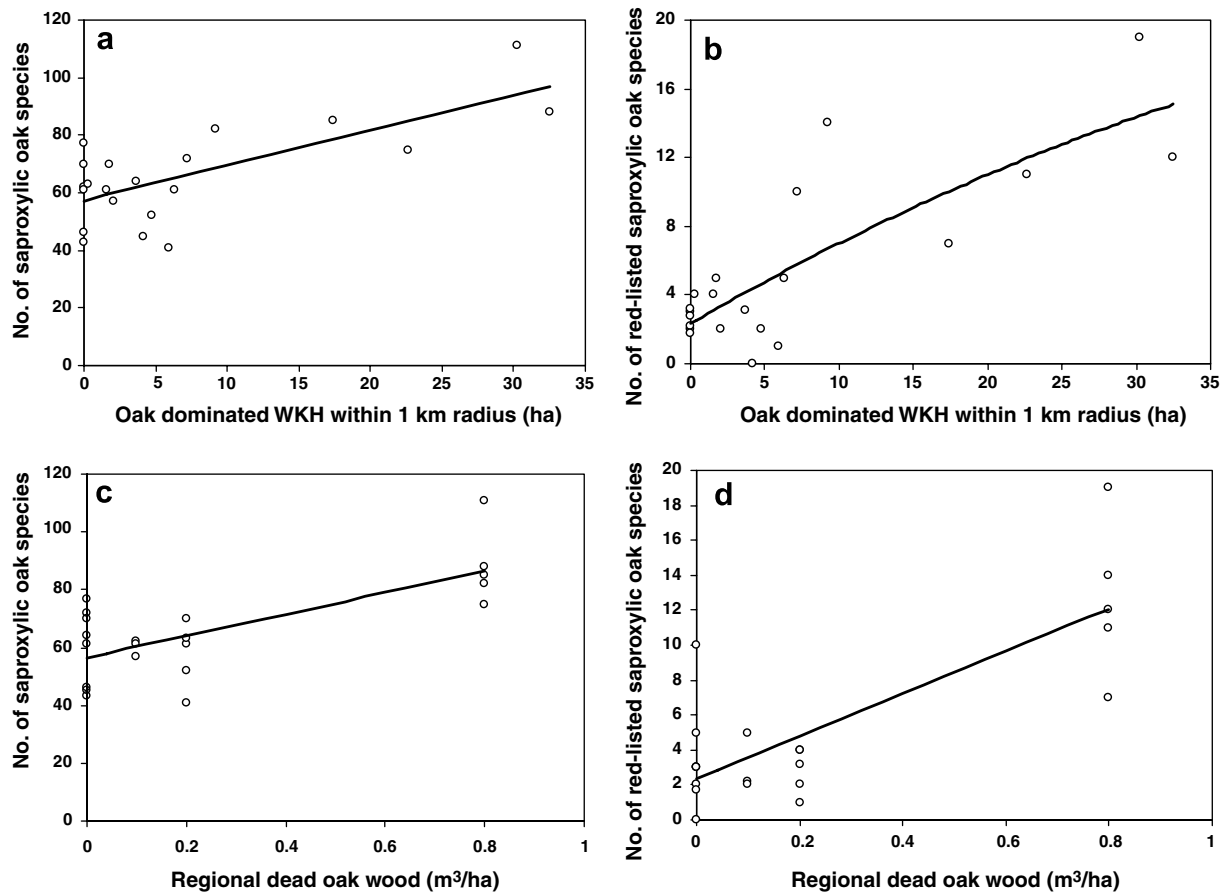


Fig. 3 – Relationship between WKHOD1 (woodland key habitat of oak dominated forest within 1 km radius of sites) and (a) number of saproxylic beetle species connected to oak, (b) number of red-listed (2000) saproxylic beetle species connected to oak, and relationship between DWROAK (regional dead wood of oak) and (c) number of saproxylic beetle species connected to oak, and (d) number of red-listed (2000) saproxylic beetle species connected to oak.

Table 4 – Stepwise multiple regression in SPSS between the local site environmental variables and the dependent variables: (a) total number of saproxylic oak beetles, (b) number of obligate saproxylic oak beetles, (c) number of red-listed oak beetles (2000), and (d) red-listed 2005, with entry and removal levels 0.05 and 0.1

Dependent	Predictors ^a	Unstandardized coefficient	SE	t	p	R ² , adjusted
(a) Species on oak	CONSTANT	44.48	16.87			
	(1) BASIDIO	0.45	0.14	3.12	0.006	0.28
	(2) ELEVAT	-0.10	0.03	-3.14	0.006	0.46
	(3) BABROADL	-1.06	0.49	-2.15	0.047	0.55
(b) Obligate oak species	CONSTANT	34.58	14.59			
	(1) ELEVAT	-0.10	0.03	-3.59	0.020	0.27
	(2) BASIDIO	0.40	0.12	3.19	0.050	0.50
	(3) BABROADL	-0.95	0.43	-2.22	0.040	0.59
(c) Redlisted on oak 2000	CONSTANT	10.71	1.52			
	(1) ELEVAT	-0.05	0.01	-4.09	0.001	0.44
(d) Redlisted on oak 2005	CONSTANT	-26.42	12.66			
	(1) ELEVAT	-0.02	0.01	-3.38	0.004	0.34
	(2) ASCOM	-0.23	0.05	-4.50	<0.001	0.56
	(3) TEMP	2.49	0.92	2.69	0.015	0.68

a See Table 1 for information.

The two variables were strongly correlated and might depend on the same process of agricultural landscape change from 1850 onwards.

The woodland key habitats are relatively old forest patches, rich in structures such as older trees and dead wood. They indicate continuity of dead wood, also in the landscape

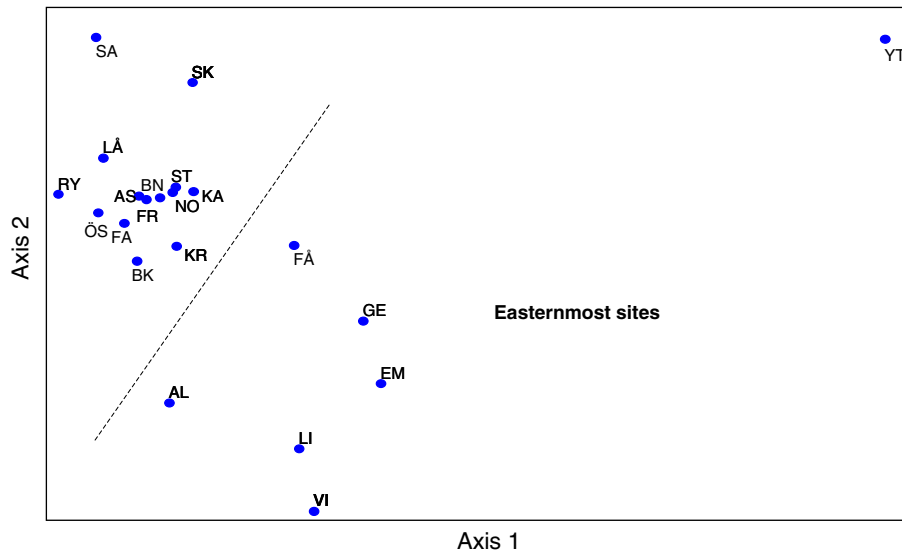


Fig. 4 – PCA ordination analysis (first two axis) of oak beetles at the 21 sites. For name and location of sites, see Fig. 1. The easternmost sites tend to be separated from the others and a tendency for clumping among the western sites can also be seen. SK and YT were collected 2002 and all others 2001, see Section 2 for more information.

Table 5 – Multiple regression for beetle species composition (PCA) and environmental variables (Table 1)

Dependent	Predictors	Coefficient	SE	t	p	R ² , adjusted
<i>WKHOD1 included, DWROAK excluded</i>						
PCA axis 1	CONSTANT	-3.12	0.97			
	(1) WKHOD1	0.44	0.08	5.43	<0.001	0.59
PCA axis 2	CONSTANT	-19.97	2.55			
	(1) CANOPY	1.09	0.15	7.26	<0.001	0.51
	(2) WKHCON10	0.03	0.01	3.81	0.001	0.68
	(3) DECF10	<0.01	<0.01	2.57	0.020	0.76
<i>DWROAK included, WKHOD1 excluded</i>						
PCA axis 1	CONSTANT	-3.12	0.97			
	(1) DWROAK	12.02	2.85	4.22	<0.001	0.46
PCA axis 2 ^a						

a Identical results as PCA axis 2 above.

if there is high coverage of WKH. The predictive power of WKHOD1 suggests that earlier distribution of habitats may be important for species richness today, supporting theories regarding continuity of substrates (Nilsson and Baranowski, 1997) and connectivity of habitat patches (Lindborg and Eriksson, 2004).

This study and those of Siitonen (1994) and Økland et al. (1996) indicate that local site variables (amounts of dead wood) have weak relationships with species richness of saproxylic beetles. One possible reason is the dispersal capacity of the beetles, allowing them to visit substrates over larger area than the local stand. Our measure of dead wood at the sites, although based on fairly large sampling in about 2 ha (Nordén et al., 2004a), may not reflect dead wood at a scale that is relevant to beetles, whereas WKHOD1 likely reflects deadwood at such scale. However, our model including only local variables suggested a relationship between beetles and fungi, which was expected and deserves more study.

Our findings of likely landscape impact on species richness of saproxylic beetles (and on red-listed ones) are consistent with three earlier studies: Økland et al. (1996), who found strong relationship between species richness of saproxylic beetles in boreal forest and ecological variables at 1 and 4 km²; Kehler and Bondrup-Nielsen (1999) who found effect of spatial isolation (25–2000 m between woodlots) on incidence of the beetle species *Bolitotherus cornutus*; and Rukke and Midtgaard (1998) who found increased chance of the presence of the beetle species *Bolitophagus reticulatus* on larger habitat islands, size 8000–20,000 m². These studies found impact on the largest landscape level studied, but presented results relevant only to a maximum of 2 km radius and not for the larger landscape scales analysed here (10 km radius and regional landscape). Spatial limitations of size or distance are common in most studies. Our study also indicates impact of large landscapes (for dead wood; Fig. 1), and even though we cannot specify upper limits of this landscape, its potential importance should be considered in landscape studies.

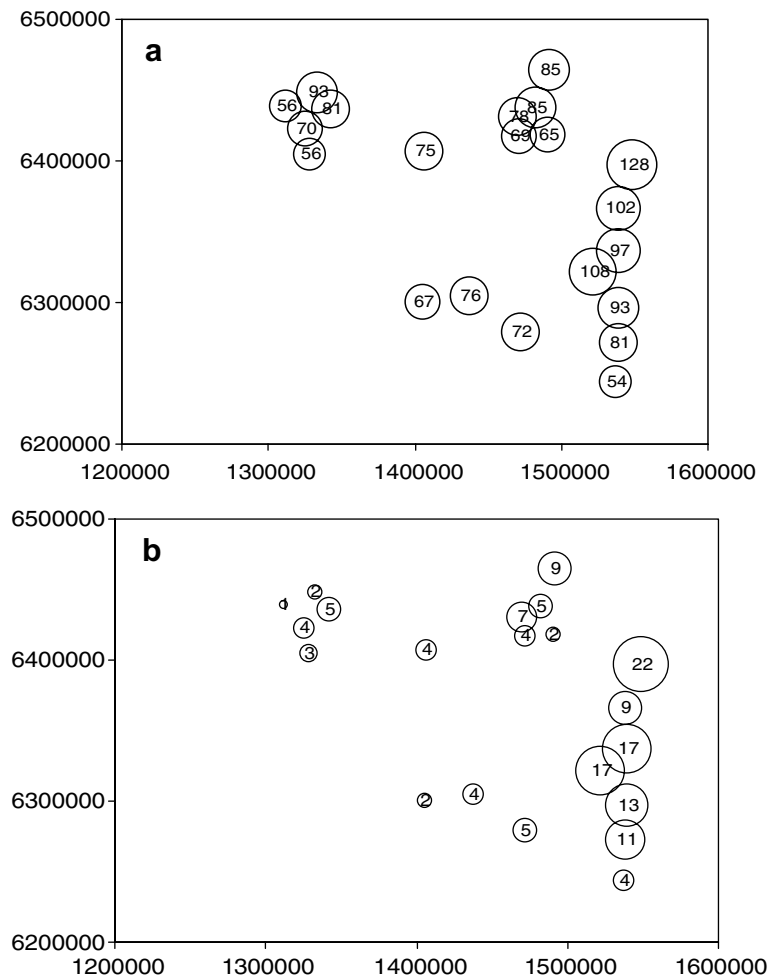


Fig. 5 – Species richness of: (a) saproxylic and (b) red-listed (2000) saproxylic oak beetles increasing at the sites from west to the east. The area of circles is proportional to species richness, and number of species is given in circles. For sites, see Fig. 1. Y- and x-axes correspond to the Swedish Grid (system of co-ordinates).

In 2002 a study on fungi and deadwood dependent mycetophilids (Sciarioidea) was carried out at 15 of our forest sites (Økland et al., 2005). The mycetophilids increased in species richness towards northwest, i.e. almost the opposite pattern to the saproxylic beetles. In the regression model, precipitation had a strong positive influence on the mycetophilids (Økland et al., 2005), compared to WKHOD1 in this study. This suggests that results for saproxylic beetles cannot be generalized to other forest dwelling insects that depend upon dead wood and fungi, at least not without further studies.

We studied an environment in transition, changing from open or semi-opened to essentially closed canopy forest. We expected to find some sun-preferring species, but found few (compared to, e.g. Ranius and Jansson, 2000). This result indicates a passed or almost passed state of extinction debt, rather than an active state (see Hanski and Ovaskainen, 2002). This is also suggested by the lack of predictive power of the historical variables OAK1795 and OAK1825 in the models.

4.2. Species composition

In terms of species composition, the southeastern sites were separated from the remaining sites in the ordination.

WKHOD1, and DWROAK separately, were the best predictors of observed variation in the ordination (first axis of PCA). Increased population sizes (lower extinction risk) and increased diversity of substrates for oak beetles probably comes with increasing area of WKHOD1, and these factors likely explain at least part of the result. The high species richness in the east implies a larger community that contributes to larger compositional variation, reflected in the ordination (Fig. 4). The second axis of the ordination was best predicted by canopy closure, which is related to sun exposure of substrates. Species richness of saproxylic beetles overall and of red-listed species seems to be favoured by sun exposure (Jonsell et al., 1998; Lindhe and Lindelöw, 2004). Also abundance of many oak connected beetle species seems to increase with increased sun exposure of substrate (Ranius and Jansson, 2000). The ordination (first two axes) only explained 22% of the variation in species composition, implying that other factors or different distribution ranges can be of significant importance.

4.3. Implications for conservation work

In this study, many potentially important factors were examined and the result is clear: amount of oak dominated key

habitat and dead wood of oak in the landscape strongly predict oak beetle species richness at the stand (local) level. It seems that forest patches identified by the national survey of WKHs are of high conservation value, and that their importance increases with increasing patch density at landscape level. The current Swedish forest reserve strategy (Naturvårdsverket, 2005) focuses on larger valuable forest tracts and core areas, which is supported by our results. Within 1 km of stands, oak WKHs were a small fraction of the landscape (0–10%). The patches of oak WKHs were also small (mean 2.5 ha, range 0.02–28 ha, $n = 847$), but clusters of such WKHs, and high amounts of dead wood in the larger landscape, should be in focus in conservation work for saproxylic beetles, including red-listed ones. Many forest areas in northern Europe probably have too low density or area of woodland key habitats and will not provide for long-term protection of many saproxylic beetles. Therefore, restoration work at the landscape level should be important.

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REFERENCES

- Ahti, T., Hämet-Ahti, L., Jalas, J., 1968. Vegetation zones and their sections in northwestern Europe. *Annales Botanici Fennici* 5, 169–211.
- Andersson, M., 2002. *Detaljtypskatalog – Mark och vegetation*. Lantmäteriet, Gävle, Sweden.
- Bouget, C., Duelli, P., 2004. The effects of windthrow on forest insect communities: a literature review. *Biological Conservation* 118, 281–299.
- Casgrain, P., Legendre, P., 2001. *The R Package for Multivariate and Spatial Analysis, version 4.0 d9 User's Manual*. Département de sciences biologiques, Université de Montréal, Montreal. Available from: <<http://www.fast.umontreal.ca/BIOL/legendre/>>.
- Christensen, M., Hahn, K., Mountford, E., Ódor, P., Standovár, T., Rozenbergar, D., Diaci, J., Wijdeven, S., Meyer, P., Winter, S., Vrska, T., 2005. Dead wood in European beech forest reserves. *Forest Ecology and Management* 210, 267–282.
- Cox, C.B., Moore, P., 1999. *Biogeography: An Ecological and Evolutionary Approach*, sixth ed. Division of Life Sciences, King's College, London.
- Dahlberg, A., Stokland, J.N., 2004. Vedlevande arters krav på substrat. 7, Skogsstyrelsen, Rapport No. 7, Jönköping, Sweden. (in Swedish).
- Diniz, J., Bini, L., Hawkins, B., 2003. Spatial autocorrelation and red herrings in geographical ecology. *Global Ecology and Biogeography* 12, 53–64.
- Eliasson, P., 2002. *Forest, power and people. An environmental history of the Swedish forest 1800–1875*. Monograph. Lund University, Lund (in Swedish).
- Forman, R.T.T., 1999. *Land Mosaics – The Ecology of Landscapes and Regions*. Cambridge University Press, Cambridge.
- Fridman, J., Walheim, M., 2000. Amount, structure and dynamics of dead wood on managed forestland in Sweden. *Forest Ecology and Management* 131, 23–26.
- Gärdenfors, U. (Ed.), 2000. *Rödlistade arter i Sverige*. Artdatabanken, SLU, Uppsala.
- Gärdenfors, U. (Ed.), 2005. *Rödlistade arter i Sverige 2005 (The red list of Swedish species)*. Artdatabanken, SLU, Uppsala.
- Gaston, K.J., Blackburn, T.M., 2000. *Pattern and Process in Macroecology*. Blackwell Science Ltd., Oxford.
- Gaston, K.J., 2000. Global patterns in biodiversity. *Nature* 405, 220–227.
- Gilbertson, R.L., 1984. Relationships between insects and wood-rotting basidiomycetes. In: Wheeler, Q. (Ed.), *Fungus–insect Relationships*. Columbia University Press, Guildford, Surrey, New York.
- Götmark, F., Thorell, M., 2003. Size of nature reserves: densities of large trees and dead wood indicate high value of small conservation forests in southern Sweden. *Biodiversity and Conservation* 12, 1271–1285.
- Gripenberg, S., Roslin, T., 2005. Host plants as islands: resource quality and spatial setting as determinants of insect distribution. *Annales Zoologici Fennici* 42, 335–345.
- Graham, M.H., 2003. Confronting multicollinearity in ecological multiple regression. *Ecology* 84, 2809–2815.
- Gustafsson, L., 2002. Presence and abundance of red-listed plant species in Swedish forests. *Conservation Biology* 16, 377–388.
- Hanski, I., Ovaskainen, O., 2002. Extinction debt at extinction threshold. *Conservation Biology* 16, 666–673.
- Jonsell, M., Nordlander, G., 2002. Insects in polypore fungi as indicator species: a comparison between forest sites differing in amounts and continuity of dead wood. *Forest Ecology and Management* 157, 101–118.
- Jonsell, M., Weslien, J., Ehnström, B., 1998. Substrate requirements of red-listed saproxylic invertebrates in Sweden. *Biodiversity and Conservation* 7, 749–764.
- Kehler, D., Bondrup-Nielsen, S., 1999. Effects of isolation on the occurrence of a fungivorous forest beetle, *Bolitotherus cornutus*, at different spatial scales in fragmented and continuous forests. *Oikos* 84, 35–43.
- Kruess, A., 2003. Effects of landscape structure and habitat type on a plant–herbivore–parasitoid community. *Ecography* 26, 283–290.
- Lindborg, R., Eriksson, O., 2004. Historical landscape connectivity affects present plant species diversity. *Ecology* 85, 1840–1845.
- Lindhe, A., Lindelöw, Å., 2004. Cut high stumps of spruce, birch, aspen and oak as breeding substrates for saproxylic beetles. *Forest Ecology and Management* 203, 1–20.
- Lundberg, S., 1995. *Catalogous Coleopterorum Sueciae*. Naturhistoriska riksmuseet & Entomologiska föreningen i Stockholm, Stockholm.
- Martikainen, P., Kouki, J., 2003. Sampling the rarest: threatened beetles in boreal forest biodiversity inventories. *Biodiversity and Conservation* 12, 1815–1831.

- McCune, B., Mefford, M.J., 1999. PC-ORD. Multivariate analysis of ecological data. In: MjM Software, Gleneden Beach, Oregon.
- Meffe, G.K., Carroll, C.R., 1997. Principles of Conservation Biology, second ed. Sinauer Associates, Inc. Publishers, Sunderland, Massachusetts.
- Naturvårdsverket, Skogsstyrelsen. 2005. National Strategy of Formal Forest Protection. NV dnr 310-419-04, SKS dnr 194/04 4.43 (in Swedish).
- Nilsson, S.G., Baranowski, R., 1997. Habitat predictability and the occurrence of wood beetles in old-growth beech forests. *Ecography* 20, 491–498.
- Nilsson, S.G., Hedin, J., Niklasson, M., 2001. Biodiversity and its assessment in boreal and nemoral forests. *Scandinavian Journal of Forest Research Supplement* 3, 10–26.
- Nilsson, S.G., Niklasson, M., Hedin, J., Aronsson, G., Gutowski, J.M., Linder, P., Ljungberg, H., Mikusinski, G., Ranius, T., 2002. Densities of large living and dead trees in old-growth temperate and boreal forests. *Forest Ecology and Management* 161, 189–204.
- Nitare, J., 2000. Signalarter. Skogsstyrelsen, Jönköping (in Swedish).
- Nordén, B., Götmark, F., Tönnerberg, M., Ryberg, M., 2004a. Dead wood in semi-natural temperate broadleaved woodland: contribution of coarse and fine dead wood, attached dead wood and stumps. *Forest Ecology and Management* 194, 235–248.
- Nordén, B., Ryberg, M., Götmark, F., Olausson, B., 2004b. Relative importance of coarse and fine woody debris for the diversity of wood-inhabiting fungi in temperate broadleaf forests. *Biological Conservation* 117, 1–10.
- Økland, B., 1996. Unlogged forests: important sites for preserving the diversity of mycetophilids (Diptera: Sciarioidea). *Biological Conservation* 76, 297–310.
- Økland, B., Bakke, A., Hagvar, S., Kvamme, T., 1996. What factors influence the diversity of saproxylic beetles? A multiscaled study from a spruce forest in southern Norway. *Biodiversity and Conservation* 5, 75–100.
- Økland, B., Götmark, F., Nordén, B., Franc, N., Kurina, O., Polevoi, A., 2005. Regional diversity of mycetophilids (Diptera: Sciarioidea) in Scandinavian oak-dominated forests. *Biological Conservation* 121, 9–20.
- Palm, T., 1959. Die Holz- und Rindenkäfer der Sud- und Mittelschwedischen Laubbäume. *Opusc. Entomol. Suppl.* 16, 1–374.
- Pedhazur, E.P., 1997. Multiple Regression in Behavioral Research, third ed. Christopher P. Klein, Fort Worth, Texas.
- Peltonen, M., Heliövaara, K., Väisänen, R., Keronen, J., 1998. Bark beetle diversity at different spatial scales. *Ecography* 21, 510–517.
- Ranius, T., 2002. Influence of stand size and quality of tree hollows on saproxylic beetles in Sweden. *Biological Conservation* 103, 85–91.
- Ranius, T., Jansson, N., 2000. The influence of forest regrowth, original canopy cover and tree size on saproxylic beetles associated with old oaks. *Biological Conservation* 95, 85–94.
- Reese, H., Nilsson, M., Granqvist-Pahlén, T., 2003. Countrywide estimates of forest variables using satellite data and field data from the National Forest Inventory. *Ambio* 32, 542–548.
- Rosenzweig, M.L., 1995. Species Diversity in Space and Time. Cambridge University Press, Cambridge.
- Rukke, B.A., Midtgaard, F., 1998. The importance of scale and spatial variables for the fungivorous beetle *Bolitophagus reticulatus* (Coleoptera, Tenebrionidae) in a fragmented forest landscape. *Ecography* 21, 561–572.
- Saab, V., 1999. Importance of spatial scale to habitat use by breeding birds in riparian forests: a hierarchical analysis. *Ecological Applications* 9, 135–151.
- Samuelsson, J., Gustafsson, I., Ingelög, T., 1994. Dying and Dead Trees – A Review of their Importance for Biodiversity. Swedish Threatened Species Unit, Uppsala.
- Schiegg, K., 2000. Effects of dead wood volume and connectivity on saproxylic insect species diversity. *Ecoscience* 7, 290–298.
- Siitonen, J., 1994. Decaying wood and saproxylic coleoptera in 2 old spruce forests – a comparison based on 2 sampling methods. *Annales Zoologici Fennici* 31, 89–95.
- Siitonen, J., Martikainen, P., 1994. Occurrence of rare and threatened insects living on decaying *Populus tremula* – a comparison between Finnish and Russian Karelia. *Scandinavian Journal of Forest Research* 9, 185–191.
- Siitonen, J., 2001. Forest management, coarse woody debris and saproxylic organisms. Fennoscandian boreal forests as an example. *Ecological Bulletins* 49, 11–41.
- Similä, M., Kouki, K., Martikainen, P., 2003. Saproxylic beetles in managed and seminatural Scots pine forests: quality of dead wood matters. *Forest Ecology and Management* 174, 365–381.
- Söderström, B., Svensson, B., Vessby, K., Glimskär, A., 2001. Plants, insects and birds in semi-natural pastures in relation to local habitat and landscape factors. *Biodiversity and Conservation* 10, 1839–1863.
- Speight, M.C.D., 1989. Saproxylic Invertebrates and their Conservation. Council of Europe, Publications and Documents Division, Strasbourg.
- Stevens, G.C., 1989. The latitudinal gradient in geographical range: how so many species co-exist in the tropics. *American Naturalist* 133, 240–256.
- Sverdrup-Thygeson, A., 2001. Can 'continuity indicator species' predict species richness or red-listed species of saproxylic beetles? *Biodiversity and Conservation* 10, 815–832.
- ter Braak, C.J.F., Smilenaer, P., 2002. CANOCO Reference Manual and CanoDraw User's Guide: Software for Canonical Community Ordination (Version 4.5). In: Microcomputer Power. Ithaca, NY.
- Weibull, A.C., Östman, O., Granqvist, A., 2003. Species richness in agroecosystems: the effect of landscape, habitat and farm management. *Biodiversity and Conservation* 12, 1335–1355.
- Wright, D.H., 1983. Species-energy theory: an extension of species-area theory. *Oikos* 41, 496–506.