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Predicting the occurrence of Middle Spotted Woodpecker *Dendrocopos medius* on a regional scale, using forest inventory data

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ABSTRACT

The Middle Spotted Woodpecker (*Dendrocopos medius*) is the bird species which Germany has the greatest global responsibility to protect. It is an umbrella species for the entire assemblage of animals associated with mature broadleaved trees, especially oak. Even though well studied in small to medium scale stands, the validity of habitat suitability analysis for this species in larger forests has not previously been proved. Aim of this study was to test suitability of permanent forest inventory plots for modelling its distribution in a 17,000 ha forest landscape and to derive habitat threshold values as a basis for formulating management guidelines. Based on 150 randomly selected 12.5 ha plots we identified mean age and basal area of oaks as the most important habitat factors using a backward selection logistic model. Internal validation showed an AUC of 0.89 and a R^2_N of 0.58. Determination of thresholds using maximally selected rank statistics found higher probability of occurrence in stands with a mean age >95 years. Above that age the probability increased again in stands with more than 6.4 m^2 basal area oak/ha.

Our results show that widely available forest inventory data can serve as a valuable basis for monitoring the Middle Spotted Woodpecker, either within the framework of the Natura 2000 Network, or more generally in integrated forest management with the aim of providing suitable habitats for the entire assemblage of species on old deciduous trees, especially oak.

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1. Introduction

Global threats to biodiversity are mainly anthropogenic, a fact which is shown to be accepted by the response, which has included international agreements such as the convention on biological diversity (CBD). Following this convention, the Europe-wide Natura 2000 Network was established in 1990 to protect endangered species and habitats in the European Union, based primarily on two EU Directives, the Birds Directive and Council Directive on the Conservation of Natural Habitats and of Wild Fauna and Flora, or "Habitats Directive" (Donald et al., 2008). Member states are bound by the Directives to improve the conservation status of species therein named by protecting or enhancing their habitats, e.g. for birds by designation of special protected areas (SPAs). The status of target species should be monitored at intervals and reported to the EU (Ostermann, 1998).

Due to the practical problems involved in surveying population levels in large and complex areas such as woodlands within periods of only a few years, the condition of a population of a species is usually assessed using three groups of criteria: population estimates, habitat quality and quality of threats. The larger the area, the greater is the relevance of habitat quality estimation. Two major problems affect approaches at larger scales. Firstly, a model for habitat–species relations has to be built and tested. Secondly, an adequate database for models must be available.

We selected the Middle Spotted Woodpecker *Dendrocopos medius* as an example demonstrating the value of forest inventory data for evaluating habitat suitability and monitoring, for the following reasons:

1. *D. medius* is listed in Annex I of the Birds Directive. These species shall be the subject of special conservation measures concerning their habitat in order to ensure their survival and reproduction within their area of distribution.
2. It is resident in the temperate continental climatic zone of Europe, and first in priority of 255 species ranked by the responsibility of Germany for their global protection (Denz,

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2003). Europe holds 75% of the world's population (10,000–22,000 pairs). The decrease by 39% in Central European countries from 1970 to 1990, caused by forest clearance and radical changes in forest management highlights the actuality of the threat (Mikusinski and Angelstam, 1997; Pasinelli, 2003).

3. *D. medius* is considered to be a 'relict of European virgin forests'. Its occurrence is restricted to mature broadleaved forests with rough-barked tree species. According to the composition of broadleaved tree species in German forests (beech 15%, oak 10%, alder 2%, ash 2%, popular 1%), oak is the most important rough-barked genus (BWI, 2007). Its strong preference for oaks and old trees makes *D. medius* a suitable umbrella species for all species attached to mature broadleaved forests, especially of *Quercus*, in Central Europe (Angelstam et al., 2003). Protection of this bird, which many people find fascinating and is easy to identify, benefits several other less conspicuous species with similar habitat requirements. The majority of 515 saproxylic beetles in the study area is associated with mature broadleaved trees, and with 57 tree specialist beetle species, *Quercus* possesses a larger number than any other tree genus in this region (Müller and Goßner, 2007). 37 of these specialized beetles are listed in the Red Data Book of endangered animals (Schmidl et al., 2003). A similarly high number of moths are associated with oak. With 205 specialist moth species feeding mainly or exclusively on oak in southern Germany, *Quercus* is at the top of the list of tree genera with respect to species richness (Hacker and Müller, 2006).
4. Since parameters measured in classical forest inventories happen to be those which have a strong influence on *D. medius*, we expected a realistic model to result when constructed using inventory data. Even although some studies reported the importance of snags or cavities (Schumacher, 2005), structures which are not normally assessed in forest inventories, in most studies these factors were found to be of lesser significance (Jöbges and König, 2001; Müller, 2005).

Pasinelli (2003) reviewed research on *D. medius*, showing an increasing number of publications in the most recent decades. As a result of the high level of effort required for field studies in forests, most of these studies were made in small stands of 10–50 ha. Densities over areas of thousands of hectares were recorded only in a few cases (Bühlmann, 1993). The influence of habitat fragmentation, with small scattered patches of oak spread over the landscape, has been studied especially intensively in Switzerland (Müller, 1982). According to the large amount of knowledge contained in these studies, the quality of habitat assessment for the purposes of conservation in small to medium sized forests seems to be acceptable when based on direct searches, particularly using the reliable response of *D. medius* to tape playback (Südbeck et al., 2005). By contrast, habitat evaluation of large forested areas (>10,000 ha), which are often Special Protected Areas, is still difficult to achieve in most regions. This situation is unsatisfactory, because these large forests contain the major part of the total population. Records from permanent forest inventories suggest themselves here as a practical source of regional data. These have been established in Bavaria since 1984 and are repeated around every 10 years. Mainly standing volume and growth rates are assessed (Fuchs and Kennel, 1994).

The aims of this study were: (1) to test the influence of occurrence of different proportions of tree genera, tree dimensions and tree age obtained from forest inventory data on the occurrence of *D. medius*; (2) to test the suitability for prediction of habitat quality of different types of species distribution models, based on different depths of inventory information; (3) to derive thresholds for practical implementation in forest management.

2. Material and methods

2.1. Study area

The ''Northern Steigerwald'' is a forest area of about 17,000 ha, located in northern Bavaria (N 49°50′; E 10°29′), dominated by broadleaves (Fig. 1). The main tree species is beech (*Fagus sylvatica*). Average daily temperatures range from 7 to 8 °C and average annual precipitation from 700 to 800 mm. The predominant vegetation types are ''*Luzulo-Fagetum*'' and ''*Galio odorati-Fagetum*'' (Walentowski et al., 2004). The proportion of beech is 40%, of oak 17%, and of conifers 32%. Alder, Ash and Maples together represent 3%. In the eastern part, the proportion of pine increases, while in the western part beech-oak forests dominate. A detailed description is given in Müller (2005).

2.2. Species under study

While foraging, the Middle Spotted Woodpecker spends most time bark probing and surface gleaning (Jenni, 1983; Pasinelli, 2000). A high preference for oak has been shown for many regions (Pasinelli, 2000). The species is however also found in forests with other typically rough-barked tree species such as *Alnus*, *Ulmus* or *Salix* (Pasinelli, 2003). Furthermore, it can occasionally inhabit fruit or olive orchards (Kristin, 2003). Pure coniferous forests are avoided (Bruland, 1993; Pasinelli, 2003). Colonisation of old beech forests is even possible where these contain a very large amount of dead wood, which provides rough surfaces (Schumacher, 2005). However, this type of old, pure beech stand without oaks is only available on a small scale in Central Europe. The species is not restricted to inner forest areas, as is made evident by presence of breeding pairs in orchards close to forests (see above). Therefore we neglected the spatial proximity of sampling areas to forest edges in our analyses.

The ready response of Middle Spotted Woodpecker to playback has made this approach the standard method for mapping the species throughout Germany. We surveyed all woodpecker plots using playback, following the standardised method for counting

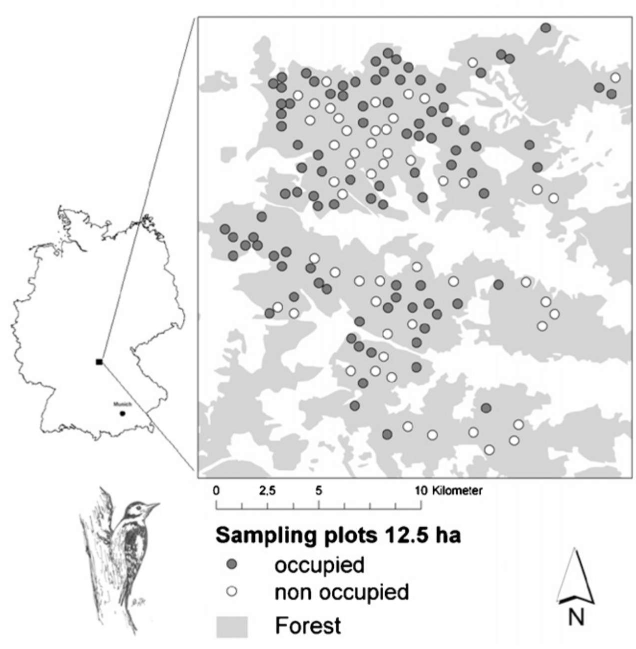

Fig. 1. Location of the 150 circular sampling plots (black dots) in the ''Steigerwald'' – forest in Southern Germany (N 49°50′; E 10°29′).

breeding birds (Südbeck et al., 2005). From March to the end of April each plot was surveyed three times, while slowly walking along a circle in each sampling plot. The playback was at low volume, so that only individuals within the sampling plot were attracted. The distance between plots guaranteed that individuals from other plots were not attracted. Both sexes can be attracted by playback, even if mainly males respond. The method allows estimation of presence absence of the species with high accuracy. We used the presence and absence of the species as the response, which is binary coded as 1 and 0, summarised for all three sampling campaigns.

2.3. Environment and study design

We randomly selected 150 circular plots, pre-stratified in 50 plot sets for three types of stands: dominated by mature beech; dominated by mature oak; and other types of stands (Fig. 1). The size of each study plot of 12.5 ha was selected in accordance with known Middle Spotted Woodpecker home ranges in Central Europe (for overview see Pasinelli, 2003). All these circular plots were intersected by the forest inventory grid. The inventory plots each had a size of 0.05 ha and their location was determined by GPS. Forest inventory data were obtained in 2003. Therefore an upward adjustment to the age of all trees was made, but no adjustment to the diameter measurements, because of the relatively slow growth of mature beech and oak. In most of our study area the density of inventory plots was one plot per 2 ha, in the eastern part (approximately one third of the area under study) it was one per 4 ha. This is caused by past changes in forest compartment sizes. Using this procedure, we found our woodpecker plots represented by 4–9 (mean 7.5) forest inventory plots. Forest inventory data comprise the spatial position of each tree, tree species, diameter at breast height (dbh) and age within the inventory plot. From these data we calculated the mean value of 13 predictor variables for each 12.5 ha circular woodpecker plot (see Table 1).

2.4. Statistical analysis

To avoid strong multicollinearity between predictor variables, we studied the correlation matrix of all 13 predictors. Where there was a strong correlation between two variables (Spearman rank correlation, $|r_s| > 0.70$), only the parameter which seems according to the literature to be more important for the species was selected for further modelling (Hosmer and Lemeshow, 2000). 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 is relevant for predicting the response variable.

To estimate the total independent contribution of the individual variables to the response, we ran a hierarchical partitioning procedure on our predictors (MacNally, 2000). This decomposes the variation in habitat occupancy into independent effects of different predictors. Thus, hierarchical partitioning helps to provide a deeper understanding of the importance of each predictor.

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). This special type of generalised linear model (GLM) for binary response variables still serves as a baseline for model comparisons with more complex machine-based approaches, yielding good results (e.g. Elith et al., 2006; Revermann et al., in press).

For variable selection, we applied Akaike's Information Criterion (Akaike, 1974; Burnham and Anderson, 2002; Oppel et al., 2004). Since the biases and shortcomings of stepwise-variable selection are known (Whittingham et al., 2006) we allowed for model uncertainty by comparing our "final" model with two alternative models, where the second important variable was exchanged with the third and fourth (cf. Binzenhöfer et al., 2008; Heisswolf et al., in press). To assess model performance, Nagelkerke's (1991) R^2_N was used for evaluation of model calibration. It quantifies the proportion of variance explained by the model. Values exceeding 0.4 indicate a good calibration (Steyerberg et al., 2001). Additionally, we checked slope and intercept of the calibration line; values of about 1 (slope) and 0 (intercept) indicate a good calibration (Harrell, 2001; Reineking and Schröder, 2006). We also calculated the area under a receiver operating characteristic (ROC) curve, the AUC value (Hanley and McNeil, 1982). To test the accuracy of the models, we applied internal validation by means of bootstrapping with 1000 replicates (Harrell, 2001; Reineking and Schröder, 2003). Additionally, we used a program provided by Schröder (2006) to calculate some threshold-dependent performance criteria such as correct classification rate and Cohen's kappa for several threshold probabilities. To avoid misinterpretation of biased parameter estimates caused by spatial autocorrelation, we tested the residuals of the final model for spatial autocorrelation (Dormann et al., 2007) using Morran's *I*.

To provide an alternative variable selection method and to derive habitat thresholds especially intended for inclusion in practical guidelines (Müller and Hothorn, 2004), we used recursive partitioning (Lausen and Schumacher, 1992; Hothorn and Lausen, 2003; Hothorn and Zeileis, in press). This approach allows simultaneous identification of a threshold and assessment of its

Table 1
Environmental parameters of 150 circular sampling plots, used in our analysis, based on means of 4–9 forest inventory plots for each theoretical *D. medius* territory (circular sampling plot).

Abbreviation	Variable	Range	Mean ± S.D. (presence)	Mean ± S.D. (absence)
baSa	Basal area of all trees (m^2/ha)	15.7–44.1	28.4 ± 4.3	28.1 ± 6.0
baConifer	Basal area of Conifers (m^2/ha)	0.0–42.2	9.1 ± 8.9	14.7 ± 8.8
baOak	Basal area of oak (m^2/ha)	0.0–26.5	13.0 ± 4.9	6.8 ± 4.9
baBeech	Basal area of beech (m^2/ha)	0.0–27.4	14.6 ± 4.3	14.5 ± 6.0
baAlder	Basal area of alder and ash(m^2/ha)	0.0–31.0	3.0 ± 4.5	3.7 ± 6.2
meanage	Mean age (years)	46.7–168.8	127.6 ± 20.0	83.9 ± 30.6
maxage	Maximum age (years)	53.0–197.0	154,28 ± 22.2	114.3 ± 35.3
maxdbh	Maximum diameter at breast height all trees (cm)	30.0–104.0	65.7 ± 9.3	56.6 ± 11.8
meandbh	Mean diameter at breast height all trees (cm)	19.0–68.0	50.1 ± 7.3	42.1 ± 11.9
maxdbhDecid	Maximum diameter at breast height broadleaved trees (cm)	28.0–104.0	65.2 ± 9.6	52.1 ± 14.1
meandbhDecid	Mean diameter at breast height broadleaved trees (cm)	4.7–49.3	65.2 ± 9.6	52.1 ± 14.1
maxdbhOak	Maximum diameter at breast height oak (cm)	0.0–104.0	56.1 ± 12.0	33.5 ± 22.8
meandbhOak	Mean diameter at breast height oak (cm)	0.0–60.5	38.8 ± 7.4	24.1 ± 16.4

significance by means of a statistical test procedure, i.e. a decision whether or not there is a relationship between some independent variable and the response. The thresholds are derived from estimates of break points by means of maximally selected two-sample statistics, and their validity is judged by multiple test procedures. The key results are those where the difference between high and low values of the dependent variable (here: occupied and non-occupied sampling plots) is largest. The approach can be applied to a single or, as in our study, to multiple environmental variables. After the dataset is divided into two subsets by the threshold with highest explanatory power, the subsets are searched for additional thresholds. The methodology provides a decision tree with *P*-values for one or more critical thresholds. Based on 5000 bootstrap samples a confidence interval (95%) was calculated for all thresholds. This methodology is a further development of some currently more popular implementations for 'recursive partitioning' or generation of 'trees', such as 'CART' (Breiman et al., 1984) or 'C4.5' (Quinlan, 1993), but solves two fundamental statistical problems of the earlier approaches: overfitting and a selection bias towards covariates with many possible splits or missing values (Hothorn et al., 2006a). Method and a comprehensive model comparison are described in Hothorn et al. (2006a).

Threshold values very much depend on the datasets from which they are calculated and thus are highly critical in an ecological sense, because sharp increases or decreases along an environmental gradient are rare in nature (Dykstra, 2004). One should however keep in mind that even the use of simple logistic regression models is hardly feasible in forest management practice. This discrepancy between practical and theoretical conservation biology can be bridged by resilient target values (thresholds) that are easily implemented in forest management planning (Angelstam et al., 2003; Bütler et al., 2004; Müller and Hothorn, 2004; Guénette and Villard, 2005; Suorsa et al., 2005).

We carried out all statistical modelling with R 2.6.0 (R Development Core Team, 2007). Hierarchical partitioning was conducted using the 'hier.part' package (version 1.0, MacNally and Walsh, 2004). Maximally selected rank statistic was run on the 'party' package (Hothorn et al., 2006b). We assessed and internally validated logistic regression models by applying the 'Hmisc' (version 3.0–12) and 'Design' libraries (version 2.0–12) provided by F. Harrell Jr. Morran's *I* was calculated with 'spdep' (version 0.4–24) provided by Yo and Bivand. Response curves were plotted using the program 'LR mesh' provided by Rudner (2004).

3. Results

In 96 of 150 sampling plots *D. medius* was recorded at least once during the three sampling campaigns (Fig. 1). Our inspection of the environmental correlation matrix revealed a high correlation between MAXAGE (maximum age) and MEANAGE (mean age), and MEANDBHDECID (mean diameter breast height broadleaved trees) and MEANAGE. Therefore we retained only MEANAGE. Similar results were obtained for MAXDBH (maximum breast height) and MAXDBHDECID (maximum breast height broadleaved trees), as well as MAXDBHDECID (maximum breast height broadleaved trees) and MAXDBHOAK (maximum breast height oak), so that MAXDBHDECID and MEANDBHOAK were also omitted. Finally, our dataset contained eight independent variables.

3.1. Selection and relevance of predictors

The final model considers only two predictors with a strong effect on the probability of occurrence (Table 2). We found that increasing MEANAGE and BAOAK (basal area of oak) lead to increasing probabilities of occurrence. We conducted a hierarchical partitioning procedure to quantify the independent contribution of the predictor variables to the response. The results show the relative importance of MEANAGE (38%), BAOAK (23%) (i.e. the two predictors in the final model) as well as MAXDBHOAK (19%). The MEANDBH contributed slightly less than 10% to explaining the occurrence of *D. medius*, and all other variables were of minor influence. Testing the residuals of the final model for spatial autocorrelation, Moran's I showed no significant autocorrelation, indicating that spatial effects do not have to be considered in our model.

Since hierarchical partitioning indicates some influence of MAXDBHOAK and MEANDBH as well, we included each of them in two alternative models together with MEANAGE to assess the loss of predictive power resulting from a lower level of measurement effort, firstly using only the dbh of largest oak (MAXDBHOAK), and secondly the simple MEANDBH of trees irrespective of tree species.

Table 2
Parameter estimates of the final logistic regression model (residual deviance = 110.86 on d.f. = 147, null deviance = 196.03 on d.f. = 149).

Variable	Regression coefficient	S.E.	*P*
Intercept	−6.30957	1.077524	<0.001
BAOAK	0.176857	0.055556	0.001
MEANAGE	0.047240	0.009038	<0.001

Corresponding response surface is shown in Fig. 3.

3.2. Model evaluation

The final and both alternative models were evaluated using performance criteria after internal validation based on 1000 bootstrap samples. Our final model explains nearly 60% of the overall variance of the response variable in our training dataset (R^2_N 0.58). The model also shows an excellent discriminative power with an AUC of 0.89 (Table 2). The alternative models exhibit an almost negligible loss of predictive power; their performance was still excellent, with AUC of 0.86 and 0.85 (Table 3). The explained variance decreased from 58% in the final model to 50% in the model with poorest performance where no tree species determination was conducted.

3.3. Thresholds as guidelines for management

To corroborate the selection of predictors made with the GLM procedure and to derive useful values for management guidelines, we also used maximally selected rank statistics. Based on this, probability of occurrence was greatest in forest stands older than 94.75 (95% CI = 89.33–102.75) years. In these older stands, occurrence increases from 0.5 to 0.9/ha in stands with more than 6.24 (95% CI = 5.0–14.0) m^2/ha basal area of oak. The statistically different approach of this methodology resulted in the selection of the same independent variables, thus supporting the results of the backward selection.

Table 3
Performance of the final and three alternative models after internal validation with 1000 bootstraps.

	Model 1: MEANAGE + BAOAK	Model 2: MEANAGE + MAXDBHOAK	Model 3: MEANAGE + MEANDBH
AUC	0.887	0.855	0.850
R^2	0.581	0.542	0.506
Slope	0.975	0.969	0.963
Intercept	−0.003	0.017	0.022

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

	Model 1			Model 2			Model 3		
	P_{fair}	P_{kappa}	$P = 0.5$	P_{fair}	P_{kappa}	$P = 0.5$	P_{fair}	P_{kappa}	$P = 0.5$
Threshold probability (P_{crit})	0.690	0.600	0.500	0.735	0.432	0.5	0.735	0.470	0.5
Sensitivity	0.802	0.927	0.937	0.791	0.968	0.947	0.759	0.958	0.937
Specificity	0.796	0.778	0.741	0.777	0.722	0.722	0.759	0.740	0.740
Correct classification rate	0.800	0.873	0.867	0.786	0.880	0.866	0.753	0.880	0.866
Kappa	0.580	0.720	0.701	0.551	0.726	0.698	0.487	0.728	0.701

4. Discussion

4.1. Model evaluation

ROC curves are useful for evaluating predictive species distribution models (see (Pearce and Ferrier, 2000; Schröder, 2006). Because it is independent of prevalence, this technique is one of the best criteria for assessing the discriminative power of SDMs (Fielding, 2002), although this was recently discussed controversially (cf. Lobo et al., 2008). The AUC value of our final model indicates that its discriminative power is good, approaching excellent, according to Hosmer and Lemeshow (2000). However, both alternative models also seem to possess high predictive power (Table 4). Kappa, a satisfactory indicator of model predictive performance (Manel et al., 1999), ranged from 0.5 to 0.6, which indicates good predictive power (after Monserud and Leemans, 1992).

Apart from the statistical validation, we also have to prove that the importance of the selected parameters accords with existing biological knowledge. There are three basic hypotheses about natural habitat requirements of *D. medius*: the association with old deciduous trees (Pasinelli, 2007), the requirement for rough-barked trees, and a specific association with the genus *Quercus* (Pasinelli, 2000). The first is important, because older forests contain more dying and partly dead trees. The species can only make cavities in those trees with soft, dead wood. Additionally, these trees are much richer in insects on and under the bark (Müller, 2005). Age of the tree is of greatest importance in beech, where healthy trees retain a smooth bark surface until they reach high ages. The rough-barked trees are of great significance, because with increasing roughness the density of insects and therefore the food supply for this bark-gleaning species is increased (Pasinelli, 2000). Oak exhibits these traits in high measure: it has rough bark, high insect diversity and often the crowns are partly dead, even in otherwise healthy trees (Pasinelli, 2000).

In our dataset, tree age had the greatest independent explanatory power in our GLM model and also dominated the threshold analysis, with a confidence range around 90–100 years (Fig. 2). This is congruent with the value of >60–100 years age described by Pasinelli (2003) as suitable habitat in oak forests. For almost pure beech stands Müller (2005) found a significant threshold for age at 137 years, but this is only applicable to beech-dominated stands, which need higher ages to be attractive because of the smooth bark of *Fagus*. Schumacher (2005) also found regular breeding only in over-mature beech stands in North-eastern Germany. For oak forests, the conclusion that a high preference exists for stands older than 180 years was drawn by Jöbges and König (2001). Studies in stands of alder also pointed out the preference of *D. medius* for stands of greater age (Weiss, 2003). Even if our results underline that age is a highly valuable factor for modelling occurrence of this species, we have to bear in mind that the study area considered here was dominated by broadleaved trees. Although there are conifer plantations in the lowlands which are of similar age, they are not suitable for *D. medius*. In these stands, which are rare because conifer plantations are generally logged earlier than broadleaves, or killed by bark beetles in the case of spruce, the model is therefore not applicable. It should be used only in broadleaf-dominated forests, especially those of oak and beech.

The second important factor was the basal area of oak trees, with a threshold at 6.24 m^2/ha. This was also found in several previous studies conducted within smaller areas. Pasinelli (2000) found a minimum of 63 large oaks in breeding territories, which corresponds approximately to 6.5 m^2/ha basal area. In Sweden, the lowest value of oak basal area in successful breeding territories was around 10 m^2/ha (Pettersson, 1984), in South Germany 12 m^2/ha (Coch, 1997), in North-east Switzerland 10 m^2/ha (Bühlmann and Pasinelli, 1996) and in Austria 7.9 m^2/ha (Michalek et al., 2001). All these values are within our 95% confidence interval for basal area threshold.

The third important factor, maximum size of oak trees, used in the first alternative model, is also corroborated by reliable literature, which reports oaks as being attractive to *D. medius* only at a dbh above 36 cm (Schmalzer, 1990; Pasinelli, 1992; Hertel, 2003). Even our last factor, the average dbh, has been reported elsewhere as being important in oak forests (Bühlmann and Pasinelli, 1996). In our study, the significance of presence of other rough-barked tree species was low, which can mainly be explained by their scarcity in the beech-oak dominated landscape of the study area. In most other studies, oak was also the most important tree genus, which is in accordance with frequency rates of tree species in general (but see exception Weiss, 2003). Based on

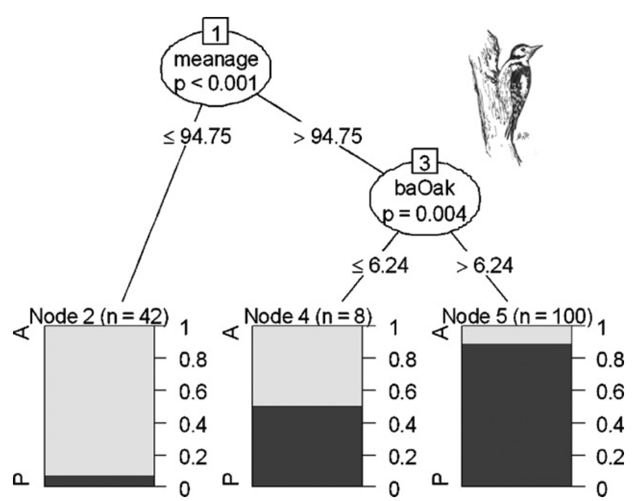

Fig. 2. Conditional inference tree for the *Dendrocopos medius* data. For each inner node, the Bonferoni-adjusted *P*-values are given. The fraction of plots with *D. medius* occurrence (presence = P, absence = A) is displayed for each terminal node, MEANAGE = mean age of forest inventory plots representing one woodpecker sampling plot. BAOAK = mean basal area of oak in m^2/ha.

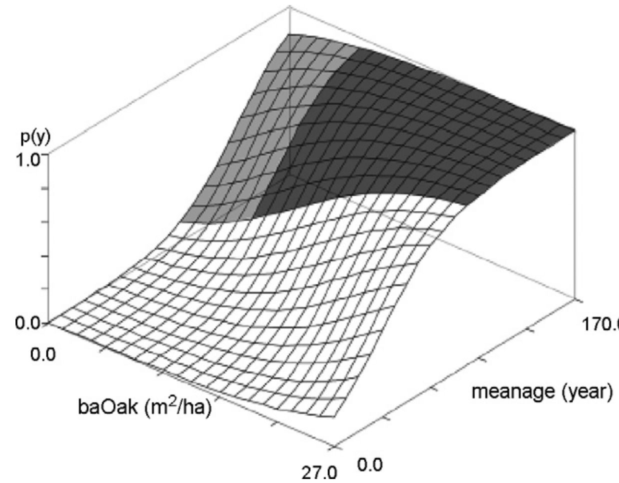

Fig. 3. Bivariate response surface for the two predictors included in the final model. The estimated occurrence probability *P*(y) of *Dendrocopos medius* is plotted against the two continuous predictors. Occurrence increases with increasing mean age and basal area of oak per ha. The areas with high probability (dark grey) and medium probability (light grey), identified by maximally selected rank statistics (see Fig. 2).

a review of the extensive literature on this species, we can conclude that our model closely reflects the current state of knowledge, even in other Central European regions.

4.2. Forest inventory: a suitable database

One should bear in mind that our model was constructed using only 4–9 inventory plots, which is only 1.6–3.6% of our theoretical territory sampling plot of 12.5 ha. Although this database seems small, we were able to build a model with high predictive power. This leads to the question of suitability of forest inventory data in monitoring and habitat evaluation.

The great advantage of forest inventories lies in their representative survey of large woodland areas with the help of a grid. Approximately every 10 years, exact data on tree species and dimensions of all individual trees on these plots are collected. For about 20 years, volume of dead wood has also been calculated in some regions. Where qualities useful for modelling are revealed for a species by these data, each repeated survey can be used to rapidly obtain information on these habitat qualities at the landscape scale.

The repeated sampling also enables alterations in habitat suitability to be identified and tested on a statistically validated basis. *D. medius* appears to be excellently suited to this approach. A similar promise of success appears to exist for other species, particularly those with a requirement for old trees or for particular tree species. Too much should not however be expected of this approach, because occurrence of many species is tied to cryptic structures which have not previously been recorded during inventory, e.g. hollow trees or trees with persisting fungal brackets. Nevertheless, it would appear important to attempt modelling for further species, while continuing to investigate which additional parameters require to be surveyed. Forest inventory, originally purely intended as an economic instrument, can in this way be developed into an integrative tool of use in the quest for ecological sustainability, as is already being attempted in a similar way in other regions (Marzluff et al., 2002).

4.3. Value of species distribution models

Financial constraints have commonly caused monitoring in large protected areas to only be carried out on small areas, with subsequent use of expert knowledge to apply these data to assessment of the entire area. On large areas such as those of our study area, this procedure is plagued by numerous sources of error (Südbeck and Flade, 2004). To improve this situation, development of statistically validated species distribution and dispersion models is increasingly being attempted. These permit a more objective evaluation of areas of habitat and can also be applied at the landscape scale, for e.g. *Cerambyx cerdo*, Coleoptera (Buse et al., 2007), *Osmoderma eremita*, Coleoptera (Ranius and Heding, 2001), *Cupido minimus*, Lepidoptera (Binzenhöfer et al., 2005), agricultural steppe birds (Suárez-Seoane et al., 2002) or the Great Reed Warbler (Woithon and Schmieder, 2004). As shown in the present study and the previous work cited, species distribution models are very suitable instruments for filtering out important habitat parameters and for revealing habitat qualities. In contrast to simple surveys of status, models permit scenarios for various environmental changes to be assessed before these occur, e.g. the effects of management such as harvesting (Schröder et al., 2008), climate change scenarios (von dem Bussche et al., 2008), or comparisons between different inventory periods with the present situation.

For small areas of woodland and the majority of species whose relationships to the habitat parameters are little understood, a direct survey or assessment by experts will remain the standard tools in future. Wherever possible, however, an attempt should be made to translate expert knowledge into models, so that more flexible tools for planning are made available (Petit et al., 2003; McPherson et al., 2006).

The species under study is one of the most prominent forest birds in Central Europe in the context of logging and conservation. Combined with tree-based stand simulators (Pretzsch et al., 2002), our distribution model allows derivation of detailed prognoses for different logging intensities on old broadleaf trees, especially for oak. The requirements of old broadleaf trees and a minimum basal area of oak per hectare are best fulfilled by a logging regime concentrating on single trees instead of clear-felling, and the integration of old decaying trees in all stands. Additionally, the conservation of areas of oak with trees older than 100 years seems to be highly important, an aspect not considered in the commercial perspective of forest sustainability, with a focus only on tree species area.

5. Conclusion and management implication

Our results allow derivation of concrete recommendations for forestry management, aiming at habitat improvement for *D. medius*; a bird species for which we in Germany bear a high global responsibility and which is representative of a large number of animals associated with mature, broadleaved forest. Our model allows a rapid assessment of suitable forest areas, together with a means for identification of important core zones of populations and isolation effects (Müller, 1982).

An improvement in habitat quality can be achieved by increasing the area of broadleaved stands of more than 90–100 years age, and by raising the amount of oak in older stands above a basal area of 6.25 m^2/ha by careful logging. The high accuracy of our model enables an evaluation of suitability of stands for designation as reserves for this endangered forest bird. Finally, the model could be very helpful in preparing the next reports on *D. medius* for the European Commission.

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