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Modelling habitat and spatial distribution of an endangered longhorn beetle – A case study for saproxylic insect conservation

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ABSTRACT

Saproxylic insects are characterised by their exceptional diversity and high proportion of threatened species. No recent studies have demonstrated the validity of habitat suitability analysis for scientifically based habitat management for these species. We studied the habitat requirements of the endangered longhorn beetle *Cerambyx cerdo*, a species with a supposed keystone function for the saproxylic insect community living on oaks. We used species distribution modelling based on datasets from Central Europe to understand the species–habitat relationships and to find the environmental variables responsible for habitat selection of *C. cerdo*. Our results show that the most important parameters, insolation, presence of oak sap, bark depth and the distance from the next colonised tree, are able to predict the presence of *C. cerdo* very well. A spatial validation procedure revealed very similar predictive power, indicating the general validity of our model. Tree-level parameters were shown to have a stronger effect on the occurrence probability than landscape-level predictors. To improve the tree-level conditions (e.g. insolation on the trunk) habitat management in the form of semi-open pasture landscapes is recommended from which many other taxa will also draw considerable benefit. The provision of such conditions over decades is the essential key in the conservation of this longhorn beetle species. The success of the European network of conservation areas "Natura 2000" heavily depends on broad biological knowledge of the designated protected species. The present paper shows that species distribution models can give valuable contributions for conservation in saproxylic insects.

1. Introduction

Habitat models for species of conservation interest are of key importance and value in landscape planning and reserve development (Fleishman et al., 2002). Despite the large number of threatened species of wood-dependent insects there is no recent verification whether an habitat suitability analysis is useful for a scientific based habitat management in these species. We chose the longhorn beetle *Cerambyx cerdo* L. (Coleoptera, Cerambycidae) for this study on saproxylic insects because of its vulnerability and because there is considerable interest in conserving the remaining populations of this

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beetle throughout Europe. Saproxylic insects are defined by Speight (1989) as invertebrates 'that are dependent, during some part of their life cycle, upon the dead or dying wood of moribund or dead trees or upon wood-inhabiting fungi, or upon the presence of other saproxylics'.

This longhorn beetle is one of the protected species explicitly named in the Habitats Directive with the goal of maintaining existing populations and establishing long-term survival (Council of the European Communities, 1992). Furthermore, the species is receiving worldwide attention through the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES).

Many saproxylic species are affected by modern forestry and the shortage of old trees in our landscape today (Ranius and Jansson, 2000; Lindhe and Lindelöw, 2004) with the result that more than 60% of saproxylic beetle species in Central Europe are currently threatened by extinction (Geiser, 1998). Surprisingly, detailed studies have been conducted on the habitat requirements of only a few saproxylic beetles (e.g. Ranius and Nilsson, 1997 for *Osmoderma eremita*; Kolb et al., 2006 for *Ips pini*).

Previous studies revealed that species distribution models can make a significant contribution to the conservation of different taxa: such as for birds (Manel et al., 1999), ground beetles (Bonn and Schröder, 2001; Matern et al., 2007) and butterflies (Binzenhöfer et al., 2005). Quantitative assessment of the contribution of the three components patch area, isolation and habitat quality to patch occupancy in insects has demonstrated the key importance of the factor habitat conditions (e.g. Dennis and Eales, 1997; Gutiérrez et al., 1999; Thomas et al., 2001; Heikkinen et al., 2005). Statistical habitat models provide a method to combine terms of isolation and patch area with simple habitat parameters into a complex model (Kuhn and Kleyer, 1999; Guisan and Thuiller, 2005). Taking into consideration that one major group which determines insect diversity in Central Europe belongs to saproxylic insects, we test this approach on a wood-dwelling species as a case study.

Over the past 100 years there has been a sharp decline in the number of populations and in population sizes of *Cerambyx cerdo* (Klausnitzer et al., 2003). Changes in landscape structure as a result of altered agricultural and forest management practices have led to a decline in potential suitable habitats for this longhorn beetle species. This monophagous beetle in Central Europe only occurs on oaks which fulfil its specialised habitat requirements. Recent threats are a decrease in the number of old oak trees and oak dominated semi-open landscapes in general. The species was once widespread throughout Northern Africa and Europe wherever oaks grow, with the exception of Great Britain (Bílý and Mehl, 1989). A recent survey of its distribution in Europe exhibits last viable populations in France, Germany, Poland and the Mediterranean region (Luce, 1997). The surveyed populations in Germany are among the last known populations in northern Central Europe. In order to create management plans and develop protected areas it is necessary to make a close analysis of the species habitat requirements.

The aim of our paper is to test whether a habitat suitability model, considering patch area, isolation and habitat quality, can also be derived for saproxylic insects. With the help of spatial validation and conservation suggestions from our results we intend to extrapolate a nature conservation strategy with which to conserve the species rich community associated with *C. cerdo*.

2. Materials and methods

2.1. Species

With a body length of up to 55 mm, *C. cerdo* is one of the largest longhorn beetles living in Europe. Larval development takes 3–5 years in oak trunks – in Central Europe mainly *Quercus robur* (Bílý and Mehl, 1989; Luce, 1997). The adult stages can be found on colonised trees from the end of May until the beginning of August. Emergence is not synchronised to specific years. Colonised trees can be identified by visible holes made by the larvae on the trunk or thick branches (Müller, 2001). These holes can persist over many years or even decades. Typical signs of recent activity are wood meal and fresh holes with red-coloured interior sides. Trees with many dead wood in the canopy, which is a result of larval feedings, are often colonised by *C. cerdo*.

2.2. Study areas

The study area was located in the 'Gartower Elbmarsch' (53°1′N, 11°27′E) where the last population of this species in Lower Saxony is to be found. This area covers approximately 105 km^2 and is strongly influenced by the Elbe river. The 'Gartower Elbmarsch' is an ancient cultural landscape with large areas widely covered by pastures interspersed with groups of trees and small woodlands. Most trees on which *C. cerdo* occurs are located in a narrow strip of pasture between the dike and the river. Another important location is a three kilometre long avenue with a mixture of oak trees of different ages on both sides.

The second study area primarily used for external validation in our test of model transferability in space is located about 150 km away in Saxony-Anhalt. This region still harbours the greatest number of oak trees colonised by *C. cerdo* in Germany and is well known for its park landscape with a huge number of solitary oaks. We examined sites around Dessau (51°50′N, 12°15′E) and in the 'Ochsenbusch' nature reserve near Diebzig. Both these study areas are part of the MAB (Man-and-Biosphere)-reserve "River landscape Elbe".

2.3. Environmental and species data

2.3.1. Sampling strategy

For sampling we applied a stratified approach concentrated within different transects (see Hirzel and Guisan, 2002). We first searched for all colonised trees in the known region in order to set the transects and then recorded all oaks within these transects. Additional samplings were made taking care to obtain a long gradient in the habitat variables. We recorded all colonised trees in our primary study area. Each tree was counted as a single case in the modelling process. In total, we have analysed 267 oak trees in the area in Lower Saxony and 144 oaks for the validation in Saxony-Anhalt.

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2.3.2. *Predictor variables*

In total we investigated 10 habitat variables presented by these oaks (Table 1). Our dataset consists of predictor variables measured on different scales. Categorical independent variables were coded with indicator coding into design variables (Jongman et al., 1995; Hosmer and Lemeshow, 2000).

2.3.3. *Tree-level*

Investigations in this study were carried out on both the landscape and the tree-level (see Maurer, 2002). Following expert knowledge and literature (Neumann, 1985; Müller, 2001) we focussed on a relatively small number of potential predictor variables. Some of these are recorded in ordinal scale, because, for instance, it is impossible to measure the vitality of the trunk or tree canopy. The diameter of the oak trunk is an expression of the amount of available resources and is comparable to patch area. Besides these direct resource variables we used indirect gradients such as insolation, an expression of the heat conditions. To depict the potential insolation, we created an index based on an approximation of sunshine intensity, related to light incidence and sun-exposed sides of the tree, according to Hill and Binford (2002). The average bark depth was calculated as an average from three measurements at different representative locations on the trunk.

2.3.4. *Landscape-level*

At the landscape-level the isolation of trees is considered as a predictor. We therefore measured isolation of trees in terms of (i) the distance to the next uncolonised oak tree and (ii) the distance to the next recently colonised oak tree. Distance to the next colonised or uncolonised oak was transformed into log-scale ($\log_{10}$), because of the large range. Finally, we recorded the position of the oak tree in the landscape, placing the tree in a category such as 'solitary' or 'avenue'.

2.3.5. *Response variables*

As response variable we surveyed the intensity and the current state (presence/absence/old presence) of occurrence on each tree using visual indicators such as wood meal or fresh exit holes used from the imagines. Old infestations observed, due to visible old holes and larval feeding ways were not considered in the modelling process because habitat conditions possibly changed over decades; thus, considering old holes would yield biased parameters. We used the presence and absence of the species as the response, which is binary coded as 1 and 0.

2.4. *Statistical analysis*

To identify strong correlation between predictors, we investigated their correlation structure (Fielding and Haworth, 1995). Since the maximum bivariate correlation between predictors was $r_s = 0.384$ (Spearman rank correlation), multicollinearity is negligible. The significance of interaction terms and quadratic functions of the parameters was tested before building the final model and it was found that none of them are relevant for predicting the response variable.

Table 1 – Predictor variables measured from each of the oak trees

	Classes	df	Number of cases in presences		Number of cases in absences	
Categorical predictor variables						
Canopy vitality	0 = mostly dead; 1 = partly dead; 2 = vital	2	0 = 14; 1 = 39; 2 = 10		0 = 3 ; 1 = 16 ; 2 = 135	
Trunk vitality	0 = dead parts without bark; 1 = entire bark vital	1	0 = 19; 1 = 44		0 = 7; 1 = 147	
Oak sap	0 = no sap locations; 1 = sap location (s)	1	0 = 30; 1 = 33		0 = 137; 1 = 17	
Understorey vegetation	0 = half trunk length and higher; 1 = lower vegetation	1	0 = 12; 1 = 51		0 = 27; 1 = 127	
Position in landscape	0 = solitary; 1 = woodland edge; 2 = patchy site; 3 = woodland; 4 = avenue	4	0 = 9; 1 = 7; 2 = 27; 3 = 1; 4 = 19		0 = 14; 1 = 12; 2 = 48; 3 = 25; 4 = 55	
	Units		Mean of presences	SD	Mean of absences	SD
Continuous predictor variables						
Trunk diameter (DBH[a])	Measured at breast height in metre	1	1.22	0.36	0.96	0.31
Distance uncolonised	in [$\log_{10} m + 1$]	1	1.02	0.37	0.87	0.29
Distance colonised	in [$\log_{10} m + 1$]	1	1.32	0.51	1.58	0.81
Sun index	[0 = heavily shaded, no direct sun] to [12 = sun from all directions]	1	8.05	3.58	5.79	3.82
Bark depth	Mean of three independent measures in mm	1	32.03	12.01	24.08	8.52

[a] Diameter at breast height.

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2.4.1. *Logistic regression*

Binary logistic regression with backwards, stepwise variable selection is a common statistical method used in conservation biology to estimate occurrence probabilities in relation to predictors (Kleyer et al., 1999; Cowley et al., 2000). We developed two different models. The so-called final model uses all significant predictors which are thought to have a contribution independent from the species presence. To calculate an alternative model we added the variables 'canopy vitality' and 'trunk vitality', which are biased by the species presence, on the dataset. The application of the last one will be discussed later in the paper. The significance of coefficients in the logistic regression model was assessed via the likelihood ratio test. We applied AIC (Akaike's Information Criterion, Akaike, 1974; Burnham and Anderson, 2002) as criterion in backward selection to compromise between model performance and complexity (cf. Oppel et al., 2004). Nagelkerke (1991) R_N^2 was used for the evaluation of model calibration. To evaluate model discrimination, we calculated the area under a receiver operating characteristic (ROC) curve, the AUC-value (Hanley and McNeil, 1982; Fielding and Bell, 1997). In an ROC-plot, sensitivity, i.e. the proportion of correctly predicted occupied sites, is plotted against the term (1-specificity, i.e. 1 minus the proportion of correctly classified absences) for each possible threshold probability. A random prediction as well as a null model would yield an ROC-curve equivalent to the 45°-line, whereas a perfect classification would follow the *y*-axis ($x = 0$) and $y = 1$. The area enclosed by this curve is called AUC (area under curve) which is 0.5 in the null model case and 1.0 if classification is perfect. We calculated AUC with a 95% confidence interval along with some threshold-dependent performance criteria such as correct classification rate and Cohen's kappa for several threshold probabilities applying a program provided by Schröder (2006). This software is used to assess model transferability by testing the significance of AUC-values after applying the model to independent test data. To estimate the total independent contribution of the single variables to the response, we ran a hierarchical partitioning procedure (MacNally, 2000). By this procedure, the variation in habitat occupancy is decomposed into independent and joint effects of different predictors (cf. Heikkinen et al., 2005). Thus, hierarchical partitioning helps to provide a deeper understanding of the importance of those predictors.

We carried out the statistical analyses with R 2.2.0 (R Core Development Team, 2005). Hierarchical partitioning was conducted using the 'hier.part'-package (version 1.0, MacNally and Walsh, 2004), and the 'Hmisc' (version 3.0-12) and 'Design' library (version 2.0-12) (provided by F. Harrell) were used for the logistic regression procedure. Response curves were plooted using the program LR-mesh provided by Rudner (2004).

3. Results

Only 62 out of 267 (24%) oaks investigated were recently colonised; 154 (58%) trees were without any characteristic signs of presence. 51 oaks (19%) were classified as old presence trees. Thus, our final sample size is $n = 216$ trees.

3.1. *Habitat parameters related with species presence*

The final model considers four predictors with a strong effect on the occurrence probability (see Table 2 with response surfaces shown in Fig. 1). We found that increasing bark depth, sun intensity and presence of oak sap leads to significant higher occurrence probabilities in *C. cerdo*. Increasing distance to the next colonised tree leads to weaker conditions for colonising an oak (Fig. 1). This is the only significant landscape effect in the regression procedure Table 3.

The parameters 'distance to next uncolonised tree', 'understorey vegetation height', 'trunk diameter (DBH)' and 'position in landscape' were removed in the stepwise model selection process. No interaction term and no quadratic term was significant.

The vitality of the canopy and trunk were included in the alternative model which shows that these predictors are of great importance in predicting the occurrence probability. The parameters 'understorey vegetation height' and 'DBH' were also considered to be significant predictors of species presence so that the alternative model consisted of seven predictor variables.

We conducted a hierarchical partitioning procedure to quantify the independent contribution of our predictor variables considered in the final model to the response (Fig. 2). The results show the relative importance of the presence of oak sap on the trunks (44%). Depth of the bark, which is highly correlated with trunk diameter, contributed 30% to explaining the occurrence of *C. cerdo* on the oaks, whereas the influence of the power of the sun contributed only 16% and the distance to the next colonised tree a little less than 10%. All four variables are highly significant predictors of presence of *C. cerdo*.

3.2. *Model validation*

The final model explains nearly 50% of the overall variance of the response variable in our training dataset ($R_N^2 = 0.498$). The model also shows a high discriminative power with an AUC-value of 0.87 (CI$_{95\%}$: 0.82–0.92). The alternative model with seven predictors yields a considerably better general fit ($R_N^2 = 0.753$) and a higher AUC of 0.96 (CI$_{95\%}$: 0.93–0.99). There are several classification thresholds, depending on the research goal (Table 4). To achieve the best balanced predictive performance, we used P_{fair} as the appropriate classification

Table 2 – Parameter estimates of the final logistic regression model (residual deviance = 166.55 on 211 degrees of freedom, null deviance = 258.97 on 215 degrees of freedom)

	Variable	Regression coefficient	SE	*p*
β_1	Oak sap	2.636	0.457	<0.0001
β_2	Distance to next colonised tree	−1.081	0.357	0.0025
β_3	Sun index	0.211	0.058	0.0003
β_4	Bark depth	0.102	0.022	<0.0001
β_0	Intercept	−4.491	0.921	<0.0001

Corresponding response surfaces are shown in Fig. 1.

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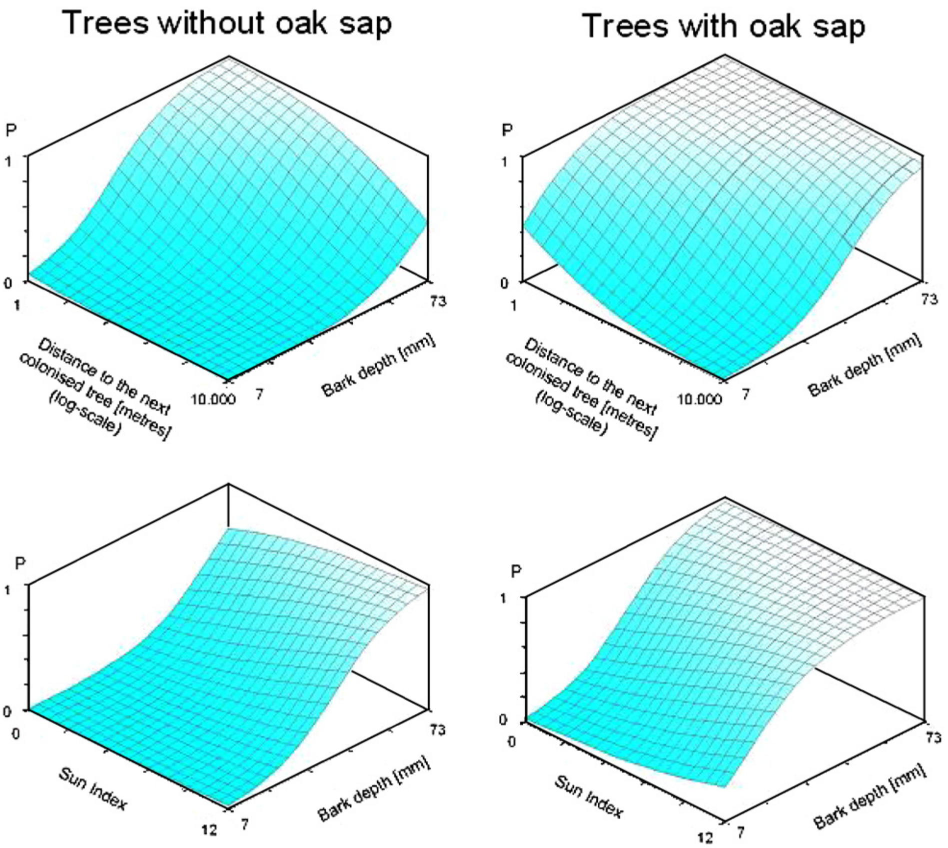

Fig. 1 – Bivariate response surfaces of the four predictors included in the final model. The estimated occurrence probability (*P*) of *C. cerdo* is plotted against the three continuous predictors. Left and right surfaces represent the different levels of the fourth predictor. Sun index is fixed to be 6 for the first row, distance to the nearest occupied tree is 141 m in the second row. The occurrence of *C. cerdo* increases with increasing bark depth, insolation and oak sap as well as decreasing distance to the nearest occupied tree.

Table 3 – Parameter estimates of the alternative logistic regression model (residual deviance = 129.57 on 211 degrees of freedom, null deviance = 258.97 on 215 degrees of freedom)

	Variable	Regression coefficient	SE	*p*
β_1	Oak sap	1.790	0.499	0.0003
β_2	Canopy vitality [partly dead]	3.131	0.488	<0.0001
β_3	Canopy vitality [mostly dead]	3.873	0.776	<0.0001
β_4	Diameter	2.231	0.688	0.0012
β_0	Intercept	−5.397	0.910	<0.0001

threshold for the final model (cf. Jiménez-Valverde and Lobo, 2006). Evaluation of kappa after Monserud and Leemans (1992) indicates fair predictive power for the final model and very good predictive power for the alternative model with a higher number of predictors.

3.3. *Is the habitat model transferable in space?*

We validated our final model testing its transferability to an external dataset from Saxony-Anhalt. We analysed 144 oaks from different stands, of which 55 were found to be colonised and were entered into the dataset (38%). The regression equation from the training dataset was applied to predict the spatial distribution for this external test dataset. The model resulted in an AUC-value of 0.87 ($CI_{95\%}$: 0.83–0.93) within the test dataset. Surprisingly, there is a slightly better performance within the test data as regards the prediction of both presences and absences (Table 5). We also tested alternative model building with the dataset from Saxony-Anhalt and further validation on the data from Lower Saxony. The data from Saxony-Anhalt provided a better model, but also a poorer predictive performance in the spatial validation procedure using the Lower Saxony data. The importance of the individual parameters changed only slightly (results not shown).

4. Discussion

4.1. *Parameters describing aspects of the realised niche*

Our model exhibits relevant habitat factors which are essential for habitat selection in the longhorn beetle *Cerambyx cerdo*. We are able to predict occupancy patterns in this beetle species with only a few analysed variables. Species distribution models based on field data predict the realised niche in the study area (Guisan and Zimmermann, 2000). Our results show that the bark depth of the trees is one of the significant predictors for species presence. Bark depth and trunk diameter are highly correlated. We measured colonised oaks with trunk diameters from 0.64 m to 2.32 m. Increasing age and diameter of the oak trees improves the occurrence probability for our study species. Ranius and Jansson (2000) have shown that trunk diameter is an important determinant of saproxylic species richness in common as well as rare red-listed beetles associated with oaks. Tree diameter also restricts occupancy of other highly endangered beetles (e.g. *Tenebrio opacus*, Ranius, 2002). The latter species also occurs in the research area in Lower Saxony. The bark depth also seems to be very important for successful egg development in our study species with female beetles preferentially using protected deep slits in the bark for oviposition (Döhring, 1955).

Our alternative model considers oak vitality as a powerful predictor indicating high occurrence probabilities on trees with a large number of dead branches or damaged sections of trunk bark. The vitality of trunk and canopy appeared to be another important parameter for predicting the presence of this saproxylic beetle species. A correlative analysis such as logistic regression leads to such simple mechanistic results, but is this not a misinterpretation of causes and effects? Müller (2001) reported oaks with physiological failings and trees with damage as a typical habitat for *C. cerdo* and Zuppke (1993) described dead branches as useful signs of presence. Our study species belongs to a small number of longhorn beetle species which are able to attack living trees (Bense, 1995). In fact, we know that the larvae of *C. cerdo* need fresh wood to feed and have become extinct on dead trees (Neumann, 1985). The larval damage to living wood strongly affects the water and nutrient supply network inside the tree, which in turn leads to the death of some branches in the canopy. This means that this beetle is effecting changes in its own essential habitat which amount to a destruction of habitat conditions for the following generations. Therefore, a low vitality of oak canopy and trunk reflects an unsuitable habitat for the larvae of *C. cerdo* and is the result of larval feeds. For this reason these parameters were not included in our final predictive habitat model.

Oak sap is sometimes suggested as an important food resource for the adults (Neumann, 1985). There are some observations showing that *C. cerdo* is attracted by oak sap on trees (Weckwerth, 1954; Döhring, 1955). Sap spots are common on most trees of the genus *Quercus*. Some species from the beetle family Nitidulidae are known for their specialisation in feeding on sap spots of different tree species (e.g. Juzwik et al., 2004; Zeran et al., 2006). These sap spots are often the door for disease infections transmitted by sap visiting insects (Ambourn et al., 2005). Our model predicts a higher likelihood of occurrence if there are oak sap spots on the tree. As Fig. 2 reveals, this is the most important predictor. Therefore, re-

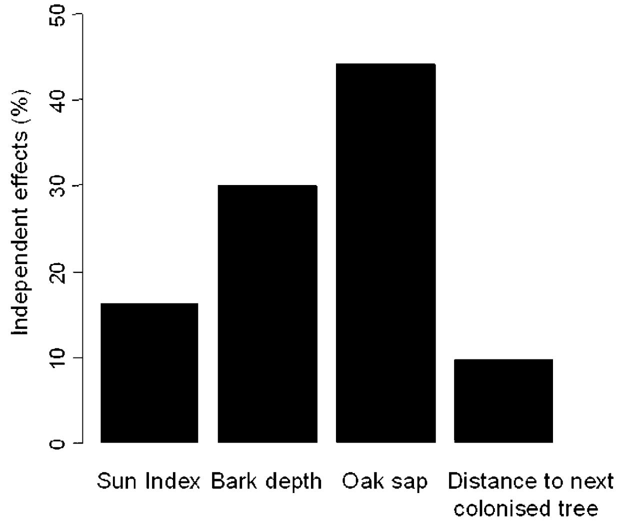

Fig. 2 – Contribution of the individual predictors to the final model response (independent effects calculated by hierarchical partitioning with respect to the log likelihood as goodness-of-fit criterion).

Table 5 – Performance of the final model and results for the spatial validation on the test dataset

Parameter	Training data ($n = 216$)	Test data ($n = 144$)
AUC with 95% CI	0.87 [0.82–0.92]	0.87 [0.83–0.93]
Sensitivity	0.79	0.80
Specificity	0.78	0.82
Correct classification rate	0.78	0.81
Kappa	0.51	0.61

AUC (Area Under Curve) is provided as a threshold independent criterion. Threshold dependent criteria are given with respect to P_{fair} which is the classification threshold where the performance for presences (sensitivity) and absences (specificity) is nearly balanced (see also Table 4).

Table 4 – Different classification thresholds and their effects on prediction success according to Schröder and Richter (1999), calculated with ROC_AUC Schröder (2006)

Criteria	Final model			Alternative model		
	P_{fair}	P_{kappa}	$P = 0.5$	P_{fair}	P_{kappa}	$P = 0.5$
Threshold probability P_{crit}	0.2775	0.515	0.500	0.400	0.460	0.500
Sensitivity	0.787	0.639	0.639	0.855	0.839	0.807
Specificity	0.779	0.929	0.909	0.863	0.902	0.902
Correct classification rate	0.781	0.847	0.833	0.861	0.884	0.874
Kappa	0.513	0.601	0.571	0.679	0.723	0.698

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lated infections may be important for the ability of *C. cerdo* to attack these weakened trees.

In the case of many other saproxylic beetles (Grove, 2002; Ranius, 2006), the distance to the next colonised oak tree is a significant predictor of occurrence probability. According to Schiegg (2000) habitat fragmentation in saproxylic beetles occurs on a more local scale (<150 m). Considering that *C. cerdo* uses a transient resource there is only a poor dispersal power in this species.

In search of a better prediction of occupancy we combined habitat quality, patch size and isolation to develop a model which satisfies a primary connection between the habitat and metapopulation approach in the sense of Armstrong (2005). Despite the fact that the use of all spatial scales in species distribution modelling sometimes leads to better classification results and better general fit (Johnson et al., 2002), the only significant landscape predictor is the distance to the next colonised oak. The position of the trees in the landscape does not affect occurrence probabilities. But the influence of landscape structure is visible in the sun conditions/exposition on the trunks. It is expected that a more open landscape offers more sun-influenced trunks than a closed woodland.

Surprisingly, the influence of the sun exposition of the bark is of subordinate importance for the likelihood of occupancy. This parameter gives significant changes in the outcome, but with relatively low contributions compared to the other variables. Sun-exposed trees, especially those which are south exposed seem to be favourites for colonisation. Zuppke (1993) observed oaks at the northern boundaries of woodlands where *C. cerdo* was present, and postulated that the degree to which the trees are exposed to open spaces has an additional effect on colonisation. Species richness and number of red-listed saproxylic beetles are found to be significantly higher in sun-exposed trees (Lindhe and Lindelöw, 2004). Therefore, sun-exposed trees play a major role in the conservation of many saproxylic beetles. However, the larval development of *C. cerdo*, which takes place in the interior of the trunk, is favoured by increasing insolation.

4.2. *Model evaluation and validation*

ROC-curves are a useful evaluation tool for predictive species distribution models (see Fielding and Bell, 1997; Pearce and Ferrier, 2000; Reineking and Schröder, 2006). Because it is independent of prevalence, this technique gives an appropriate measure of accuracy (Fielding, 2002). The AUC-value of the final model indicates excellent discriminative power according to Hosmer and Lemeshow (2000). Kappa, a satisfying indicator of model predictive performance (Manel et al., 2001), ranged from 0.5 to 0.6, which indicates good predictive power (after Monserud and Leemans, 1992).

One goal of our research was to analyse the general fit of the model when applied to another geographic region (see Schröder and Richter, 1999; Randin et al., 2006). The spatial validation shows similar predictive and discriminatory power to that in the model building region. This means that the model can further be applied to other geographic regions of Central Europe. There is no effect of altered habitat requirements between our tested regions for the species we investigated.

4.3. *Application to habitat management and implications for conservation*

To facilitate survival by establishing high habitat quality for *C. cerdo*, management strategies should focus on opening up wood stands and trees. Semi-open wood stands are thought to be suitable landscape structures. This kind of landscape also harbours a great variety of different microhabitats in dead wood, which has a strong impact on overall saproxylic species richness (Lindbladh et al., 2003; Gibb et al., 2006). *C. cerdo* depends on semi-open wood stands, which also meet the habitat requirements of *Osmoderma eremita* and some other highly endangered beetles (Ranius and Nilsson, 1997). These threatened beetle species have similar habitat requirements on the landscape level, in particular with respect to tree conditions, a fact which should be taken into account in management of nature conservation areas.

Recent studies have shown that both saproxylic and species rich epigaeic insect communities (e.g. Falke et al., 2000) and the plant communities associated with natural disturbance (Poschlod et al., 2002; Mountford and Peterken, 2003) will benefit considerably from an interesting new approach involving large herbivores in wood pasture landscapes. Grazing with large herbivores, such as horses or cattle, promises the best impact to generate suitable landscape and tree-level conditions on oaks for occurrence of *C. cerdo*. Because of their ability to feed on the lower canopy branches and leaves large herbivores are important for opening the trunks to the sunlight. Surprisingly, grazing seems to be important for oak recruitment. Vera (2000) found no new young generations of oak trees in the closed forest reserves he studied. Despite the discussion about the natural landscape structure in Central Europe (closed forest vs. park landscape; see Vera, 2000) there is a distinct man-made component in the potential suitable habitats for our study species. Elements of cultural landscapes, for example tree avenues or parks, can also harbour viable populations of *C. cerdo*. A large number of today's remnants colonised by *C. cerdo* are either still or were formerly used as wood-pasture (as for instance the nature reserve 'Ochsenbusch' in Saxony-Anhalt).

One problem affecting population survival of our study species in our recent landscapes is the shortage of trees with sufficient trunk diameter for colonisation and establishment of a stable population over a number of years. A large number of the recently colonised oaks in the Elbe region were planted in the past to protect the dikes against iceshore drift in winter. If this measure were to be taken up again today in the area between the dike and the river, this would help provide a large number of oaks for the future.

Ranius and Jansson (2000) made valuable suggestions for the conservation of rare saproxylic beetles associated with hollow oaks. They proposed the resumption of former management activities in areas with old oaks and a restoration of regrown sites. One of these former uses should be wood pasture which has been recommended as a successful tool in nature conservation for a number of different threatened taxa (Redecker et al., 2002). In the re-introduction of wood pasture, the focus should be on a large spatial scale and on low grazing intensity to allow for recruitment of oak seedlings (Vera, 2000) and moderate disturbance.

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Jonsell et al. (2004) point out the value of man-made deadwood substrate in modern forestry. Their results show that naturally created stumps can provide a greater overall species richness in the case of saproxylic beetles. Therefore, we should aim to conserve saproxylic species richness using natural processes.

5. Conclusion

We have shown that a habitat suitability analysis is useful for scientifically based habitat management of saproxylic species. Our research provides basic information for an evaluation of the remaining areas as well as for reserve selection in the endangered longhorn beetle *Cerambyx cerdo* in Central Europe. A derived evaluation index of trees or areas can easily be developed from our results. This would be very helpful for the next reports to the European Commission.

Important results obtained from our research are the knowledge and quantification of a number of aspects of the realised niche, and of the habitat conditions necessary on tree and landscape level to maintain existing populations of *C. cerdo*. This species prefers distinct habitat conditions and this allows us to make very good predictions of its spatial distribution based on a relatively small dataset.

Regarding the key function of *C. cerdo* for occurrence of other highly endangered saproxylic beetles, we are able to recommend an integrative approach for habitat management which will also be of great benefit to other taxa.

The vitality of the oak trees included in the alternative model may be used in future to detect unknown presences of *C. cerdo* in the field. As a parasite of oaks, *C. cerdo* depends on a fairly large number of suitable trees in its proximity. The provision of such conditions over decades is the essential key in the conservation of this protected and highly endangered longhorn beetle species.

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