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Evaluating habitat suitability for the middle spotted woodpecker using a predictive modelling approach

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This paper explores the influence of forest structural parameters on the abundance and distribution of potential habitats for the middle spotted woodpecker (*Dendrocopos medius*) in three different forest landscapes in Poland. We applied predictive habitat suitability models (MaxEnt) based on forest inventory data to identify key environmental variables that affect the occurrence of the species under varying habitat conditions and the spatial configuration of suitable habitats. All models had good discriminative ability as indicated by high AUC values (> 0.75). Our results show that the species exhibited a certain degree of flexibility in habitat use, utilizing other habitats than mature oak stands commonly associated with its occurrence. In areas where old oak-dominated stands are rare, alder bogs and species-rich deciduous forests containing other rough-barked tree species are important habitats. Habitat suitability models show that, besides tree species and age, an uneven stand structure was a significant predictor of the occurrence of middle spotted woodpecker. The total area of suitable habitats in the studied forests varied from 9% to 60%. Predictive habitat models identified several concentrations of suitable habitats (clusters) with the average distances between them ranging from 3.2 to 5.0 km. Although these distances lie within the species' dispersal ability, the migration of individuals between these sites might be difficult due to the necessity of travelling long distances through unsuitable forest types.

Introduction

Identifying the habitat structure and composition that fulfils critical requirements for threatened or indicator species is an important step in developing promising conservation strategies. In particular, if habitats are subjected to human exploitation, responsible management decisions must be based on reliable, quantitative habitat models (Angelstam *et al*. 2003, 2004, Angelstam & Donz-Breuss 2004, Roberge *et al*. 2008). In recent years, predictive modelling of species distributions has become an important tool for supporting conservation planning, i.e., for the selection of representative habitat networks to meet species conservation goals (e.g. Rodriguez *et al*. 2007, Suárez-Seoane *et al*. 2008, Stachura-Skierczyńska *et al*. 2009, Fernández & Gurrutxaga 2010, Mateo *et al*. 2013).

The scope of most studies on forest-dwelling birds, such as woodpeckers (family Picidae), is limited due to the cost and time required to execute the study. Environmental variables used to explain the habitat selection of birds are frequently derived from small sample plots (e.g. Pasinelli 2000, Kosiński & Winiecki 2004, Müller *et al*. 2009, Delahaye *et al*. 2010, Rehnus *et al*. 2011). It is accepted, as is apparent from the management or conservation implications developed by various authors, that results obtained from a limited area can be used effectively for habitat management at a larger scale, e.g. on a landscape or regional scale. However, habitat variation occurs across multiple scales, and detected patterns should not be generalized beyond the extent of a given study (Wiens 1989). Since it is not easy to obtain reliable extrapolations of data from small to larger areas, their applicability by conservationists and land managers may be limited. Therefore, to gain knowledge that would be applicable to forest management at the landscape or regional scale, studies of the habitat requirements of species should be conducted at different spatial scales (e.g. Rolstad *et al*. 2000, Robles *et al*. 2007b) and replicated in several regions (Dunning 2002, Roberge *et al*. 2008).

Due to the long-term exploitation of European forests, majority of primeval woodpecker habitats have either disappeared or been replaced by semi-natural or artificial commercial stands with lower tree species diversity and only a selection of the few most productive tree species (Mikusiński & Angelstam 1997). Such human activities have apparently degraded primary habitats for middle spotted woodpeckers (*Dendrocopos medius*) (Petterson 1985a, 1985b, Pasinelli 2003, Roberge & Angelstam 2006, Robles *et al*. 2007a, Ciudad *et al*. 2009), a habitat specialist restricted to mature stands with rough-barked tree species, mainly oaks (Müller 1982, Jenni 1983, Török 1990, Pasinelli & Hegelbach 1997, Pasinelli 2000, Kosiński 2006, Müller *et al*. 2009). Other potential habitats are rarely reported and include mature alder stands (Noah 2000, Weiß 2003) and very old pure beech forests (Winter *et al*. 2005). Oak forests have been favoured by humans for centuries as sources of brushwood, timber, and acorns for pigs (Kasprowicz 2010). However, incidences of oak decline in central Europe have occurred repeatedly during the past three centuries as well as in the most recent decades. This decline has resulted from the interaction of biotic and abiotic factors and has a mass character with periods of higher and smaller disease intensity (Thomas *et al*. 2002, Sonesson & Drobyshev 2010). The appearance of oak decline may affect the survival of middle spotted woodpecker in the future. Therefore, identification of factors affecting the persistence of the middle spotted woodpecker in different types of forests is essential to maintaining viable populations across the species range. Moreover, identification of key habitats for middle spotted woodpeckers and their protection may also benefit non-vertebrate species with similar habitat requirements, e.g. saproxylic beetles and moths associated with oaks (Müller & Goßner 2007, Ranius *et al*. 2009). The middle spotted woodpecker is listed in Annex I of the European Community Birds Directive (Directive 2009/147/UE). Therefore, it is the subject of special conservation measures concerning its habitat in order to ensure its survival and reproduction.

Most studies regarding middle spotted woodpecker habitat selection have been confined to small spatial scales, i.e., nest-site selection (Pasinelli 2000, Kosiński & Winiecki 2004, Kosiński *et al*. 2006) and the trees used for foraging (Pasinelli & Hegelbach 1997). Studies at larger, macrohabitat scales describe the habitat use or population with regard to the area, age and type of forest (deciduous *vs*. coniferous), as well as to the size and density of potential nesting/foraging trees (Kosiński & Winiecki 2005, Robles *et al*. 2007b, Müller *et al*. 2009). Moreover, some studies focus on habitat use, demography and population persistence at the macrohabitat scale (Kossenko & Kaygorodova 2001, Robles *et al*. 2007a, Robles *et al*. 2008, Ciudad *et al*. 2009, Robles & Ciudad 2012). Since habitat suitability is correlated with population persistence (Cabeza *et al*. 2004, Rodriguez *et al*. 2007, Robles & Ciudad 2012), an understanding of the factors influencing habitat suitability for middle spotted woodpeckers is necessary for identification and protection of optimal areas and for guiding forest management.

Environmental features important for the middle spotted woodpecker are most often those that are recorded in classical forest inventories (Müller *et al*. 2009, Walczak *et al*. 2013). Moreover, some additional characteristics describing the complexity of within-stand structure can be simply obtained directly from basic data (Kurlavicius *et al.* 2004, Stachura-Skierczyńska *et al.* 2009). Some studies have reported the importance of decaying or cavity trees, which are not normally included in forest inventories; however, these factors have usually been found to be of lesser significance (Pasinelli 2000). Nevertheless, environmental parameters describing tree species composition, the vertical structure of stands, etc., are frequently omitted in studies of habitat selection of the middle spotted woodpecker (however, *see* Pavlik 1994, Roberge *et al.* 2008, Delahaye *et al.* 2010, Walczak *et al.* 2013).

In this study, we analyze environmental factors affecting the occurrence of middle spotted woodpecker in three forests sited within Special Protection Areas, and differing in size, spatial structure, habitat conditions and history of use. Our goal was to develop a landscape-scale predictive model of potential nesting habitats for middle spotted woodpeckers. In particular, our objectives were: (1) to identify key environmental variables that affect the presence of middle spotted woodpecker under varying habitat conditions, (2) to evaluate the spatial distribution of key habitats for middle spotted woodpeckers in various spatial contexts, and (3) to provide a focus for conservation efforts.

Methods

Study area and the middle spotted woodpecker population

We developed models for three Special Protection Areas (SPAs) designated by national authorities in Poland within the framework of the European Birds Directive (2009/147/UE) (Fig. 1): Krotoszyn Oak Forest (PLB300007), Forest at the Drawa River (PLB320016), and Knyszyn Forest (PLB200003).

Krotoszyn Oak Forest (KOF; 17°32´17´´E, 51°38´36´´N) consists of several isolated forest patches totalling about 15 600 ha, and surrounded by agricultural areas. The whole site is protected as one of the largest concentrations of old oak forests (mainly *Quercetea-robori petreae*, locally *Calamagrostio arundinaceae–Quercetum petraeae*) in central Europe (Kasprowicz 2010). Stands with dominant oak (mainly Pedunculate oak *Quercus robur*) comprise about 47% of the total forest area. More than 60% of oak-dominated stands are over 100 years old. The average age of stands (80 years) is therefore much higher than the average for Poland (56 years; Anon. 2012). KOF consists mainly of productive forests, with a few reserves covering less than 1% of the total forest area. As an important source of high quality oak hardwood, the site has been exploited since the end of the 19th century. Small, elongated clearcuts are the most common type of regeneration in oak-dominated stands.

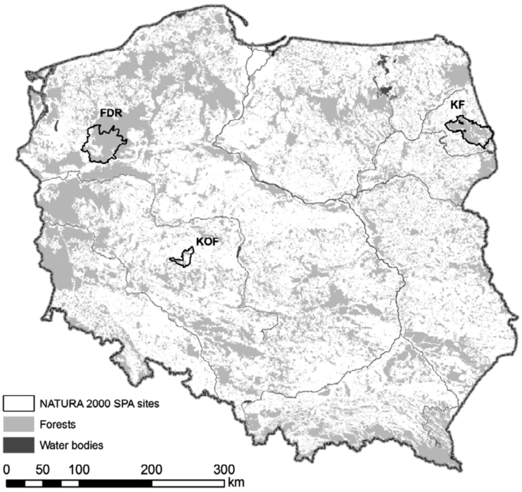

Fig. 1. Distribution of study sites across Poland (KOF: Krotoszyn Oak Forest, FDR: Forest at the Drawa River, KF: Knyszyn Forest).

Forest at the Drawa River (FDR; 15°53´37´´, 53°02´32´´N), located in northwestern Poland, consists of about 115 000 ha of forested area. Before the 20th century wars, the whole site was a mosaic of forests, extensive farmlands and meadows. Nowadays, it is covered by an almost continuous forest. Pine stands (Scots pine *Pinus sylvestris*) have replaced abandoned fields and grasslands, as well as the primary broadleaved and mixed forests destroyed during wars. Deciduous stands (mainly *Melico-Fagetum*, *Luzulo pilosae-Fagetum*, riparian ash-alder communities belonging to the *Fraxino-Alnetum* association) still cover about 11 200 ha, mainly over moraine hills in the southwestern part and along water courses. Among the broadleaves, oak is the dominant species, followed by birch (*Betula* spp.), beech (*Fagus sylvatica*) and alder (*Alnus glutinosa*). The central part of the area is protected within the boundaries of Drawieński National Park. In total, protected forests cover about 9% of the total forest area.

Knyszyn Forest (KF) is located in eastern Poland (23°24´18´´E, 53°03´23´´N) and encompasses about 92 000 ha of forested area. Pine is the dominant species, followed by spruce (*Picea abies*), birch and alder. Unlike in the other two forests, beech is absent from KF. The site has been an important timber growing area for a long time. Timber has been exported from here since the 16th century, with several episodes of wanton exploitation during wars (Czerwiński 1995, Angelstam & Donz-Breuss 2004). Nowadays, deciduous stands cover about 12 000 ha, including subcontinental oak–lime–hornbeam communities (*Melitti-Carpinetum*, *Tilio-Carpinetum*, *Tilio-Piceetum*), rare maple–lime forests (*Aceri-Tilietum*) in the north-central part, ash–alder riparian communities (*Circaeo-Alnetum*, *Fraxino-Ulmetum*, *Piceo-Alnetum*) and alder bogs (*Carici elongatae-Alnetum*) along water courses and near surface springs, mainly in the northern, western and central parts of the area. Reserves cover approximately 4% of the site area (Stachura-Skierczyńska *et al*. 2009) and protect the most valuable parts of deciduous forest communities. The remaining deciduous stands are subjected to various forms of group fellings and alder bogs are usually clear-cut.

KOF is the second most important middle spotted woodpecker site in Poland, with a population estimated at ca. 480 pairs (Wilk *et al*. 2010). In contrast, in FDR the middle spotted woodpecker is rare, with the whole population estimated at only 40–60 pairs (Wilk *et al*. 2010). KF, with recent estimates at 160–200 pairs (T. Tumiel unpubl. data from 2011–2012), ranks as one of the most important sites in Poland (Wilk *et al*. 2010).

Woodpecker occurrence data

For the purpose of this study, we used presence records for the middle spotted woodpecker obtained from 1 km × 1 km study plots, selected at random, during pre-breeding periods in 2010 (KOF), 2010–2011 (FDR) and 2011–2012 (KF). We surveyed birds in a total of 19 sample plots in KOF, 67 in FDR and 50 plots in KF. Each plot was surveyed in one year only. Within plots, all habitats were checked twice. As a way of overcoming difficulties in detection and mapping, the survey was based on the well-described and recommended audio stimulation (playback) method (Kosiński *et al*. 2004, Kosiński & Winiecki 2005). To provoke responses from territorial birds, taped calls (rattle- and advertising-calls of males) were used. To reduce the probability of some individuals being attracted away from their territories through the use of the playback technique, the following parameters were applied: a minimum distance of 150–200 m between points, a maximum time of 40 seconds for the stimulation in one bout, and a minimum interval of 1–2 minutes for listening. A second bout of playback was rarely performed. After the first bird response, the taped calls were stopped to determine the initial location of the bird. The woodpecker's position, behaviour, type of call and movements were recorded and mapped. Special attention was paid to register simultaneously active birds (Tomiałojć 1980). In this way, the number of birds holding territory on the study plots could be assessed. It was assumed that two registrations are required to accept a territory (Kosiński *et al*. 2004). On the basis of experience from previous studies, we can assume that up to 80% of all territories can be found during one visit (Kosiński *et al*. 2004), and two visits allow an experienced observer to find almost 100% of territories (Z. Kosiński unpubl. data). All surveys were performed in good weather conditions, without rainfall or strong wind. The approximate centre of bird activity was identified on the basis of all collected observations for each individual/breeding pair and GPS-marked. An earlier study suggests that the distribution of nest-sites corresponds to the territories delineated during the pre-breeding season (Kosiński *et al*. 2004).

During the surveys, 70, 49 and 46 woodpecker territories were found in KOF, FDR and KF, respectively. Since the model algorithms used in this study allow for presence-only data from various sources (Phillips *et al*. 2006) and in order to improve model performance, we also used additional records collected outside the sample plots within the frameworks of broader inventories conducted in 2010 in KOF and 2011–2012 in KF. In total, we used 142, 49 and 129 middle spotted woodpecker locations from KOF, FDR and KF, respectively.

Environmental data

For modelling purposes, we used variables describing the following: stand age, structure, presence of wet habitat types and percentage share of particular tree species. All the information was assigned to a 16 ha square grid. For different categories of stands, we calculated their percentage coverage in the grid cell; for tree species, we calculated their proportional (stand area weighted) presence in the cell. Basic descriptive statistics for all variables in the study areas are provided in Appendix 1. The grid resolution (16 ha) corresponded to the approximate size of an average winter home range of middle spotted woodpeckers (Pasinelli *et al*. 2001), ensuring all ecological requirements for survival and reproduction. For males and females, winter home ranges overlap to a major extent and during the breeding season pairs limit their territories to the core area (Pasinelli *et al*. 2001, Pasinelli 2003). Moreover, Kosiński (2006) reported that the probability of the occurrence of middle spotted woodpeckers increased up to 90% in plots of 16 ha containing optimal habitats. Therefore, for modelling purposes it can be assumed that a 16-ha grid cell represents the minimum area necessary for a pair of woodpeckers during the whole year. Adjusting the model resolution to the average home range is a widely used and justified approach (Guisan & Thuiller 2005).

Forest age: Four age classes were distinguished, corresponding to the four main forest growth stages: young (0–39), premature (40–79), mature (80–119) and old (120 and more years).

Structure: We identified stands with a well-developed uneven vertical structure as those where trees of different ages were present, with at least 30 years of age difference and the proportion-weighted average age of all trees was 80 years or more. We adopted and modified this criterion after Kurlavicius *et al*. (2004). In order to assess the diversity of tree species, we calculated the total number of species in each stand's canopy (excluding the understory) and distinguished three categories: low (1–3), medium (4–6), and high (7 or more species). Finally, we used the forest inventory classification for canopy density (closure): high (partially overlapping crowns, no openings), medium (gaps between crowns might occur, but smaller than one single crown), low (gaps wide enough to fit one or two mature trees), and sparse (individual trees growing at some distance, no competition for light between trees).

Wet habitat types: This category included all wet, bog and riparian forest types, according to the forest inventory classification. We used this as additional information, supplementing the percentage of particular tree species.

Species composition: We calculated the relative percentages of the most abundant tree species (those that appeared as the dominant species in more than 1% of all stands in the given study area). The more abundant deciduous species (alder, birch, oak, beech and ash *Fraxinus excelsior*) were included in the model as separate variables. For less common species (hornbeam *Carpinus betulus*, aspen *Populus tremula*, lime *Tilia* spp., maple *Acer* spp.), we calculated their combined percentage as one variable. The same was done for all coniferous species (pine, spruce and larch *Larix europaea*). In FDR, hornbeam, lime, aspen and maple were rare (in less than 1% of all stands) and were not included in the model.

Statistical analysis

Principal component analysis of environmental variables

It is assumed that models might be vulnerable to correlation in terms of variables if the correlation is high (Mertler & Vannatta 2002). For this reason, we tested the environmental variables in each study area for correlations pairwise, using Spearman's rank correlation ($p < 0.01$). Since we found a high degree of correlation in some variables, we performed a Principal Component Analysis (PCA) with a varimax rotation to identify ecologically meaningful relationships between environmental variables and used factor scores as new predictor variables in the models. Models based on individual variables were also retained as an additional source of information regarding the response of predicted values to the change in particular variables, while taking into account the relationships between variables and their importance for the ecology of model species. Analyses were performed using SPSS (ver. 20.0, IBM Corp.).

Prediction models

We modelled the probability of the occurrence of the middle spotted woodpecker using the maximum entropy method implemented in MaxEnt, ver. 3.3.3k (Phillips *et al*. 2006, Phillips & Dudík 2008, Elith *et al*. 2011) and the genetic algorithm for rule-set prediction (GARP) implemented in openModeller Desktop, ver. 1.1 (Stockwell 1999).

We used the presence-only modelling approach because of the nature of our data, which contained both presence-absence (obtained from 1 km^2 plots) and presence-only records (obtained from the remaining area). In the case of specialist species, such as the middle spotted woodpecker, predictive distribution models seem less sensitive to the absence data than is the case with generalists (Brotons *et al*. 2004, Elith & Graham 2009); therefore, we assumed the presence-only approach to be more suitable. However, absence records were used for an additional check of model performance.

Each model consisted of 10 replicated runs (partial models). In each run, the occurrence data were randomly partitioned into training and testing samples (75% and 25% of occurrences, respectively). Results of partial models were averaged, providing a final predictive map of habitat suitability. Final models were compared using the area under the curve (AUC) of the receiver operating characteristics (ROC). AUC values exceeding 0.75 indicated informative and potentially useful models, and models with AUCs above 0.9 were considered excellent (Elith 2000).

Both models use the subsample of presence records for self-assessment of the prediction error. In the case of GARP, the output is binary (0 = absence, 1 = presence) and it is possible to compute the omission rate of the test sample as the ratio of false absence predictions to all presence records. This ‘false negatives’ rate allows an assessment of the risk of a Type II error (omitting potentially suitable habitats for the species). In the case of MaxEnt, the model output is the continuous logistic function of the input variables, with values ranging between 0 and 1. This estimate is often interpreted as the direct probability of species’ occurrence (Yackulic *et al*. 2013). However, MaxEnt output is not analogous to occurrence probability, since typical presence localities (locations where species have been recorded in the field) can already have the corresponding logistic output value (lower presence threshold, LPT) of 0.5. Here, we treat the MaxEnt logistic output as the index of habitat suitability which, by definition, affects the species’ occurrence probability, but it is not the same as the binary probability value (i.e. in GARP). As a form of self-assessment, MaxEnt uses the subsample of input presence records to test the null hypothesis that predictions for these points are no better than those for a random sample within the same fractional predicted area and computes the omission rate for a default fixed cumulative value of a raw prediction. In addition, we compared the MaxEnt prediction with actual presence data. We adjusted LPT using Jenks’ natural breaks classification, which determines the best arrangement of values into classes by iteratively comparing the sums of the squared difference between observed values within each class and class means. The optimal classification identifies breaks in the ordered distribution of values that minimizes within-class sum of squared differences (Jenks 1967). We applied two break values, thus dividing MaxEnt habitat suitability estimates into three classes. All grid cells in the third class (with the highest estimate) represented optimal habitats and were considered typical presence localities, while all grid cells in the second class (between the lower and higher natural break values) represented suboptimal habitats (possible presence localities). With this assumption, we compared predicted false absence records with all presence points, therefore obtaining an approximation of the risk of a Type II error. Finally, we used 'real absence' data from sample plots (described in the Methods section) to estimate the risk of a Type I error (predicting the presence of species in locations that are actually unsuitable). Since the area of the sample plot (1 km^2) was bigger than the spatial resolution of the model output grid (16 ha), we assumed that the grid cell falls within the plot if its centroid is inside the plot; therefore, all cells in plots where no woodpeckers have been detected are considered absence records.

The effect of individual model variables on predicted habitat suitability was estimated from the variables' response curves. The relative contribution of variables was assessed with the jackknife analysis, which shows how each variable affects the predictive power of the model. During each iteration of the training algorithm, values of an individual variable for presence and background data are randomly permuted; then, the model is re-evaluated and the increase in regularized gain is added to the contribution of the corresponding variable. This is done for each variable in the model. For the purpose of interpretation, the corresponding increase in the model gain is normalized to percentages.

Spatial analysis

In the first step, we analyzed the spatial distribution of forest stands potentially suitable for middle spotted woodpecker, according to the current state of knowledge (stands with oaks over 80 years and/or alder over 60 years old). We applied the *Average Nearest Neighbour* tool (ArcGIS ver. 9.3, ESRI Inc.) to compare mean pairwise distances between the nearest stands with the hypothetic random distribution (with the same number of features covering the same total area). If the average distance between features is less than the average for a random pattern, the feature distribution is clustered; otherwise, it is considered dispersed.

We applied a cluster and outlier analysis (ArcGIS ver. 9.3, ESRI Inc.), using the predictive habitat suitability map as an input layer, to identify where the best woodpecker habitats concentrate spatially. The cluster and outlier analysis seeks spatial autocorrelation among grid cells by calculating the local Moran's I value (LMI) for each cell (Anselin 1995). Positive LMI values accompanied by a high positive Z score indicate that both the analyzed grid cell and surrounding cells have similar high values (here: a high habitat suitability index) and therefore form a 'high cluster'. In order to smooth cluster boundaries (exclude single isolated spots outside the main range), we applied Hawth's tools kernel density estimate (Beyer 2004), using 90% of all grid cells classified as 'high clusters'.

Results

Distribution of potentially suitable forest types in study areas

On the basis of state-of-the-art knowledge, we compared the proportions of potentially suitable forest types among study areas: stands containing oaks at least 80 years old, and stands containing alders at least 60 years old; both were considered either as the dominant species or as an admixture. Stands with beech over 200 years that could also qualify as suitable were practically absent from the study area; therefore, we considered them insignificant.

In comparison with the other sites, KOF was the most outstanding area, with mature oak stands relatively common, large and located close to each other. Alder stands at least 60 years old were generally rare; however, in KF both their total area and the average stand size were more than twice as big as in the other two study areas. In all cases, the studied habitats had a clustered spatial distribution (Table 1).

Correlations of the environmental variables

In all three areas, we found positive correlations (Spearman's $\rho \geq 0.6$) between some environmental variables: In KOF, between 'oak' and 'old', 'uneven stands' and 'beech'; in FDR between 'oak' and 'beech'; and in KF between 'uneven stands' and 'mature', 'high number of species' and 'other deciduous'. Also, in all three areas 'alder' and 'wet habitats' were correlated. In some cases, significant positive correlations also occurred between other variables (i.e. 'coniferous', 'low number of species' or 'young'); however, taking into account the ecological demands of middle spotted woodpecker, we considered them unimportant.

For KOF, FDR and KF respectively, we found seven principal components with an initial value exceeding one, altogether explaining 71%, 68% and 71% of the total data variance (Appendix 2). In general, relationships between environmental variables commonly associated with middle spotted woodpecker were similar in KOF and FDR. In both areas, the variables 'uneven stands', 'old' and 'oaks' were positively correlated with the first component (PC1). The variables 'low canopy closure' in KOF, and 'beech' and 'medium number of species' in FDR were also positively correlated with PC1. However, in KF, PC1 depicted the variables 'high number of species', 'oak', and 'other deciduous species' ('ash' was also moderately correlated with this component). Neither 'old', nor 'uneven stands' were significantly correlated with PC1 in KF. The variables 'wet habitats' and 'alder' were positively correlated with PC3 in all study areas.

Evaluation of predictive models

All MaxEnt models had high mean AUCs, indicating their good discriminative abilities (Table 2). There were very small differences in AUC values among models based on all variables and PCA scores, although PCA-based models performed slightly better. GARP models had generally lower AUC values as compared with MaxEnt, and PCA improved the results only in the case of KOF. In all cases, models with the lowest number of presence records (FDR) had the highest AUC. This high score might be an artifact of the AUC statistics being based on a small sample size. However, a comparison of model predictions with real presence and absence data also indicates fairly good discriminative abilities for the model for FDR (Table 2).

In general, GARP models performed better in detecting suitable areas with a high probability of species' occurrence, while MaxEnt was more likely to misclassify as unsuitable areas where the species was actually present (Table 2). However, it appeared that GARP generally tended to overestimate habitat suitability and predicted the species' presence on plots where it had not

Table 1. Spatial characteristics of forest types potentially suitable for the middle spotted woodpecker. Distribution patterns were analyzed with ArcGIS Average Nearest Neighbour test. NN distance = distance to the nearest neighbour; NN ratio = ratio of the observed *vs.* expected NN distance; *Z* and *p* are the statistics of the Average Nearest Neighbour test.

	Percentage of forest area	Mean patch size ± SE (ha)	NN distance (m)	NN ratio	*Z*	*p*
Oak 80+ dominant						
KOF	34.8	39.3 ± 18.4	675	0.60	–8.93	< 0.001
FDR	3.0	9.4 ± 1.4	856	0.66	–12.60	< 0.001
KF	0.3	7.3 ± 1.8	1147	0.68	–3.57	< 0.001
Oak 80+ present						
KOF	25.2	15.5 ± 1.9	526	0.64	–10.35	< 0.001
FDR	7.0	7.9 ± 0.4	575	0.72	–17.25	< 0.001
KF	7.7	16.1 ± 0.2	641	0.70	–12.19	< 0.001
Alder 60+ dominant						
KOF	0.9	2.2 ± 0.3	830	0.53	–46.97	< 0.001
FDR	0.9	2.4 ± 0.2	680	0.54	–18.38	< 0.001
KF	2.2	5.7 ± 0.5	710	0.63	–13.38	< 0.001
Alder 60+ present						
KOF	6.3	7.2 ± 0.9	623	0.58	–9.35	< 0.001
FDR	2.2	4.3 ± 0.2	636	0.59	–19.36	< 0.001
KF	7.0	9.1 ± 0.7	538	0.69	–15.82	< 0.001

been detected more often than MaxEnt did. This error was particularly common in KF. Since the general purpose of this paper is to identify the best potential habitat areas for the middle spotted woodpecker, it seems more appropriate to rely on models that are better at discriminating suitable habitats from unsuitable ones, even at the risk that some suitable spots might be omitted. Therefore, for further analysis we use MaxEnt outputs.

Analysis of the importance of variables

In all the study areas, PC1 made the highest contribution to predictive models. In KOF and FDR, it contributed to 84% and 96% (respectively) of normalized model training gain, which makes it the most important predictor of middle spotted woodpecker occurrence in both areas. Other PCs were considered unimportant, since their individual contributions were disproportionately small (below 5% in each case). In KF, PC1 corresponded to 55% of the training gain and the second most important variable, PC3, corresponded to 35%. Again, the individual contribution of the remaining PCs did not exceed 5% in each case.

Both in KOF and FDR, ‘oak’ made the highest contribution among all variables (39% and 73%, respectively). The response curve for ‘oak’ shows that predicted habitat suitability increases along with the increase of variable value. It can be observed that even a relatively small amount of oak (around 10%–20% in the 16 ha grid cell) can substantially improve habitat suitability, as indicated by the rapid growth of response (Fig. 2). However, as we overlapped model predictions with real stand-level inventory data, it appeared that stands qualified as optimal habitats had a much higher average share of oak (mean ± SD): 90% ± 10% and 62% ± 21% in KOF and FDR respectively. The average age of oaks in these stands oscillated around 100 years (104 ± 55 in KOF and 102 ± 54 in FDR). The second variable, ‘old’, corresponded to 19% and 7%, respectively. Here, it can be seen that response curves started from already high values of the corresponding habitat suitability index. The curves rose very quickly until the variable ‘old’ reached 10%–20%, then the growth became much slower. This means that even with a very small proportion of old stands, the grid cell might be a high quality habitat. However, in both study areas the variables ‘oak’ and ‘old’ were correlated and their individual input should be interpreted with caution. The next variables — ‘young’ in KOF and ‘uneven stands’ in FDR — contributed to 5% and 6% of the training gain, respectively; the effect of ‘young’ on predicted habitat suitability was negative.

In KF, the situation seems more complex, since there were more variables with individual inputs exceeding 5% of the model training gain. Among these, ‘alder’, ‘high number of species’ and ‘uneven structure’ positively affected habitat suitability (as indicated by the rise in response

Table 2. Evaluation of predictive models for all studied areas.

	KOF		FDR		KF	
	All variables	PCA	All variables	PCA	All variables	PCA
MaxEnt						
Mean AUC	0.79	0.81	0.97	0.97	0.90	0.91
False negatives rate[a]	0.39	0.25	0.33	0.27	0.29	0.26
False positives rate[b]	0	0	0	0.03	0.05	0.10
GARP						
Mean AUC	0.74	0.78	0.96	0.93	0.83	0.72
False negatives rate	0.13	0.17	0.04	0	0.01	0
False positives rate	0.06	0.06	0	0.19	0.52	0.51

[a] Ratio of predicted false absence *vs.* all presence records.

[b] Ratio of predicted false presence *vs.* all ‘true absence’ records from sample plots.

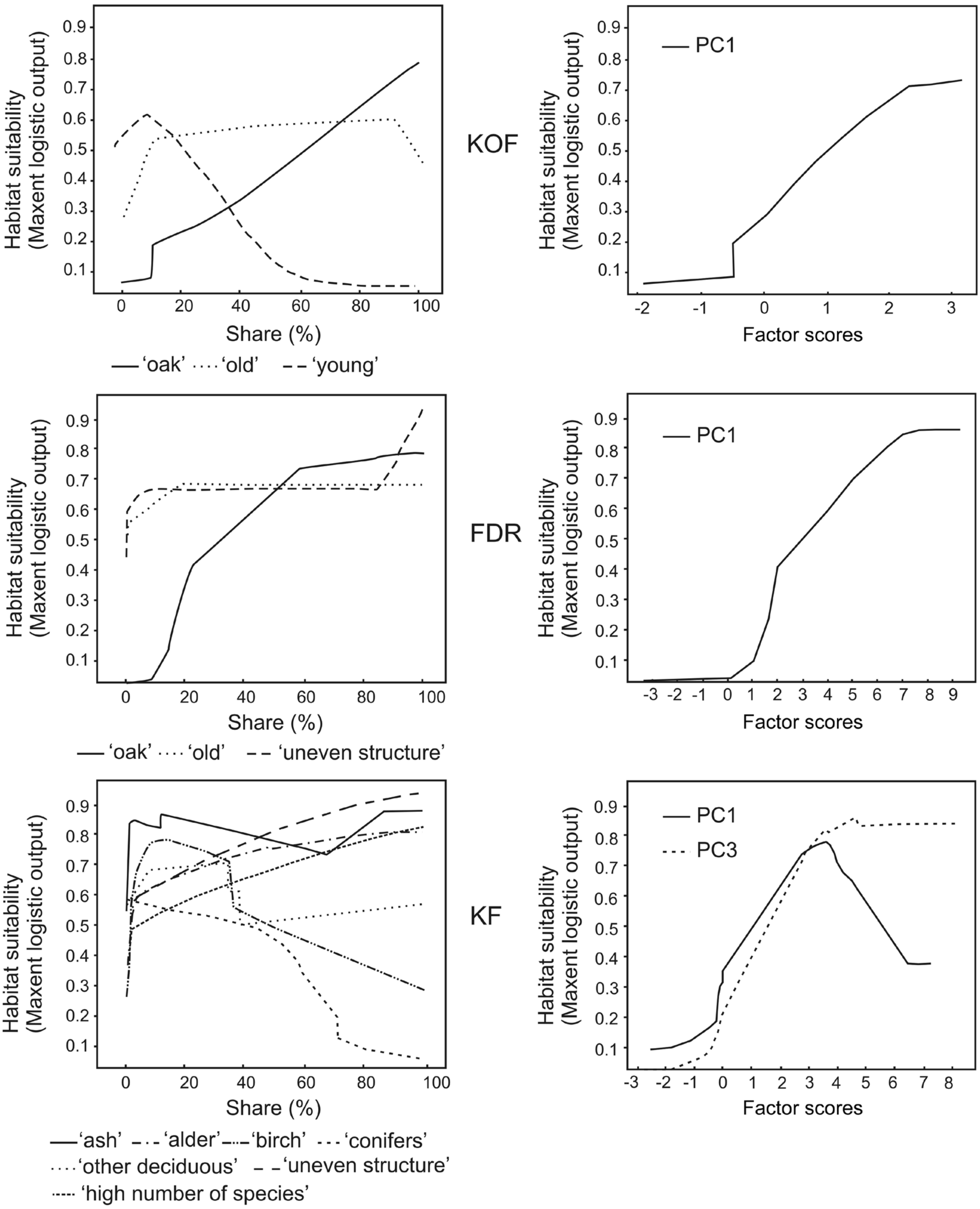

Fig. 2. Response curves of individual environmental variables and principal components used in predictive models (only variables that contribute to at least 5% of the training gain are shown). The curves show how the logistic prediction (habitat suitability) changes as each variable is varied, while all other variables remain at their average values.

curves); while 'birch' and 'conifers' had a negative effect (Fig. 2). It is interesting to note that in KF 'oak' was not present among variables with high individual contribution to the model. The average share of oak in stands qualified as optimal was relatively high (42% ± 14%), but its average age was only 40 ± 25 years. On the other hand, the average age of alder in these habitats was 70 ± 29 years and its share oscillated around 56% ± 19%.

Response curves for PCs show that both PC1 in all study areas and PC3 (in KF) positively affect habitat suitability (Fig. 2). However, due to the fact that these variables are based on principal component analyses, it is not possible to relate the shape of curves to the corresponding relative percentages of particular species or age classes in the grid cell.

Despite the input of individual environmental features, none of them affected the model AUC substantially. This is due to existing correlations between variables, such that a single one seldom provided specific information that was not present in other variables. As the variable was removed from the model, other correlated variables replaced it in the model. For PCs, which are not correlated by definition, the situation is different. The results of a jackknife test on test sample AUC for all PCs show that both in KOF and FDR, PC1 made the highest contribution to AUC when used in isolation; moreover, it decreased the model's predictive power the most when it was omitted (Fig. 3). For other PCs, the corresponding fall in AUC was negligible. This means that the information carried by PC1 was both the most useful and the most specific of all the information. A similar situation was observed for KF, but here both PC1 and PC3 had the most significant effect on AUC and the input of other PCs was disproportionately low.

Spatial distribution of suitable habitats

In all study areas, we classified suitable habitats as either suboptimal (lowest presence thresholds: 0.16, 0.15, 0.14) or optimal (lowest presence thresholds: 0.43, 0.44, 0.43) in KOF, FDR and KF, respectively. In FDR and KF, the proportion of optimal habitats in total forest area was generally low (approximately 4% in FDR and 10% in KF) and substantially higher in KOF (around 26%). In total, suitable habitats (both optimal and suboptimal) covered approximately 9% of the total forest area in FDR, 27% in KF and over 60% in KOF.

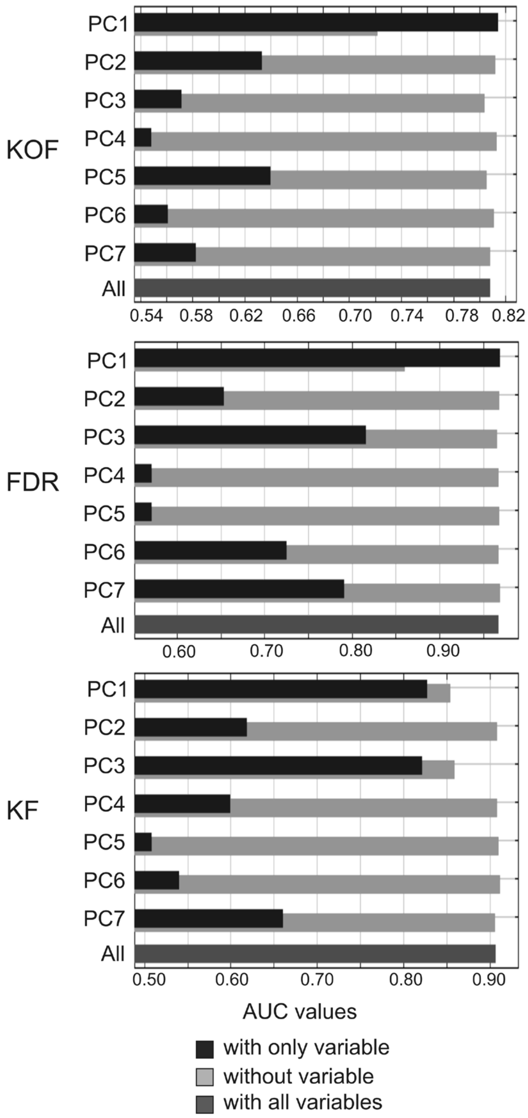

Fig. 3. Results of the jackknife test of principal components using the AUC on test data. Black bars represent the effect of individual variables on the AUC value; light grey bars: the drop in AUC while the tested variable is removed from the model.

The concentrations (clusters) of grid cells with high habitat suitability index included more than 85% of all actual occurrences of the middle spotted woodpecker. The fraction of total forest area included within clusters was smallest in FDR and largest in KOF. The average area of clusters in all three areas ranged between 2157–2540 ha, with the highest variation from the average in KF (Table 3). In each study area, at least one very big cluster was identified, surrounded by several smaller ones (Fig. 4). Clusters had a dispersed spatial pattern (Average Nearest Neighbour test: Nearest Neighbour distance ratio > 1, $p < 0.001$). Distances between clusters (measured as distance between cluster boundaries) were smallest in KF and largest in FDR (Table 3).

Discussion

Habitat selection patterns

Our results highlight the diversification of environmental factors that affect the spatial distribution of the middle spotted woodpecker. Depending on local conditions, the species exhibited a certain degree of flexibility in habitat use.

Our results confirm that the relationship between species' presence and environmental factors is mainly connected with the proportion of oaks in a given area (e.g. Pasinelli 2000, 2003, Kosiński 2006). The middle spotted woodpecker can benefit even from a relatively small increase in the proportion of oak, especially in those regions where oak-dominated stands are not common (Winter *et al*. 2005). In our study, in FDR grid cells with approximately 20%–30% share of oak (which corresponds to ca. 3–5 ha of oak-dominated stands) had a habitat suitability index that already qualified them as optimal middle spotted woodpecker habitats. However, both in KOF and FDR the average share of oak in optimal habitats was much higher. In general, the species' preferences in both KOF and FDR could be summarized briefly as 'the more oak, the better'. The abundance of old age classes (120 and older) also positively influenced the probability of woodpecker occurrence. The predicted habitat suitability was already very high at a relatively low proportion of old stands (around 20% of the total forest area within the grid cell). Although in our study these two predictors were correlated and the response of the probability function should be interpreted cautiously, the results are in line with previous studies, thus confirming the strong positive relationship between the presence of old, oak-dominated stands and the presence and abundance of middle spotted woodpeckers (Pasinelli 2000, Müller *et al*. 2009). Kosiński (2006) showed that the probability of woodpecker occurrence increased with the area of the optimal habitat, with patches of 16 ha having a 90% probability of encountering woodpeckers. In our study, for both KOF and FDR the probability of occurrence also increased steadily with the increasing percentage of oak. Middle spotted woodpeckers can inhabit oak forests over 80 years old (e.g. Pasinelli 2000, Kosiński 2006, Müller *et al*. 2009). In our study areas such forests were available, but woodpeckers clearly preferred the oldest stands wherever possible and the average age of oak stands in optimal habitats oscillated around 100 years. Predictors other than forest age and proportion of oak were less important when considered separately. However, variables associated with the uneven structure of stands and/or the presence of gaps in the canopy layer were positively

Table 3. Spatial characteristics of concentrations (clusters) of suitable habitats for the middle spotted woodpecker in the study areas. NN ratio = ratio of the observed *vs*. expected distance to the nearest neighbouring cluster; *Z* and *p* are the statistics of the Average Nearest Neighbour test.

Cluster characteristics	KOF	FDR	KF
Percentage of total forest area	46.4	16.6	22.6
Percentage of MSW[a] occurrences included	85.9	100.0	88.6
Mean area ± SD (ha)	2157 ± 2310	2540 ± 3077	2340 ± 4989
Mean (min–max) distance[b] (km)	4.4 (2.5–6.2)	5.0 (1.8–12.6)	3.2 (0.5–10.6)
NN ratio	2.38	2.32	1.56
Z	5.90	7.99	3.86
p	< 0.001	< 0.001	< 0.001

[a] Middle spotted woodpecker.

[b] Distance between cluster boundaries.

correlated with the presence of oaks and the high age of stands. Old deciduous stands can develop such unevenness, either due to natural gaps in dynamic processes, or, in the case of productive forests, due to management practices, e.g. shelterwood cutting. Such structures can also benefit middle spotted woodpeckers. Less dense canopies, with small openings provide more sunlight, which favours the abundance of arthropods, their main source of food (Pasinelli & Hegelbach 1997, Pasinelli *et al*. 2001). However, if the preferred old trees (oaks ≥ 36 cm dbh) become too sparse, the home range size increases (Pasinelli 2000). Therefore, even when total forest size remains stable, the carrying capacity of the habitat is lowered, decreasing population density and the probability of species' occurrence in a given location (Pasinelli 2000). This explains why neither stands with high canopy density, nor those with sparse, separated trees were preferred by woodpeckers.

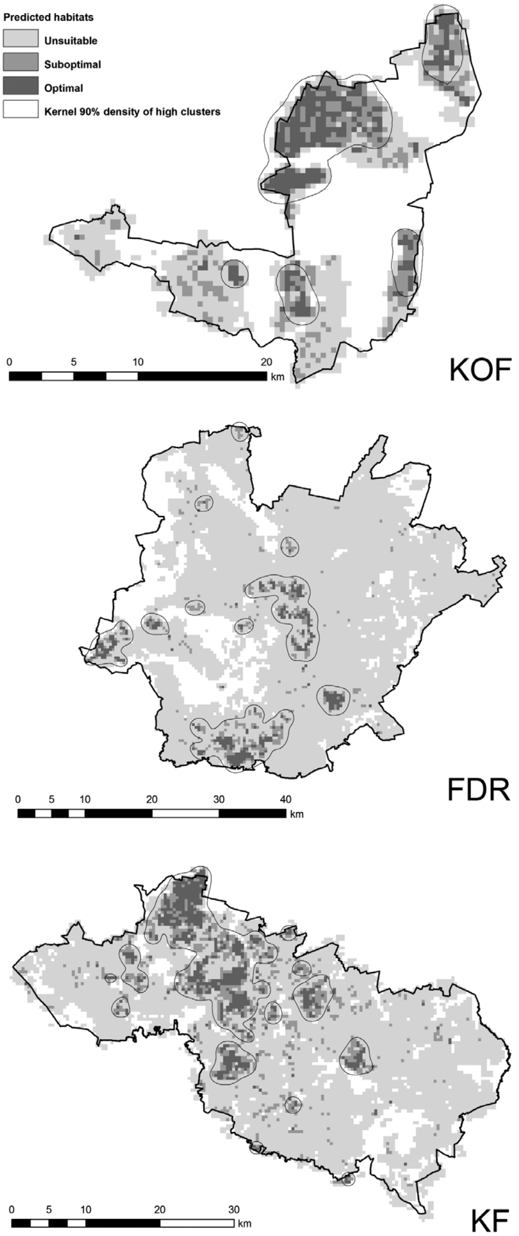

Fig. 4. Spatial distribution of suitable middle spotted woodpecker habitats in the study areas. Black outlines represent concentrations of cells with high habitat suitability index, delineated with the cluster and outlier analysis and kernel density estimate.

The habitat selection choices in KF were quite different. Unlike in the other two areas, there were more predictor variables of relatively high contributions, and neither the proportion of oak nor the presence of old stands were among them. Although the woodpeckers generally responded positively to an increasing proportion of alder, stands with uneven structure and high number of species, the individual effect of predictor variables was difficult to estimate. In KF, middle spotted woodpeckers preferred two types of habitats: deciduous forests with a high number of tree species, including oak (but not always as the dominant species), and alder–ash bogs. These habitat types are often located near alder–ash, wet and bog communities along streams and surface springs (Czerwiński 1995), creating large concentrations of suitable habitats, able to maintain local populations of 10–30 pairs (T. Tumiel unpubl. data). Such preferences suggest that these types of stands are important habitats for middle spotted woodpeckers in an area where oak-dominated forests are scarce. In KF, patches of forest with dominant oak are usually small and young. Oak-dominated stands over 80 years old occur in just a few locations in the northern and central parts of the area. However, middle spotted woodpeckers can inhabit rich deciduous stands where not only oaks, but also other rough barked species, such as lime, maple and ash, can be found. It is worth noting that in the near-primeval lowland forests in Białowieża National Park (Poland), middle spotted woodpeckers inhabit all types of broadleaved forest stands, including ash–alder forests, alder-swamp forests and oak–hornbeam–lime forests (Wesołowski *et al.* 2002).

There are few records regarding the local occurrence of middle spotted woodpeckers in alder bogs. Weiβ (2003) reported from eastern Germany that woodpeckers inhabiting a large continuous alder forest tract preferred trees with at least 22 cm of diameter for foraging. In our study area, this value corresponded to an age threshold of 53–54 years; however, the average age of alders thicker than 21 cm in KF exceeded 70 years, with a substantial admixture of trees with 40–50 cm of diameter and an approximate age of 100 years and more. In KF, we found that in stands classified as optimal habitats, where old oaks were rare or absent, the average age of alder oscillated around 70 years and its average share around 56%. Another study on a large population (around 100 breeding territories) from eastern Germany assumed that old alder stands (above 60 years) have the same attributes which are important for the foraging ecology of the middle spotted woodpecker as old oak stands and, therefore, the species is able to reach similar population densities in both types of habitats (Noah 2000). Our study confirms these findings. Compared with oaks, it takes much less time for alder trees to become attractive for woodpeckers, which explains why older age classes (over 80 and over 120 years) were not important as predictors of middle spotted woodpecker occurrence in KF. It suggests that the size of the preferred trees, and not the age, is an important predictor of woodpecker occurrence (Pasinelli 2000, Robles *et al.* 2007b, Delahaye *et al.* 2010), and the correlation between age and size depends on tree species and local site conditions.

Model performance

The final models predicting the distribution of middle spotted woodpecker habitat performed well, as demonstrated by the high rate of woodpecker-presence localities included in kernel-delimited patches. In each study area, more than 85% of actual woodpecker occurrences (up to 100% in the case of FDR) were found within the kernel density clusters of suitable habitats. Previous censuses of a well-known population in KOF have shown a high coincidence with the location of predicted suitable habitats and actual population status (Kosiński & Hybsz 2006, Kosiński & Kempa 2007). These results provide additional evidence that modelling based on forest inventory data is reliable in predicting suitable breeding habitats for the middle spotted woodpecker.

Fragmentation of habitats

In each study site, at least one large concentration of suitable habitats was identified, surrounded by several smaller ones. It is generally assumed that large patches of suitable habitat are better for the survival of a species than the same amount of habitat in smaller isolated fragments (Hanski 1998, Hanski & Ovaskainen 2003). As a resident specialist forest species, the middle spotted woodpecker is vulnerable to both habitat loss and habitat deterioration (Müller 1982, Petterson 1985a, 1985b). Simulation studies of the dynamics of the middle spotted woodpecker metapopulation in open agricultural landscapes revealed that the lack of any large patches resulted in a serious decrease in the performance of the population (Schippers *et al.* 2009). Moreover, this study suggests that metapopulations perform equally well or better in heterogeneous landscape types that are a mix of small linear elements, which facilitate dispersal and large and small patches which secure the population in the long run. However, a few empirical studies concerning the effect of habitat fragmentation on the population viability of middle spotted woodpeckers suggest that habitat fragmentation does not seem to have a strong influence on middle spotted woodpecker demography. Kossenko and Kaygorodova (2001) did not find any significant negative effect of fragmentation on the proportion of eggs fledged. Moreover, nestling losses and total reproductive output measured as fledgling number did not differ between fragmented and continuous habitats (Kossenko & Kaygorodova 2007). Robles *et al.* (2008) found that the pairing success of territorial males was lower in smaller and more isolated patches, but these patches also had low population sizes, and patch size, patch isolation and population size in patches were significantly correlated, so it is difficult to know which factor actually influenced pairing success. Furthermore, these authors did not find any significant effects of fragmentation on the reproductive parameters of middle spotted woodpeckers (Robles *et al*. 2008), or post-fledging, first-year and adult survival (Robles *et al*. 2007a). However, it is worth noting that a decrease in forest patch size negatively affected clutch size and the number of fledglings in the great spotted woodpecker (*Dendrocopos major*) (Mazgajski & Rejt 2006), considered the most ubiquitous woodpecker species in Europe. On the other hand, habitat fragmentation seems to have a negative effect on the habitat distribution and population density of the middle spotted woodpecker (Müller 1982, Petterson 1985a, 1985b, Kossenko & Kaygorodova 2001). Robles and Ciudad (2012) found that small patches were less likely to be occupied by woodpeckers than larger patches, which may also suggest a negative effect of habitat loss and fragmentation on woodpecker occupancy. In addition, these authors found that better quality patches (with a high density of large oaks) were more likely to be occupied and colonized. This suggests that habitat quality (abundance of suitable foraging trees) is more important than habitat fragmentation in explaining patch-occupancy dynamics, since high-quality patches were more likely to be colonized and populations there remained more stable than in lower quality patches (Robles & Ciudad 2012).

In our study, we described three different situations: (1) a high abundance of excellent habitats in isolated forest patches within the matrix of an open agricultural landscape (KOF), (2) a large forest complex with a substantial proportion of good habitats located relatively close (KF), (3) a large forest complex with a low abundance and high dispersal of good habitats (FDR). The key question is whether woodpeckers migrate between local concentrations of suitable habitats, ensuring gene flow and the viability of the entire population. The middle spotted woodpecker is a resident forest bird which spends most of its lifetime in or below tree canopies (Jenni 1983, Pettersson 1983, Pasinelli & Hegelbach 1997). It is to be expected that while moving to new territories, birds would follow habitat patches that offer better foraging conditions. When a potentially suitable habitat patch is surrounded by unsuitable habitat (i.e. coniferous forest), or the distance between potentially suitable patches of habitats is too large, the middle spotted woodpecker might not reach it (Müller 1982).

In KOF, the spatial configuration of habitats resembles the one described by Shippers *et al*. (2009). Here, high quality patches are large enough to maintain viable populations, in most cases exceeding the threshold of 50 individuals necessary to avoid inbreeding depression (Frankham & Ralls 1998). In FDR and KF, patches of suitable habitats are located within a matrix of generally unsuitable continuous forest, which is more similar to the situation described from southwestern Russia, where the average sizes of suitable habitat patches (oak stands) were 8.3 ha and distances between neighbours ranged between 0.5–2 km (Kossenko & Kaygorodova 2001). Müller (1982) found that forests larger than 30 ha and lying closer than nine km to mainland populations are more likely to be colonized.

Since the same habitat (old, rough-barked tree stands) provides the most suitable foraging opportunities both to breeding adults and postfledging juveniles (Ciudad *et al*. 2009), connectivity between patches of suitable habitats is the main factor of concern for metapopulation performance (Schippers *et al*. 2009). We do not have any quantitative information regarding juvenile survival and dispersion in the studied areas. According to the few studies regarding dispersal potential of middle spotted woodpeckers, juvenile birds can disperse at an average distance of 1.3 km (up to 10.5 km) from their natal nest, in a continuous habitat most frequently < 3.5 km (Pasinelli 2003), or 0.9–4.8 km in a mosaic landscape (Ciudad *et al*. 2009). Therefore, it can be assumed that within clusters of suitable habitats in our studied areas individuals can disperse successfully. However, the average distance between neighbouring cluster boundaries approaches or exceeds the maximum dispersal distance found in earlier studies (Pasinelli 2003, Ciudad *et al*. 2009). Therefore, some clusters might be too far to be reached by young birds from other local populations, especially in FDR and KF. This problem is probably of least concern in KOF, where the majority of its large population is concentrated in one core area. KF, with the smallest average distances between neighbouring clusters, also has the potential to maintain connectivity within the population, although overall habitat suitability is lower than in KOF.

Irrespective of physical barriers to movement, e.g. inter-patch distance, behavioural inhibitions often coincide with landscape features such as ecotones, habitat gaps, and matrix habitat types. However, the mechanisms driving behavioural inhibitions to cross landscape are unknown (Harris & Reed 2002). It has been hypothesized that resident, habitat specialist and solitary species, such as the middle spotted woodpecker, are more inhibited in crossing ecotones or habitat gaps than are their ecological counterparts (Harris & Reed 2002). It is likely that both higher costs entailed in the search for suitable habitats and predation risk may be driving factors in a bird's decision to take a route across open landscape or a forest matrix, i.e. unsuitable, coniferous stands (Matthysen & Currie 1996, Ciudad *et al*. 2009). In this case, small and isolated concentrations of suitable habitats in FDR and KF might be less frequently reached during postfledging dispersal and be more vulnerable to extinction due to lower pairing success and demographic stochasticity.

Conservation implications

Habitat suitability models based on quantitative local probabilities of occurrence are considered important tools for evaluating the performance of protected area networks in species' conservation (e.g. Williams & Araújo 2000, Cabeza *et al*. 2004, Fernández & Gurrutxaga 2010). This approach, incorporating the dispersal pattern of suitable habitat patches, should provide a first step in the assessment of the possibilities of metapopulation persistence (Loiselle *et al*. 2003). Although niche-based models have proved useful in assessing the amount of suitable habitats and the influence of different management scenarios on target bird species (Suárez-Seoane *et al*. 2008, Stachura-Skierczyńska *et al*. 2009), they are still seldom applied as a decision-making support for particular sites (Fernández & Gurrutxaga 2010), the reason being that detailed environmental datasets and/or sufficient species distribution data are often not available at the local scale (Brambilla *et al*. 2009). Our study offers a background for responsible management planning not only for NATURA 2000 sites but also for non-protected sites through the identification of areas of high importance for the middle spotted woodpecker and the key environmental factors driving its spatial distribution in different forest landscapes. Our results suggest that, in order to improve conditions for the middle spotted woodpecker, conservation activities should be aimed at maintaining and improving habitat quality. In our study, areas inhabited by middle spotted woodpeckers consisted mainly of managed forest; nevertheless, two of them contained more than 1% of the national population, which makes them crucial for the survival and reproduction of the species according to the European Bird Directive. This example shows that the responsibility imposed by the Bird Directive to maintain a species and its habitats in favourable state lies mainly with forest managers. It is possible to simultaneously preserve suitable habitat conditions for middle spotted woodpeckers and maintain the commercial exploitation of a forest with a reasonable economic return. Responsible forest management must take into account the necessity to create future generations of trees suitable for foraging and nesting by providing a continuous supply of trees of all age classes. In particular, this refers to oak-dominated stands characterized by uneven age distribution, with a disproportionate ratio between old and middle-age classes (Pasinelli 2000, Pasinelli *et al*. 2001). Some forests, e.g. KOF, where the majority of oak-dominated stands are older than 100 years, do not contain enough middle-aged oak trees to replace old stands. In some cases, it might be advisable to increase the felling age for oak in order to allow younger trees to reach maturity and to provide new foraging bases for woodpeckers. Moreover, it might be recommendable to adopt a system of shelterwood cuttings and continuous cover management instead of clear-cuts, in order to maintain current woodpecker territories as long as possible and to create a more diverse stand structure in the future. Such practises could counteract the fragmentation of most valuable habitat patches. However, due to the lack of an effective natural regeneration of pedunculate oak in oak-dominated forests, e.g. in KOF (Kasprowicz 2010), shelterwood cuttings would not be an effective practice to regenerate cohorts of younger trees. In an area where oak-dominated forests are scarce forest management should focus on alder bogs and species-rich deciduous forests containing other rough-barked tree species for supporting middle spotted woodpeckers.

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Appendix 1. Descriptive statistics of environmental variables used in the model for all study areas. *n* = number of forest stands/number of records in the database.

Variable	KOF (*n* = 1338)					FDR (*n* = 9608)					KF (*n* = 8128)				
	Min.	Max.	Mean	SE	Var.	Min.	Max.	Mean	SE	Var.	Min.	Max.	Mean	SE	Var.
Uneven stands	0	100	32.31	0.86	1032.25	0	99.29	6.29	0.15	208.76	0	100	14.62	0.27	581.45
High canopy closure	0	46.07	0.73	0.10	13.44	0	100	17.20	0.23	510.08	0	95.63	4.98	0.13	137.95
Medium canopy closure	0	100	31.71	0.81	920.96	0	100	36.35	0.31	914.51	0	100	21.20	0.28	649.99
Low canopy closure	0	100	31.49	0.85	992.06	0	100	10.97	0.18	323.94	0	100	24.91	0.31	778.16
Sparse canopy closure	0	85.44	1.50	0.16	37.05	0	72.59	0.33	0.03	7.70	0	100	4.30	0.13	145.26
Low no. of species	0	99.25	9.95	0.45	276.16	0	100	29.67	0.28	774.31	0	100	16.42	0.26	568.23
Medium no. of species	0	100	35.31	0.78	838.59	0	99.31	7.80	0.15	229.91	0	100	30.49	0.33	903.06
High no. of species	0	100	22.39	0.72	728.68	0	98.73	1.63	0.08	58.25	0	100	22.69	0.35	1014.94
Young stands	0	86.56	9.36	0.39	207.36	0	100	23.97	0.24	568.20	0	100	17.54	0.25	504.55
Premature stands	0	100	19.01	0.64	560.95	0	100	29.25	0.27	724.69	0	100	30.52	0.33	910.99
Mature stands	0	100	18.68	0.69	651.96	0	100	16.57	0.23	518.32	0	100	19.30	0.31	780.32
Old stands	0	100	20.60	0.79	855.85	0	100	2.91	0.11	107.93	0	100	2.24	0.11	92.34
Wet habitats	0	98.13	2.96	0.25	85.45	0	100	3.28	0.10	103.31	0	100	8.52	0.21	349.24
Alder	0	73.06	1.47	0.13	24.09	0	88.76	1.95	0.06	35.13	0	89.69	3.36	0.09	68.33
Birch	0	55.81	6.13	0.20	56.77	0	79.96	5.66	0.07	50.06	0	100	7.79	0.11	90.43
Oak	0	100	32.21	0.85	1000.34	0	97.91	3.92	0.10	102.09	0	92.56	3.99	0.08	52.23
Ash	0	27.31	0.28	0.04	2.37	0	23.10	0.09	0.01	0.51	0	28.69	0.33	0.02	2.16
Beech	0	71.25	3.51	0.17	38.94	0	100	3.80	0.11	114.84	–	–	–	–	–
Other deciduous	0	27.56	1.42	0.08	9.82	–	–	–	–	–	0	100	3.26	0.08	53.88
Coniferous	0	100	30.69	0.77	816.65	0	100	58.41	0.35	1 186.60	0	100	56.57	0.39	1223.55

Appendix 2. Factor analysis rotated component matrix, principal component analysis with varimax rotation.

Variable	PC1	PC2	PC3	PC4	PC5	PC6	PC7
KOF							
Uneven stands	0.842	–0.108	–0.007	0.405	0.056	0.040	0.070
High canopy closure	–0.098	0.012	–0.057	0.042	0.003	0.651	–0.038
Medium canopy closure	–0.146	0.728	–0.028	0.450	–0.090	0.002	–0.023
Low canopy closure	0.852	0.038	0.153	–0.007	0.156	0.033	0.038
Sparse canopy closure	0.171	–0.057	–0.042	0.013	–0.070	0.452	0.162
Low no. of species	0.167	0.105	0.136	0.224	–0.701	0.066	–0.106
Medium no. of species	0.328	0.629	0.026	0.051	–0.186	0.336	0.118
High no. of species	0.407	0.126	0.059	0.336	0.688	–0.133	0.048
Young stands	–0.002	0.356	0.286	–0.048	0.090	0.664	–0.069
Premature stands	–0.152	0.853	0.018	–0.117	0.044	–0.150	0.048
Mature stands	0.020	0.047	0.075	0.885	0.041	–0.014	0.153
Old stands	0.901	–0.108	–0.063	–0.167	–0.063	0.055	–0.038
Wet habitats	–0.016	0.064	0.911	0.039	–0.071	0.015	0.077
Alder	–0.027	0.063	0.900	0.046	–0.034	–0.002	0.031
Birch	0.145	0.592	0.235	–0.130	0.381	0.198	0.116
Oak	0.876	0.063	–0.143	–0.039	0.047	–0.025	0.199
Ash	–0.016	–0.040	0.343	0.040	–0.001	0.026	0.706
Beech	0.328	–0.021	–0.087	0.367	0.504	0.202	–0.028
Other deciduous	0.188	0.100	–0.133	0.072	0.121	0.060	0.766
Coniferous	–0.108	0.625	0.106	0.523	–0.122	0.176	–0.275
Eigenvalue	3.938	3.223	1.865	1.524	1.428	1.097	1.069
Variance explained (%)	17.9	13.0	10.1	9.0	7.5	6.7	6.6
FDR							
Uneven stands	0.737	0.170	0.084	–0.048	–0.174	0.143	0.026
High canopy closure	–0.033	–0.047	–0.038	0.844	0.013	–0.026	–0.028
Medium canopy closure	0.197	0.609	–0.040	–0.149	0.423	–0.461	0.026
Low canopy closure	0.163	0.146	0.088	–0.116	0.085	0.869	–0.040
Sparse canopy closure	0.030	0.053	0.073	0.028	–0.034	0.022	0.658
Low no. of species	–0.095	0.821	–0.088	–0.170	0.111	0.258	0.028
Medium no. of species	0.722	0.041	0.191	–0.103	0.064	–0.176	–0.180
High no. of species	0.288	–0.086	–0.072	–0.048	–0.007	0.068	0.441
Young stands	–0.033	–0.019	0.056	0.889	0.013	–0.057	0.019
Premature stands	–0.171	0.276	–0.078	–0.156	0.847	0.015	–0.002
Mature stands	0.298	0.723	0.100	–0.106	–0.474	–0.068	–0.058
Old stands	0.641	–0.141	–0.157	0.024	–0.006	*0.433*	0.223
Wet habitats	0.029	–0.058	0.916	0.011	0.092	0.032	0.125
Alder	–0.017	–0.063	0.886	–0.005	0.008	0.034	0.110
Birch	0.067	–0.052	0.301	0.223	0.617	0.059	–0.076
Oak	0.734	–0.040	–0.055	–0.007	–0.004	–0.017	0.073
Ash	–0.020	–0.049	0.287	–0.025	0.000	–0.116	0.557
Beech	0.621	–0.047	–0.067	0.048	–0.033	0.128	0.350
Coniferous	–0.165	0.767	–0.187	0.357	0.307	0.013	–0.122
Eigenvalue	3.082	2.636	2.001	1.740	1.330	1.197	1.003
Variance explained (%)	14.3	12.3	10.3	9.5	8.7	7.0	6.3
KF							
Uneven stands	0.067	0.847	0.024	–0.030	–0.086	0.054	0.333
High canopy closure	0.147	–0.027	0.002	0.121	0.597	–0.086	–0.042
Medium canopy closure	0.110	–0.105	0.010	0.756	0.198	–0.202	0.131
Low canopy closure	0.209	0.273	0.138	0.070	–0.233	0.768	–0.095
Sparse canopy closure	0.231	0.367	0.210	–0.012	–0.009	–0.130	0.261
Low no. of species	–0.342	–0.181	–0.072	–0.017	0.351	0.659	0.108
Medium no. of species	–0.266	0.463	0.105	0.620	0.177	0.021	–0.224
High no. of species	0.814	0.176	0.115	0.131	–0.117	0.015	0.247
Young stands	0.027	–0.100	0.073	0.009	0.894	0.096	0.021

continued

Appendix 2. Continued.

Variable	PC1	PC2	PC3	PC4	PC5	PC6	PC7
Premature stands	0.192	–0.298	0.082	0.755	–0.219	0.377	–0.079
Mature stands	0.113	0.901	0.026	–0.033	–0.122	0.113	–0.105
Old stands	0.021	0.130	0.025	0.033	–0.010	0.016	0.892
Wet habitats	–0.012	0.062	0.931	–0.008	–0.036	0.033	0.086
Alder	0.022	–0.005	0.880	–0.007	–0.044	–0.052	0.007
Birch	0.329	0.095	0.602	0.117	0.256	0.125	–0.039
Oak	0.709	–0.018	–0.103	0.075	0.289	–0.001	0.014
Ash	0.490	0.012	0.309	–0.119	0.110	–0.046	–0.089
Other deciduous	0.797	0.071	0.043	0.021	0.006	0.019	–0.036
Coniferous	–0.007	0.431	–0.214	0.645	0.135	0.485	0.142
Eigenvalue	3.369	2.418	2.224	1.863	1.445	1.157	1.041
Variance explained (%)	13.3	12.4	11.9	10.6	8.8	8.0	6.2