

Species co-occurrence and environmental factors and their effect on the distribution of forest birds in mature forests

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Measures of species co-occurrence, as a proxy of biotic interactions, may be as important as environmental factors when explaining the distribution of many species. We assessed the relative effect of both species co-occurrence and environmental factors in predicting the occurrence (presence/absence) of woodpeckers and passerines in mature forests of the Northern Iberian Peninsula. We hypothesized that woodpecker occurrence would affect the occurrence of passerines. We calculated the occurrence of woodpecker species using models that included environmental factors aggregated at three spatial scales (200, 500 and 1,000-m²). The occurrence of passerine species was then modelled by using either species co-occurrence (including the occurrence of woodpecker species) or environmental factors at the 200-m² cell scale. The occurrence of five out of nine passerine species was best explained by the co-occurrence of woodpeckers alone, whereas the occurrence of the remaining passerines was best explained using a combination of species co-occurrence (i.e. woodpeckers and/or other passerines) and environmental factors. In Southern Europe, woodpeckers are expanding their distribution in line with forest maturation, and this could increase the diversity of bird communities in forest systems.

Introduction

Biotic interactions, such as competition, mutualism, and predation, are important for explaining the distribution of many species (Araújo and Luoto, 2007; Hof *et al.*, 2012; Giannini *et al.*, 2013). However, studies aimed at understanding the factors which affect distribution typically only assess the correlations between environmental factors (e.g. climate, topography and/or land-use) and the occurrence (presence/absence) and/or abundance of the focal species (Elith and Leathwick, 2009). Some authors have, however, suggested that biotic interactions may play an additional role in explaining species distribution (Araújo and Luoto, 2007; Hof *et al.*, 2012; Giannini *et al.*, 2013). There is growing evidence that geographical or spatial overlap between species may be explained by positive (e.g. mutualism), or negative (e.g. predation) co-occurrence between species (Morales-Castilla *et al.*, 2015). Thus it is necessary to assess the relative influence of species co-occurrence as well as independent environmental factors when predicting the distribution of interacting species (Araújo and Luoto, 2007; Ovaskainen *et al.*, 2010).

Old-growth and mature forests are habitats with high landscape heterogeneity and host large numbers of specialized species that make up complex species communities (Fuller *et al.*, 2012). As such, these habitats are useful for studying how the occurrence of forest specialists may potentially be affected by

the occurrence (presence or absence) of other species within the community (Segura *et al.*, 2014). With respect to forest birds, afforestation, forest maturation and sustainable management practices are known to maintain natural levels of biodiversity (e.g. Mönkkönen and Forsman, 2002; Gil-Tena *et al.*, 2010; Segura *et al.*, 2014). In addition, the occurrence of keystone species likely conditions the richness of those bird communities (Heikkinen *et al.*, 2007; Segura *et al.*, 2014). Woodpeckers are one of the most specialized groups within forest systems, and their activity makes resources more accessible to other species (e.g. by facilitating shelter and/or foraging substrates; Cockle *et al.*, 2011). However, the occurrence of woodpeckers is limited by resource availability, which, in turn, is conditioned by the heterogeneity and the natural dynamics of the landscape itself (Bütler *et al.*, 2004; Roberge *et al.*, 2008).

Here we focused on the relative effect of species co-occurrence (woodpecker species and/or other passerines) and environmental factors in predicting the occurrence of forest passerines in mature forests of the Northern Iberian Peninsula. Previous work in our study system suggests that forest resources are abundant, although dependent on forest types (Rodríguez-Pérez *et al.*, 2018). However, this resource variability does not affect the composition of the bird community, which is rich and homogeneous across all forest types in the study system (Rodríguez-Pérez *et al.*, 2018). In this study, we

hypothesized that the occurrence of woodpeckers would explain the occurrence of passerines given that the former create important habitat features (e.g. cavities, deadwood) that are used by the latter. We employed two hierarchical steps to evaluate: (1) the occurrence of woodpeckers, achieved using sets of models that included environmental factors aggregated at three spatial scales (200, 500 and 1 000-m²); and (2) the occurrence of passerine species, based on species co-occurrence (i.e. the co-occurrence of woodpecker species and/or passerine species other than the species being modelled) or environmental factors.

Material and methods

Study area

Our study was carried out in the Artikutza Special Area of Conservation (European Union Habitat Directive; 92/43/EEC) (hereafter, Artikutza) located in the north of the Autonomous Community of Navarra (Spain; Figure 1). Artikutza covers ca. 3 700 ha and its climate is temperate-humid with a strong oceanic influence. Mean annual temperature is 13.2°C and annual precipitation is approximately 2 500 mm, with no dry periods in summer (source: Government of Navarra). The lowest point (250 m) of Artikutza is in the northwest and the highest (1 054 m) in the south, which generates slopes of over 35 per cent. Artikutza is highly forested and dominated by stands of common beech (*Fagus sylvatica* L.), pedunculate oak (*Quercus robur* L.) and sessile oak (*Q. petraea* (Matt.) Liebl.), which cover ca. 80 per cent of the area. The remaining 10 per cent of the forested area is unmanaged mature conifer plantations (ca. 7 per cent of forested area, planted during the 1930s) and broad-leaf plantations (ca. 3 per cent of forested area; planted during the 1950s) (Castro Gil pers. comm). In our study site, there is a narrow 5-km long road with limited access to cars and a network of paths and forest tracks which are accessible only to authorized personnel and hikers.

Environmental variables and scales

We used a Geographic Information System to extract tree-canopy variables from 1:5000-scale orthophotos of canopy cover for 14 tree species (Government of Navarra and EKILAN). Each species-specific canopy map was assigned to one of the following four tree-canopy-based forest types (henceforth, forest cover types): (1) native beech forest (comprising only *Fagus sylvatica*); (2) native oak forest (native *Quercus* species, *Alnus glutinosa* (L.) Gaertn.); (3) non-native conifer plantations (mostly *Pinus sylvestris* L., but also *P. nigra* J.F.Arnold, *P. radiata* D.Don, *Chamaecyparis lawsoniana* (A. Murray) Parl., *Larix kaempferi* (Lamb.) Carr., *Picea abies* (L.) H. Karst., *Pseudotsuga menziesii* (Mirb.) Franco and *Sequoia sempervirens* (D.Don) Endl.; and (4) non-native broad-leaf plantations (*Quercus rubra* L. and *Corylus avellana* L.) (henceforth broad-leaf plantation). In our study site the forest cover types also differed at the understory level in terms of the resources they had available for forest birds. Specifically, tree cavities were abundant in beech forests, moderately so in oak forests and broad-leaf plantations, but not common in mature conifer plantations; and deadwood values were low in beech forests, medium in oak forests and broad-leaf plantations and high in mature conifer plantations (Rodríguez-Pérez et al., 2018).

We generated three sets of grids differing in scale in terms of cell size—200, 500 and 1 000 m² (i.e. 4, 25 and 100 ha, respectively)—that covered the study area. We overlaid the corresponding digitized canopy maps and calculated the percentage abundance of canopy of each of the four forest cover types (i.e. beech and oak forests, and conifer and broad-leaf plantations; see above). Beyond our study site, the landscape is dominated by pastures, transitional heathlands, tree plantations and small forest fragments, thus we assumed that the distance to the edge of the forest (functioning as it does as an interface between woodland pastures, forest edges and forest interiors) could affect the co-occurrence of woodpeckers and passerines. At each spatial scale we calculated distance to forest edge (i.e. to expanses of any forest cover type) from the centroid of each cell. In addition, we calculated the average altitude and slope (extracted from a digital elevation model) at each spatial scale for each cell. All spatial variables were extracted, processed and manipulated in QGIS (1.12 version).

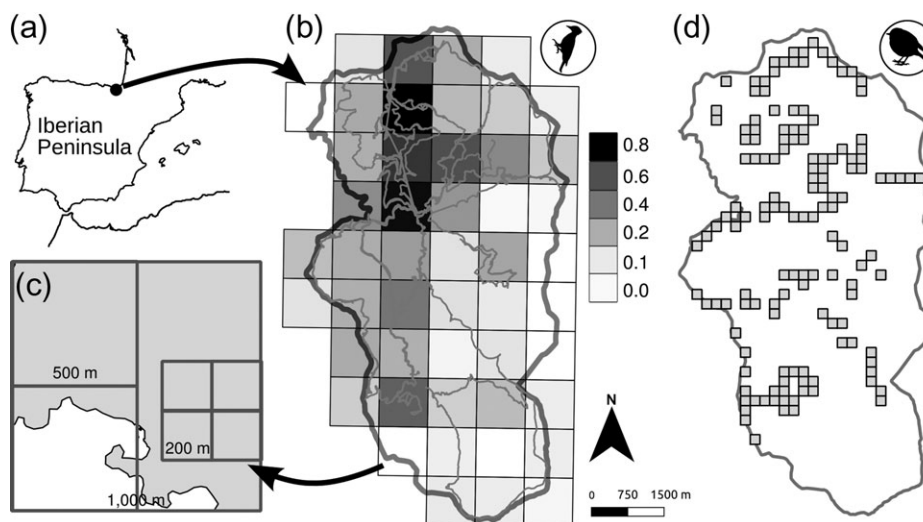


Figure 1 (a) Location of the study site (black dot) in Spain within the Iberian Peninsula. (b) Diagrammatic representation of the study area divided into 1 000 m² cells. Lines indicate the transects walked for woodpecker surveys. Increasing darkness of shade indicates higher sampling effort, for transects (lines) as well as cumulative sampling per cell. (c) Detailed view of one 1 000-m² cell subdivided into 500 and 200-m² cells. (d) Location across the study area of the 200-m² cells where passerine surveys were conducted (grey squares).

Field survey and data processing of species occurrence

From March to May 2015 we sampled encounter transects in order to measure woodpecker occurrence across our study site; this method allowed the detection of species at low-densities (Bibby *et al.*, 2000). The diurnal surveys consisted of 25 linear transects of $1\,267 \pm 1,063$ m in length (mean \pm SD) (Figure 1b) which were each walked once, at a constant pace of approximately 30 min/km. Transects, the majority of which were located in the forest interior, were performed along narrow paths and forest tracks which were localized using a GPS (see Figure 1). Transects were selected according to their accessibility within the study site, meaning that some transects shared certain sections of path/track. In order to minimize double-counting of woodpecker encounters (see also below), only one transect was surveyed each census day since some transects shared sections of path/track.

Each individual woodpecker encountered was identified by species (either visually or acoustically), and its location determined according to its distance from the surveyor (using bearing and relative distance) and position (using GPS). In order to reduce identification bias, woodpecker censuses were performed by a single person (JRP). Encounters separated by more than 15 minutes and at least 200 m were treated as independent with the aim of ensuring independent data (i.e. avoiding pseudo-replication associated with multiple encounters of the same individual woodpecker across sequential sampling intervals). Cases where more than one individual of the same species was observed in the same time frame (i.e. within 15 minutes), were considered as a single encounter. Four different woodpecker species were detected: Great spotted woodpecker (*Dendrocopos major* L.), Lesser spotted woodpecker (*Dryobates minor* L.), Iberian green woodpecker (*Picus sharpei* Sanders), and Black woodpecker (*Dryocopus martius* L.).

Between April and June 2015 we also conducted diurnal point sampling of passerine species in 140 locations, each within a different 200-m² cell identified on the GIS maps (Figure 1d). Sampling was carried out over 26 days, within a 3-hour period starting 1 hour after sunrise, in appropriate weather conditions (i.e. no heavy rain or strong wind). At each location the observer (the same person, JRP, for all sampling events) identified, either visually or acoustically, the different passerine species encountered up to a distance of 75 m from each sample point. Each survey consisted of three 5-min counts, with a 2-min break between each in order to avoid double-counting of abundant passerine species. Censuses at the same location were performed on a single day, allowing us to carry out multiple censuses at the expense of measuring between-day differences. For each species and location, data relating to their presence (i.e. more than one individual encountered) or absence (i.e. no encounters) during the three consecutive censuses were pooled across census (Julian) days.

For data processing purposes, we included only the nine passerine species which were (a) found in at least 10 per cent of the locations surveyed and (b) known to be limited by the availability of old forest structure for either feeding or breeding (Noss, 1999), namely: Coal tit (*Pariparus ater* L.), European crested tit (*Lophophanes cristatus* L.) Eurasian blue tit (*Cyanistes caeruleus* L.), Eurasian nuthatch (*Sitta europaea* L.), European pied flycatcher (*Ficedula hypoleuca* Pallas), European robin (*Erithacus rubecula* L.), Great tit (*Parus major* L.), Marsh tit (*Poecile palustris* L.) and Short-toed treecreeper (*Certhia brachydactyla* Brehm).

Data analysis

The occurrence of the four species of woodpeckers and nine species of passerines (see above) was modelled using the machine learning algorithm MaxEnt (version 3.3.3, Phillips *et al.*, 2006), a statistical technique particularly suited to evaluating predictive or response variables (either continuous or categorical variables based on environmental data) with a limited number of encounters (Pearson *et al.*, 2007). For each woodpecker and passerine species we calculated: the percent contribution of

each response variable (i.e. a measure of the percentage of increase of likelihood or total gain associated with each response variable), the permutation importance of each response variable (i.e. a measure of its ability to separate true-presences from pseudo-absences; see below), the response curves of the occurrence probability of each woodpecker and passerine species (ranging from 0 to 1, see below for how this is calculated) based on each response variable, as well as maps of occurrence probability and AUC (Area Under the ROC (Receiver Operating Characteristic) Curve) values (i.e. as an estimate of model accuracy). AUC values of below 0.7 indicate poor model accuracy, and those above 0.8 are an indication that model accuracy is good. The parameters used for each model iteration were set to their default settings. For each species, we performed 100 bootstrapping iterations in order to achieve robust estimates of model predictions despite having low sample sizes for species occurrence (see Results). For more details about this methodology see Phillips *et al.* (2006).

The habitat use of animals can be envisaged as a hierarchical spatial process of territory use (Mayor *et al.*, 2009), thus, we calculated the occurrence probability of each woodpecker and passerine species as a response to aggregated environmental factors at three spatial scales. For each woodpecker species, we first modelled their occurrence probability in relation to the aggregated environmental factors at each scale (200, 500 and 1 000 m² cell size) with the aim of detecting the spatial scale which was best at predicting woodpecker occurrence. Next, at each scale, the occurrence probability of each woodpecker species based on each individual environmental factor was calculated i.e. the percentage of beech and oak forests, the percentage of conifer and broad-leaf plantations, mean elevation and slope, and distance to forest edge; see Figure A1 in Appendix A1 for maps of environmental factors aggregated at the three spatial scales. For each woodpecker species, we therefore finally obtained a map of occurrence probability at each spatial scale.

Since modelling occurrence of woodpecker species was based on presence-only data (i.e. we were able to confidently identify those locations where they were present, but not where they were absent), we thus needed to calculate pseudo-absences (i.e. *ad hoc* randomly generated locations where specimens were not detected). Also, woodpecker locations were unequally estimated across our study site since, as mentioned in Methods, some transects shared sections of path/track, meaning that they were walked more often and hence there was a higher probability of sighting woodpeckers along these shared sections. To mimic the sampling procedure used to estimate woodpecker occurrence, we constructed maps of 'sampling effort' (Figure 1b), in an attempt to standardize the (uneven) amount of sampling effort and to accordingly generate locations of pseudo-absences. For each cell at the three different spatial scales of environmental aggregation, we summed the distances walked during sampling along each transect. For each modelling iteration, pseudo-absences were then randomly generated based on 'sampling effort' maps.

To model the occurrence of the different passerine species, we tested the relative effects of species co-occurrence (i.e. the co-occurrence of each individual passerine species and either woodpecker or another/other passerine species) and of environmental factors. For each passerine species, we ran a number of models at the 200-m² scale which varied in terms of the response variables used. Specifically, (1) 'environmental models' included the percentage of each forest cover type, mean elevation and slope, and distance to forest edge; (2) 'woodpecker models' included the occurrence probability of each woodpecker species (see Figure 2); and (3) 'species co-occurrence models' comprised those variables included in the 'woodpecker models' along with the occurrence of all the passerine species except the one species being modelled. In the case of model sets 2 and 3, we used the occurrence probability of woodpecker species (rather than the observed location of encounters) (see Figure 1). For modelling the occurrence of the different passerine species, we considered those cells where the species in

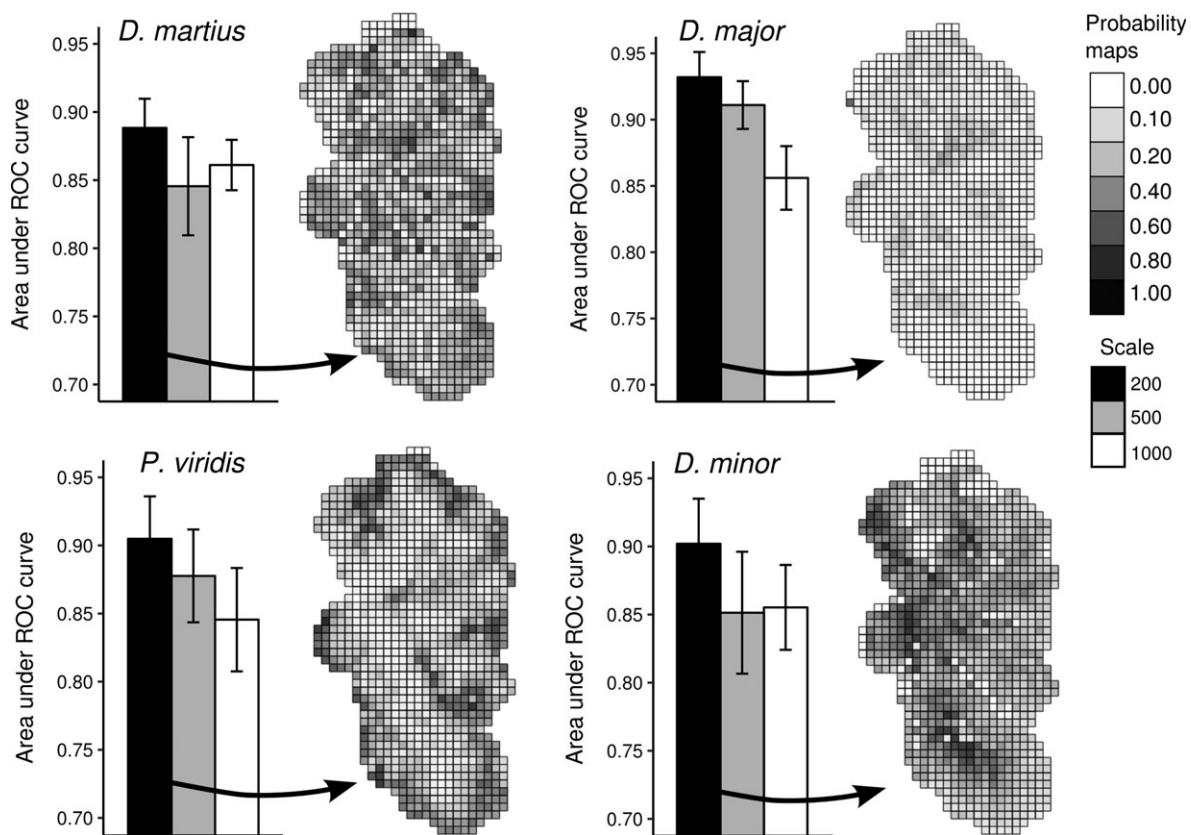


Figure 2 Model performance of the occurrence of woodpecker species based on Area Under the ROC Curve (AUC) scores (left panels) at the three spatial scales (200, 500 and 1000-m²) at which environmental variables were aggregated. Maps of woodpecker occurrence probability (right panels) were calculated from the best model and at the scale that best predicted the occurrence of woodpeckers, that is, the model which maximized AUC scores.

question was detected as true-presences, and those where it was not observed as true-absences (i.e. point sampling allows the confident measurement of both presence and absence, unlike transects).

Results

Occurrence of woodpeckers

We recorded 95 woodpecker encounters for *Dryocopus martius* (31.5 per cent of the number of total encounters, with sightings on 19 of the total 25 days over which the transects were surveyed), *Dendrocopos major* (28.4 per cent total encounters, sightings on 15 days), *Picus sharpei* (26.3 per cent total encounters, sightings on 12 days) and *Dryobates minor* (12.6 per cent total encounters, sightings on 5 days). Of the three spatial scales at which we aggregated environmental factors, we found that the smallest, i.e. 200 m² cells, provided the best fit in terms of predicting the occurrence of woodpecker species (Figure 2). Furthermore, we found that distance to forest edge, and percentage of broad-leaf plantations and oak forest were the variables that made the greatest percent contribution to explaining woodpecker occurrence, respectively accounting, on average, for 23.5 per cent, 21.6 per cent and 17.2 per cent (see Table 1). Based on the permutation importance of each variable, the percentage of broad-leaf plantations was the most important (21.0

per cent), followed by distance to forest edge (18.4 per cent) and elevation (16.3 per cent). For all four woodpecker species, model predictions were good (AUC > 0.894).

Considering each woodpecker species separately demonstrated that the occurrence of *D. martius* was positively associated with higher proportion of beech forest, and lower proportion of broad-leaf plantations and lower slope (Table 1). *D. major* was positively associated with lower elevation, medium proportions of coniferous plantations and lower proportion of broad-leaf plantations. The occurrence of *P. sharpei* was negatively associated with greater distance to forest edge and to medium proportions of oak forest, while that of *D. minor* was positively associated with lower proportion of broad-leaf plantations, lower elevation and longer distance to forest edge (see details in Figure A2 in Appendix A1).

Occurrence of passerines

We found that the most abundant passerine species (occurring in >50 per cent of cells) were *E. rubecula* and *P. major*, along with the less abundant (present in <25 per cent but >10 per cent of cells) *F. hypoleuca* and *P. ater*. At the spatial scale of 200 m², 'woodpecker models' best explained the occurrence of *E. rubecula*, *L. cristatus*, *P. major*, *P. palustris* and *S. europaea* (average AUC scores: 0.733 ± 0.041). Both 'species co-occurrence models' and

Table 1 Effect of environmental factors in explaining woodpecker occurrence at the 200 m² scale and averaged after 100 bootstrapping iterations (average values) using Maxent.

Predictors	<i>D. martius</i>	<i>D. major</i>	<i>P. sharpei</i>	<i>D. minor</i>
<i>Percentage contribution</i>				
Elevation	2.7 (NT)	25.5 (–)	1.4 (+)	10.0 (–)
Slope	12.9 (–)	4.5 (–)	2.5 (NT)	14.4 (+)
%Beech	15.4 (m)	11.8 (NT)	8.3 (+)	2.1 (NT)
%Oak	17.1 (NT)	12.9 (+)	31.9 (mI)	6.8 (NT)
%Conif	10.9 (M)	15.5 (M)	5.1 (–)	7.7 (NT)
%Bdleaf	23.7 (–)	20.9 (–)	11.5 (ML)	30.3 (–)
DistEdge	17.2 (NT)	8.8 (NT)	39.2 (–)	28.7 (+)
<i>Permutation importance</i>				
Elevation	7.4	33.3	3.1	21.5
Slope	22.7	2.6	2.6	7.8
%Beech	24.5	20.9	6.4	5.6
%Oak	8.9	19.8	23.3	6.3
%Conif	6.7	4.4	9.3	5.0
%Bdleaf	20.1	14.6	13.0	36.4
DistEdge	9.6	4.4	42.3	17.4

A summary indication of values of the percentage contribution and permutation importance of each response variable. In addition, the shape of the response curve of the occurrence probability of each woodpecker species with respect to each response variable is shown in brackets: positive (+), negative (–), minimum at intermediate values (mI), maximum at intermediate values (MI), maximum at low values (ML), minimum at low values (mL), minimum at high values (mH), or no clear trend (NT) (for specific details see Figure A2 in Appendix A1).

‘environmental models’ best explained the occurrence of *C. brachydactyla* and *C. cyaneus* (average of AUC scores across passerine species: 0.779 ± 0.001 and 0.787 ± 0.001 , respectively), whereas ‘species co-occurrence models’ alone best explained that of *F. hypoleuca* and *P. ater* (average of AUC scores: 0.858 ± 0.023 ; Figure 3). On average ‘environmental models’ had proportionally lower performance (average AUC scores: 0.688 ± 0.032) than the other two models tested across all passerine species. For *E. rubecula*, AUC scores for all models tested were low (i.e. AUC < 0.7) and thus this species was not included in subsequent analyses.

With respect to ‘woodpecker models’, the occurrence of *D. martius* and *D. major* positively influenced the occurrence of four passerine species (*C. brachydactyla*, *L. cristatus*, *P. palustris* and *S. europaea*) and negatively affected two (see Table 2 and Figure A3). The occurrence of *P. sharpei* negatively affected the occurrence of *C. caeruleus*, *P. major* and *S. europaea*, and positively affected *P. ater* and *P. palustris*, while *D. minor* had a positive effect on *S. europaea* (at intermediate values only), as well as on *L. cristatus* and *P. major*.

In terms of ‘species co-occurrence models’, higher occurrence of *E. rubecula* contributed positively to the occurrence of both *C. brachydactyla* and *F. hypoleuca*, while higher occurrence of *C. caeruleus* positively affected *S. europaea*. Interestingly, both lower occurrence of *L. cristatus* and higher occurrence of *P. palustris* had a positive effect on *F. hypoleuca* occurrence (see Table 2 and Figure A3).

The occurrence of *C. brachydactyla* and *C. caeruleus* was affected by both species co-occurrence and environmental factors (i.e. the two models performed equally well). Specifically, both species were affected positively by higher proportions of beech forest and of broad-leaf plantation and lower proportions of coniferous plantation. Occurrence of *C. brachydactyla* was, in addition, positively influenced by medium distance to forest edge and medium elevation, while *C. caeruleus* was positively impacted by greater distance to forest edge and lower elevation (see Table 2 and Figure A3).

Discussion

While it is true that biotic interactions are generally difficult to measure and detect, and it remains both controversial and a great challenge to infer such interactions from species co-occurrence (Morales-Castilla et al., 2015), this work aimed to assess the relative effect of species co-occurrence and environment in predicting the occurrence of forest bird species. To do this, we assessed the relative performance of species co-occurrence (i.e. the effect on an individual passerine species of the co-occurrence of woodpeckers or other passerine species) and of environmental factors in explaining the occurrence of passerines. We found a positive effect for the co-occurrence of woodpeckers and passerines, which may be the consequence of passerine species benefiting from the activity of woodpeckers, which increases forest resources (Cockle et al., 2011). We found that the occurrence of most of the passerine species was better explained by the occurrence of woodpeckers, which was calculated on the basis of woodpecker responses to environmental factors, than by environmental factors per se. As such, our data suggest that species co-occurrence could complement and strengthen predictions of species distribution compared to those made solely on the basis of environmental factors (Araújo and Luoto, 2007; Ovaskainen et al., 2010; Giannini et al., 2013).

Despite the apparently clear associations found in this work between the occurrence of individual passerine species and the co-occurrence of woodpeckers or other passerines, these methods have some limitations. For example, we fitted models of habitat suitability of woodpecker species based on encounter transects and presence-only models, potentially leading to bias from the repeated sightings of individual birds (Gregory et al., 2004). However, we did take a number of measures to reduce the possibility of such an effect. A second potential source of bias is that sampling along roads and trails could generate a higher association of woodpecker species with forest edges (Gregory et al., 2004). Although in our study site, the majority of trails were in the forest interior, thus reducing the probability of forest edge bias.

Occurrence of woodpeckers has been considered a potential bio-indicator of environmental variability at both the local and the landscape scale (Mikusiński et al., 2001; Segura et al., 2014). In our case, the occurrence of woodpecker species was best explained at the finer scale of aggregation of environmental factors (i.e. in the 200-m² cell scale), supporting the notion that woodpeckers prioritize local conditions in their habitat-selection decisions (e.g. Fuller et al., 2012; Dorresteijn et al., 2013). This is

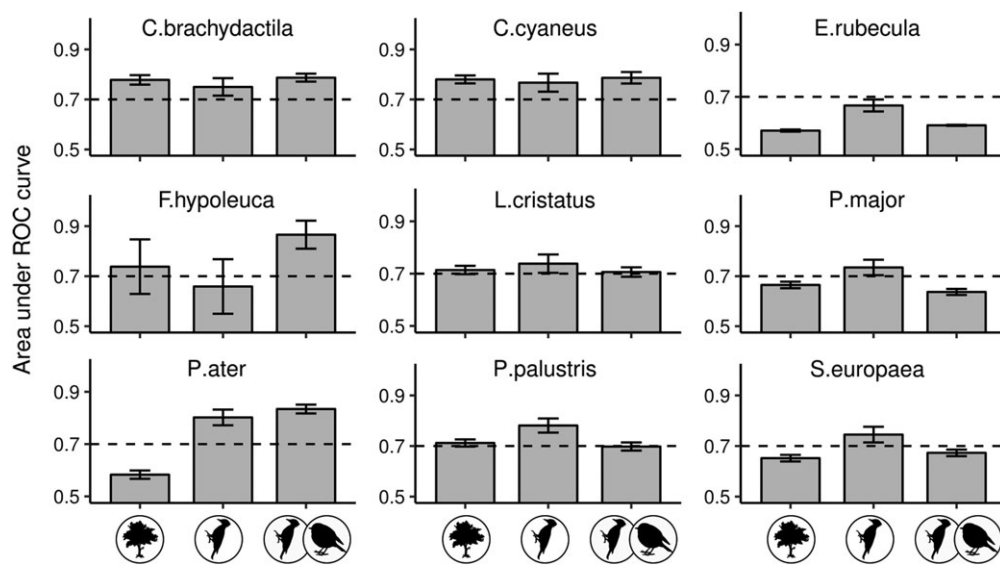


Figure 3 Model performance (in terms of AUC scores) for the prediction of the occurrence of forest bird species using the various combinations of species co-occurrence and environmental factors. Using 200-m² cells, we compared ‘environment models’, ‘woodpecker models’ and ‘species co-occurrence models’ (i.e. the latter included the occurrence of both woodpeckers and other passerine species apart from the species being modelled). Dashed lines represent the threshold score selected to indicate the minimum acceptable accuracy of model predictions (AUC = 0.7).

in line with research which shows that fine-scale forest resources (i.e. the abundance of dead and decaying wood) explain to a great extent the occurrence and activity of woodpeckers (Bütler *et al.*, 2004; Roberge *et al.*, 2008; Cockle *et al.*, 2011). In our study system, forest cover type has previously been shown to provide a good proxy of fine-scale forest resources (Rodríguez-Pérez *et al.*, 2018). For instance, beech forest, the most abundant forest cover type, has abundant resources (i.e. notably high cavity density), although our results found it to make only a small percentage contribution to explaining woodpecker occurrence. We also found that woodpecker occurrence was positively affected by mature broad-leaf plantations, which although in our study site are only at low abundance, still provide intermediate abundances of cavities and deadwood (Rodríguez-Pérez *et al.*, 2018) and thus augment the availability of forest resources for woodpeckers.

The models which included only the co-occurrence of woodpeckers (i.e. ‘woodpecker models’) better explained the occurrence of the majority of passerine species (five out of nine species), followed by those models which incorporated factors related to both species co-occurrence and environment. Shared use of environmental factors is known to promote the co-occurrence of species in certain contexts (Royan *et al.*, 2015). In our study area, we found that the occurrence of both *C. brachydactyla* and *C. caeruleus* was explained equally well by either ‘species co-occurrence’ or ‘environmental factors’, meaning that species co-occurrence in this case could, to a great extent, be a surrogate of common species responses to environmental factors. Certainly, the, generally, higher predictive power of ‘species co-occurrence’ (which included woodpecker occurrence) compared to ‘environmental factors’ suggests that a significant proportion of information derived from the former can be exclusively explained by the co-occurrence of woodpeckers and passerines

(i.e. not by shared environmental factors). Likewise, since our approach was not able to identify the underlying mechanisms of the co-occurrence of different passerine species, we cannot discard the possibility that such relationships may be a consequence of their similar responses to forest resources (Drever *et al.*, 2008), which may generate causal species co-occurrence. Nonetheless, our work supports the notion that the consideration of species co-occurrence could be valuable in improving predictions of the occurrence of passerines in mature forests (Robles *et al.*, 2012).

Considering species-specific responses, we found that distance to forest edge, along with the proportion of coniferous plantations and oak forest, best explained the occurrence of passerine species. We additionally found that the occurrence of individual passerine species was positively affected by the co-occurrence of other passerines. This supports the findings of other researchers that heterospecific attraction (partly modulated by habitat selection processes) is a potential mechanism in structuring communities of forest birds (Mönkkönen and Forsman, 2002). For example, *E. rubecula* is an abundant species that uses understory habitats similar to those of other forest passerines (Rodríguez-Pérez *et al.*, 2018). It is therefore not surprising that many of the other passerines (e.g. *C. brachydactyla* and *F. hypoleuca*) in our study co-occur or are associated with this generalist. We also found that the co-occurrence of woodpecker species (notably *D. martius*, but also *D. major* and *D. minor*) positively correlated with the occurrence of passerine species. Other studies have found that *D. martius* affects the abundance and suitability of forest resources (notably tree cavities) and this exerts a strong influence on the density and composition of cavity-dwelling birds (Heikkinen *et al.*, 2007; Camprodon *et al.*, 2008; Segura *et al.*, 2014), leading us to hypothesize that the occurrence of this, and other keystone species, could impact the structure of forest bird communities.

Table 2 Effect of environmental factors and species co-occurrence in explaining passerine occurrence at the 200-m² scale after 100 bootstrapping iterations (average values) using Maxent.

Predictors	C.bra	C.cae	F.hyp	L.cri	P.maj	P.ate	P.pal	S.eur
Percent contribution								
Elevation	32.2 (MI)	24.0 (-)						
Slope	2.6 (NT)	8.7 (ML)						
%Beech	14.1 (+)	15.3 (+)						
%Oak	7.5 (NT)	9.2 (+)						
%Conif	19.1 (-)	8.5 (-)						
%Bdleaf	6.2 (-)	11.5 (+)						
DistEdge	18.3 (MI)	24.8 (+)						
D.mar*	17.7 (+)	22.2 (mH)	0.9 (-)	20.9 (+)	11.1 (ML)	28.0 (mI)	30.4 (+)	17.3 (+)
D.maj*	4.1 (+)	16.0 (-)	3.3 (+)	23.1 (+)	10.4 (ML)	15.5 (mI)	24.3 (mI)	16.8 (mH)
P.sha*	15.7 (NT)	12.1 (-)	3.3 (-)	20.0 (NT)	14.0 (ML)	36.7 (MI)	32.6 (+)	12.9 (-)
D.min*	5.7 (ML)	6.6 (mL)	0.3 (+)	36.0 (mH)	64.5 (mI)	1.4 (MI)	12.7 (NT)	53.1.0 (+)
C.bra		2.8 (NT)	4.8 (+)			1.7 (-)		
C.cae	1.2 (NT)		2.6 (NT)			4.9 (NT)		
E.rub	33.9 (+)	2.6 (NT)	41.4 (+)			1.0 (NT)		
F.hyp	1.5 (+)	1.4 (NT)				2.4 (NT)		
L.cri	5.2 (+)	2.2 (NT)	19.3 (-)			2.3 (NT)		
P.maj	7.7 (-)	2.0 (NT)	2.5 (NT)			1.4 (NT)		
P.ate	3.2 (-)	1.9 (-)	4.3 (NT)					
P.pal	0.6 (NT)	3.3 (NT)	10.3 (+)			2.9 (NT)		
S.eur	3.4 (+)	26.5 (+)	7.0 (NT)			1.0 (NT)		
Permutation importance								
Elevation	18.7	3.3						
Slope	5.1	7.5						
%Beech	5.4	12.3						
%Oak	21.8	13.4						
%Conif	25.6	27.8						
%Bdleaf	9.9	10.9						
DistEdge	13.5	24.7						
D.mar*	13.1	9.6	2.2	16.3	21.1	35.4	20.2	20.9
D.maj*	10.8	14.6	4.7	19.9	14.6	15.9	29.9	16.2
P.sha*	15.3	20.7	7.3	23.2	21.7	29.0	26.2	25.7
D.min*	11.3	15.9	0.8	40.6	42.6	2.1	23.7	37.2
C.bra		2.8	6.3			2.8		
C.cae	0.7		2.5			1.5		
E.rub	26.6	2.6	19.0			1.1		
F.hyp	2.1	1.4				2.0		
L.cri	6.6	2.5	27.5			3.2		
P.maj	5.7	2.2	4.7			1.0		
P.ate	3.9	2.0	3.9					
P.pal	1.4	3.3	13.3			3.4		
S.eur	2.5	26.5	7.9			2.6		

The values represent percent contribution and permutation importance of each response variable, and the shape of the response curve of the occurrence probability is shown in brackets. The occurrence of woodpecker species (*) relates to occurrence probability at the 200-m² scale (see Figure 2). For *C. brachydactyla* and *C. caeruleus*, the effects of environmental variables and species co-occurrences were calculated from separate models (see Results). For other conventions see Table 1.

Conclusions

Biotic interactions affect the distribution, the complexity and the assembly of species communities, and it is therefore necessary to highlight their role in explaining species distribution (Araújo and Luoto, 2007; Ovaskainen et al., 2010; Giannini et al., 2013).

We found that the occurrence of woodpeckers strongly influenced that of passerine species in our study area, and that the association could not be explained by environmental factors alone. We suggest that the parallel developments in recent decades of large-scale forest maturation and afforestation and the recolonization of Southern Europe by woodpeckers (Gil-Tena

et al., 2010, 2013; Olano *et al.*, 2015) could have boosted the richness and expansion of forest birds by means of increasing habitat quality (i.e. cavity density and/or deadwood abundance) as well as associated interspecific interactions. Taking a broader perspective, the ongoing process of maturation of forests and the accompanying increase in the complexity of species communities provides a new opportunity to maintain levels of bird diversity in mosaics of both managed and unmanaged forest landscapes.

Supplementary data

Supplementary data are available at *Forestry* online.

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Conflict of interest statement

None declared.

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Author contributions

M.X.A compiled datasets, analysed the data and prepared the figures; J. A contributed to the principal ideas; and J.R.P contributed to the principal ideas, conducted field work and led the writing of the manuscript. All authors were involved in discussion of the results and each contributed significantly to the writing of the manuscript.

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