

# Mature non-native plantations complement native forests in bird communities: canopy and understory effects on avian habitat preferences

Javier Rodríguez-Pérez<sup>1\*</sup>, José M. Herrera<sup>2</sup> and Juan Arizaga<sup>1</sup>

<sup>1</sup>Department of Ornithology, Aranzadi – Society of Sciences, Zorrogaina 11, 20014 Donostia-San Sebastián, Spain

<sup>2</sup>CIBIO-InBIO/UE, Research Center in Biodiversity and Genetic Resources, University of Évora, Casa Cordovil 2a Andar, Rua Dr. Joaquim Henriques da Fonseca, 7002-554 Évora, Portugal

\*Corresponding author: jvr.rodriguez@gmail.com

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The habitat composition of mature non-native plantations may provide a different set of resources to that of native forests, and these differences may influence species communities. We studied a bird community in the northern Iberian Peninsula to understand whether habitat composition in either mature non-native plantations or native forests generated differences in the habitat associations of each bird species as well as the composition of the bird community. We sampled 140 4-ha plots, measuring habitat composition at both the canopy and the understory level using remote sensing data and field surveys, respectively. Using a fixed census in each plot, we also studied the bird species composition and analysed the species-specific associations for various habitat variables at the canopy and understory level. We found that mature plantations differed in understory level from native forest, but these differences in habitat did not translate into differences in bird species composition between forest types. Species–habitat associations were on average stronger at the understory compared to the canopy level, which suggests that a combination of field and remote sensing data might better represent the species-specific response to forest resources when measuring the assembly of bird communities in mature plantations. This work suggests the fact that the combination of different levels of forest resources, such as that provided by mature non-native plantations and native forests, is able to support a rich bird community.

## Introduction

Forests house a large number of species and are therefore widely accepted as key elements for the conservation of biodiversity worldwide (Bengtsson *et al.*, 2000; Lindenmayer and Franklin, 2002). In general, the presence of most forest-dwelling species is positively associated with tree canopy composition, the density of deadwood available and the presence of cracks and cavities in trees (e.g. Halaj *et al.*, 2000; Bauhus *et al.*, 2009; Rosenthal *et al.*, 2011; Burrascano *et al.*, 2013), as these elements provide important resources for feeding, roosting and breeding. In the case of mobile organisms, habitat use can be envisaged as a multi-scale process (i.e. from fine habitat composition to landscape patterns) which is dependent on species-specific requirements (Mayor *et al.*, 2009). While habitat composition and its effect on biodiversity can be studied at broad scales (i.e. using remote sensing data), habitat composition at finer scales can also influence community composition (Stein *et al.*, 2014). Mature and old-growth forests and plantations may support complex habitat structures below a homogeneous forest canopy, and we thus need multi-scale

processes (i.e. those which capture the different levels of habitat composition) to understand biodiversity patterns and the community assemblages (Canterbury *et al.*, 2000; Niemi and McDonald, 2004; Hewson *et al.*, 2011).

In Western Europe, the incidence of older, mature forests, both native forests and non-native plantations, is increasing, due to a period of afforestation in the second half of the 20th century and the application of management practices for biodiversity conservation (Brockhoff *et al.*, 2008). Current low intensity forest management has also resulted in the increased complexity of the tree canopy in many such plantations, along with the persistence of abundant large trees, a greater richness of understory plants and the presence of deadwood at levels equivalent to those found within mature native forests (Bauhus *et al.*, 2009). Many forest-dwelling birds, for example, have benefited from afforestation, reforestation and/or forest aging in recent decades (e.g. Suárez-Seoane *et al.*, 2002; Gil-Tena *et al.*, 2010). Birds are particularly good indicators of natural levels of biodiversity as they respond to habitat quality at both the finer and the broader scale (e.g. Hagan and Meehan, 2002; Brotons *et al.*, 2003; Barbaro *et al.*, 2007; Hewson *et al.*, 2011; Calviño-Cancela, 2013). Although mature

native forests are known to provide a rich and spatially-variable array of resources and support a range of species (e.g. Král *et al.*, 2014), the resource contribution made by the mature plantations across much of Europe remains little explored. Consequently, it is important to evaluate the structure and habitat attributes of plantations to determine whether they can support a comparable level of biodiversity to that of mature native forests (Felton *et al.*, 2010).

Our study assesses differences in bird species composition between mature native forests and mature non-native plantations, focusing on the northern Iberian Peninsula, an area with a long history of fragmentation and replacement of native forests with plantations. Currently, in this part of the Iberian Peninsula there are areas of mature plantation, which have not been harvested (due to low economic value), but which provide new opportunities for community restoration and biodiversity conservation (Onaindia *et al.*, 2013). We assumed that habitat quality varied vertically within both mature native forests and non-native plantations and that this variation influenced the habitat resources available for birds. We tested the hypotheses that there were differences between mature native forests and non-native plantations with regard to: (i) habitat composition at both canopy and understory level, (ii) bird species composition and (iii) the habitat associations of each bird species.

## Methods

### Study area

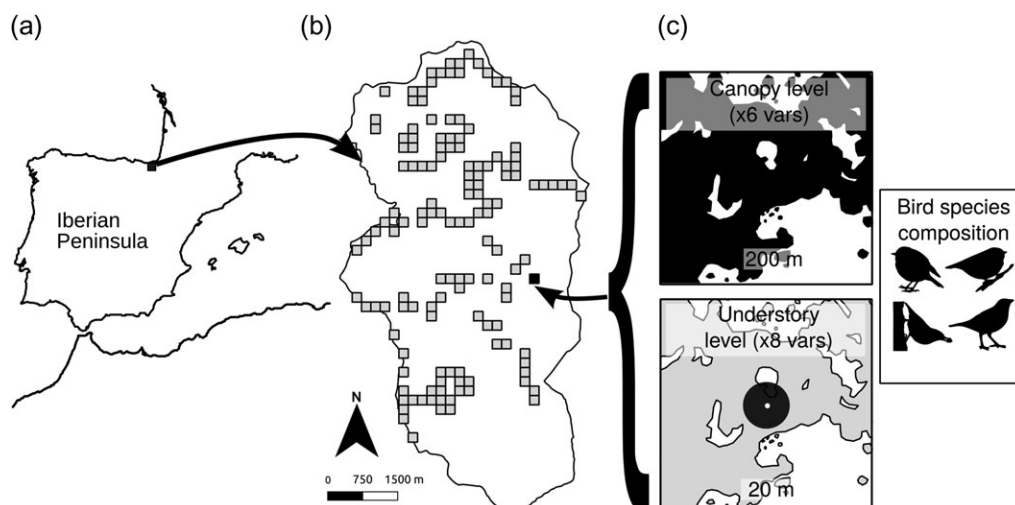
The study was conducted in the Artikutza Special Area of Conservation (European Union Habitats Directive; 92/43/EEC), a reserve comprising 3700 ha located in the north of the autonomous community of Navarre (Spain; northern Iberian Peninsula; Figure 1). The climate is temperate-humid with a strong oceanic influence (annual precipitation: 2700 mm, and mean temperature: 12.9°C). The highest point (1054 m) is in the south, and the lowest (250 m) in the north-westernmost area, generating an average slope of more than 35 per cent. This highly forested area (90 per cent is covered by forest) is mainly dominated by native species

such as beech (*Fagus sylvatica*), pedunculate oak (*Quercus robur*) and white oak (*Q. petraea*), which account for ~90 per cent of the forested area. Most of the reserve area has not suffered any significant human disturbance in the last 100 years (Castro Gil, 2009) although the remaining 10 per cent of the forested area is currently occupied by mature plantations of conifer (planted during the 1930s) and red oak (*Q. rubra* planted during the 1950s, Castro Gil pers. comm). The understory of many of these plantations currently hosts native species (mostly beech) as a consequence of natural regeneration (pers. obs.).

### Habitat surveys

We collected information on habitat composition at two vertical levels – canopy and understory – for each plot sampled. For the former habitat level, we used a highly detailed digitized thematic map of tree canopy cover (Figure 1) for each of 14 different tree species (see later in this paragraph for the names), based on field data and 1:5000-scale aerial images (Navarre regional government and EKILAN). Using a Geographic Information System (GIS), each species-specific canopy map was then assigned to one of four canopy types, namely: (1) native beech forest (*F. sylvatica* only; c. 60 per cent of forested area), (2) native oak forest (i.e. *Q. robur*, *Quercus petraea* and *Alnus glutinosa*; c. 30 per cent forested area), (3) conifer plantations (i.e. *Chamaecyparis lawsoniana*, *Larix kaempferi*, *Picea abies*, *Pinus sylvestris*, *Pinus nigra*, *Pinus radiata*, *Pseudotsuga menziesii* and *Sequoia sempervirens*; c. 8 per cent forested area) and (4) broad-leaf plantations (i.e. *Quercus rubra* and *Castanea sativa*; c. 2 per cent forested area).

Using a GIS we generated a 4-ha grid of 200 × 200 m plots to cover the whole of the study area. We then randomly selected 140 of these plots (Figure 1; see bird surveys) and overlaid the corresponding digitized canopy maps to calculate the percentage of abundance of canopy of each of the four forest types (i.e. beech and oak forests and conifer and broad-leaf plantations) in each plot. After this, each plot was classified as belonging to one of the four forest types (beech forest, oak forest, conifer plantation or broad-leaf plantation) according to the most common canopy type (i.e. >50 per cent) within it. This resulted in 63 plots being classified as beech forest, 42 as oak forest, 24 as conifer plantation and 10 as broad-leaf plantation (see Figure S1). One plot was not classified in this way due to its highly heterogeneous canopy. For each



**Figure 1** Maps of the study area with (a) the location of the study site and (b) a detailed view of the sampling scheme. The study site was subdivided into 140 plots (i.e. 200 × 200 m plots covering 4 ha in total, grey squares). In each plot (c) we measured the occurrence (presence/absence) of bird species (bird surveys), variables related to the canopy level (i.e. the grey area) and the understory (i.e. within circular plots of 20-m radius from the centroid of each plot).

plot, we also recorded the average altitude and slope (extracted from a digital elevation model) and the distance of the centroid of each plot to the nearest forest edge.

From April to June 2015, we used field methods to assess the understory habitat of the 140 plots under study (Figure 1). To do this, we established a circular-plot with a radius of 20 m at the centroid of each plot and we recorded the number of (1) trees with and without mould-filled cavities (CavityStem) and (2) trees with cavities >5 cm perpendicular to the tree trunk (Cavity5cm). We measured understory variables related to structural complexity, specifically: (3) number of trees with a broken crown (CrownBrok), (4) species richness of understory trees and shrubs (that is, the species richness of the small trees and shrubs growing beneath the tree canopy; RichUndTree) and (5) average DBH of dominant trees (SizeTree). Finally, we measured variables which serve as a proxy of the abundance of deadwood including the number of (6) snags or standing dead trunks (Snag), (7) dead trees and fallen trunks (DeadFallTree) and (8) naturally generated stumps (TreeStump).

### Bird survey

Bird censuses were conducted from 2 April to 11 June 2015 (Figure 1), a period important in the phenology of the majority of breeding birds in the northern Iberian Peninsula (i.e. the main breeding period). Censuses were carried out from fixed points located at the centroid of each plot, during which a single observer (JRP) recorded every bird heard and/or seen up to a distance of 75 m from the census point (except flyovers). All censuses were conducted within a 3-h period starting 1 h after sunrise in appropriate weather conditions (i.e. no heavy rain or strong wind). Each census consisted of three 5-min counts, with a 2-min break between each. All censuses within each plot were performed in a single day, allowing us to carry out multiple censuses at one plot at the expense of measuring between-day differences. Number of recorded incidents of presence or absence of each species, in each of the three 5-min counts were pooled for each plot. Each census (Julian) day was treated independently for statistical purposes (see below).

### Statistical analysis

We tested for differences in habitat and bird species composition between native forest and non-native plantations. Specifically, we assessed (1) the relationship between forest type and habitat variables at the canopy and the understory level, (2) differences in species composition between forest types and (3) the response of bird species to resources at the canopy and the understory level. All statistical analyses were performed in R 3.2.3 ('R: A Language and Environment for Statistical Computing,' 2010) using the following packages: *vegan* (Oksanen *et al.*, 2017), to perform analyses of canonical correspondence analyses (CCAs), non-metric multidimensional scaling (NMDS), rarefaction curves and principal component analyses (PCAs); *stats*, for generalized linear models (GLMs), CCA and *k-mean* analyses; *ggbiplot* (Vu, 2011) to perform the biplot for CCAs; and *MuMIn* (Bartoń, 2016) for model selection and averaging based on AIC scores. Unless otherwise indicated, average values are reported as mean  $\pm$  standard error.

### Composition and relationships between forest resources

We performed the direct gradient analysis of CCAs to ascertain if the habitat variables at the canopy level could be classified (or constrained) according to their relationship with those at the understory level. To this end, we constructed a first matrix of six dimensions of independent variables which comprised the percentage of abundance of canopy accounted for by beech/oak forest, or conifer/broad-leaf of plantation, the altitude and the distance to the nearest forest edge for each plot.

We also constructed a second matrix of dependent variables comprising the eight understory variables measured in the circular plots (see Habitat surveys). Axes scores were re-scaled to the unit variance. The variance inflation factor (VIF) was also calculated in order to test for collinearity between dependent variables.

### Bird species composition and differences between forest types

Since no a priori structure of bird community based on habitat composition was assumed, we used the indirect gradient analysis of NMDS to ordinate the distance-based differences in bird species composition across plots. This was performed using 'Bray-Curtis' dissimilarity matrices calculated from species presence/absence in plots. Differences in species composition in plots were ordinated in a two-axis ordinal space; in the biplot ordination we added species scores as weighted averages of ordination by plots. We excluded species which occurred in only one plot because they did not contribute to differences in species composition between plots. In addition, we calculated multi-response permutation procedures (MRPP) to confirm whether the species composition differed between forest types, a procedure based on the Monte Carlo permutation test of among- and within-group dissimilarities.

We performed sample-based rarefaction curves of species richness (Gotelli and Colwell, 2011) to describe species composition and confirm that our sampling effort was appropriate to describe our bird community. Rarefaction curves were generated by repeatedly and randomly re-sampling 1000 times (without replacement), and we computed the expected species richness function and the 95 per cent confidence interval pooled for forest types (re-scaled by the number of expected species). The expected accumulative curve of species richness in plots was fitted to non-linear regression models.

### Bird-habitat associations to forest resources

We were interested in ascertaining whether the bird species composition from the previous analyses was the consequence of species-specific habitat associations. To this end, for each species we performed (1) GLM analyses to calculate relationships between dependent species occurrence (based on presence/absence) and independent habitat variables and (2) then used PCA to classify the species-habitat relationships (i.e. their GLM estimates). Accurate species-habitat associations depend on data prevalence (i.e. the ratio between presences and absences), resulting in more accurate associations for rarer than for common species (Franklin *et al.*, 2009), while data quality is independent of data prevalence (Jiménez-Valverde and Lobo, 2006). Thus, we restricted our analysis to the 16 bird species detected in at least 10 per cent of the plots in order to achieve robust estimates of species-habitat associations (see Table S1 in Appendix S1).

First, we used GLMs (logistic regression: logit link, binomial error) to test whether the occurrence of each species was affected by independent variables (see below for description of independent variables). For each bird species tested the relationship between species occurrences and habitat variables at two levels: 'canopy' models, which included independent variables such as the proportion of tree canopy of each of the four forest types (e.g. the proportion of beech forest), the distance to the nearest forest edge and average altitude; and 'understory' models, which comprised eight independent variables (see above and Table S2). All independent variables were standardized to allow for direct comparisons of resulting coefficients. We adopted an information-theoretic approach and tested all model subsets resulting from all possible combinations of independent variables. All model combinations were ranked according to their AIC<sub>c</sub> score, retaining only those models with  $\Delta AIC_c < 2$ , which were then weighted based on their AIC<sub>c</sub> score (Burnham and Anderson, 2002). We used a k-fold cross-validation procedure (Chernick and LaBudde, 2011) to assess the predictive

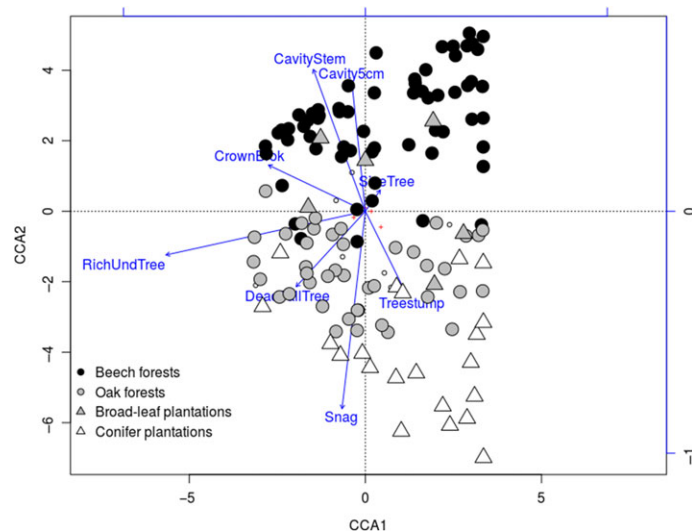
performance of the top-ranked models (i.e. with  $\Delta AIC_c < 2$ ). For each of 10 iterations, we randomly divided our data in two, using 66.6 per cent to calibrate the association of species occurrence to independent variables and 33.3 per cent to validate the results. We then calculated the average-model estimates and the area under the ROC curve (AUC) as a measure of model performance.

Second, to classify the species–habitat associations at the ‘canopy’ and ‘understorey’ levels we performed an indirect gradient analysis of PCAs to represent the relative position of species-specific associations to independent variables. We constructed a two-dimensional gradient for both ‘canopy’ and ‘understorey’ models based on the model estimates relating to independent variables and the species occurrence (see Tables S2 and S3), and these were then classified along two-PCA gradients representing the parameter reduction of six independent variables for ‘canopy’, and eight variables for ‘understorey’ models (see above in data analysis). Thus, for each species we used model estimates (i.e. average-model estimates after 10 iterations, Tables S2 and S3) as input variables for the PCA, and we calculated the position of each species within a two-dimensional space of species-specific habitat-associations.

## Results

### Composition and relationships between forest resources

We found that habitat composition at the canopy level was explained by habitat differences at the understorey level (see Figure 2). Specifically, we found that the first CCA axis (CCA1) varied along a gradient of structural complexity and the second CCA axis (CCA2) along a gradient of volume of deadwood. Overall, our CCA model was significant (ANOVA permutation test: Chi-square = 0.05,  $F = 5.5$ , d.f. = 8,  $P < 0.0001$ ) and



**Figure 2** Canonical correlation analysis (CCA) two-dimensional ordinal diagram of six variables at canopy level classifying eight variables at understorey level (see Material and methods for a detailed description of variables). Sampled plots are represented by circles, whereas the arrows represent the gradients of habitat variables at the understorey level explained by the CCA axes. The direction and the length of the arrows with respect to each axis indicate the correlation coefficient between the variable in that axis. Plots were additionally tagged and coloured according to forest type.

explained c. 20 per cent of total variance ( $\text{adj-}R^2 = 0.198$ ). The variance inflation factor (VIF) indicated low collinearity between independent understorey variables ( $\text{VIF} < 3.01$  for all variables).

In descending order of importance, CCA1 was associated with CrownBrok, RichUndTree and DeadFallTree, whereas CCA2 was related to CavityStem, Cavity5cm, Snag and Treestump (Figure 2; see Habitat surveys for abbreviations). When we tagged plots according to their assigned forest type (i.e. >50 per cent abundance of a particular species), between-group differences were found at the understorey level (Figure 2). Beech forest had low values of RichUndTree and Snag, and high values for CavityStem and Cavity5cm; oak forest had high values of CrownBrok, RichUndTree and DeadFallTree and medium values for CavityStem, Cavity5cm and Snag while conifer plantations had high values of Snag, DeadFallTree, Treestump and low values of CavityStem and Cavity5cm. Broad-leaf plantations had values which fell mid-way between those for oak and beech forest. For a cross-correlation analysis for both canopy and understorey levels, see Figure S2 and S3 in Appendix S1.

### Bird species composition and differences between forest types

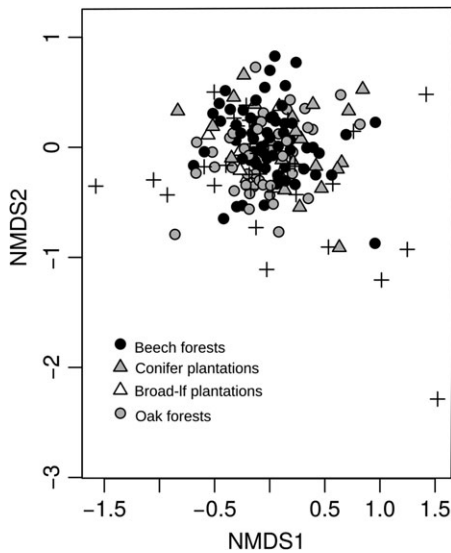
In total, we recorded 1093 of 39 bird species (see Table S1 in Appendix S1 for a complete list of the species recorded). The mean richness per plot was 10.4 species, ranging from 2 to 19. Sample-based rarefaction curves of pooled plots were not asymptotic, which suggests that our sample effort did not capture the full bird richness (see Figure S4).

Analyses of species composition across forest types resulted in a final stress of 0.282, which is within the range of reliability for community data and is unlikely to have been obtained by chance (Monte Carlo test  $P < 0.0001$ ). The two axes represented 64.9 per cent of the variation of the bird community, using a linear fit-based  $R^2$  as a measure of goodness of fit. Results of NMDS showed that the sampled plots grouped together in the two-axis ordinal space. We also tagged plots according to their forest type and we found that plots were spread out throughout the biplot, which suggests a similar bird community and shared species composition independent of forest type (Figure 3). We also calculated the biplot NMDS ordination of species scores, and found that the plots with common species were more spread out in the biplot than those classified by forest type (Figure 3). Despite these similarities between plots, the MRPP analyses showed that the weighted group mean distances were proportionally more similar between broad-leaf plantations and oak forests ( $\text{delta} = 4.306$  and  $4.277$ , respectively) than between beech forests and conifer plantations ( $\text{delta} = 3.935$  and  $3.885$ , respectively).

### Bird–habitat associations to forest resources

Habitat associations of bird species (i.e. those 16 species detected in at least 10 per cent of sampled plots; see Tables S2 and S3) were plotted on a two-dimensional PCA axis representing the relationship between species-specific associations for either canopy or understorey variables (Figure 4). In terms of associations with respect to canopy variables, we found that the majority of species (i.e. PC1 axis had 60 per cent loading) responded positively to

distance to forest border (e.g. *E. rubecula*, *C. brachydactyla*) and to altitude (e.g. *P. ibericus* and *P. palustris*) but had negative associations for broad-leaf plantations compared to the three other forest types. For the understory variables, species were more aggregated and centred around the two origins of the PCA axes. Nevertheless, the majority of species responded positively to CavityStem and Cavity5cm and to RichUndTree and Crownbrock (notably *P. ater*), while other species responded positively to the abundance of Snags (notably *T. viscivorus*).

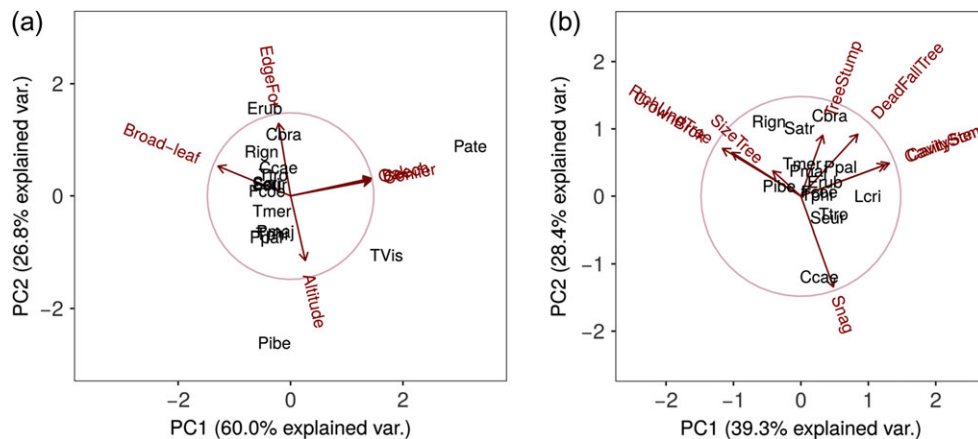


**Figure 3** Non-metric multidimensional scaling (NMDS) of bird species composition in sampled plots. We plotted the ordination (stress = 0.210) of plots based on the species composition across forest types. For illustration purposes, we represented the relative position of each plot on two-dimensional axes, with plots with similar species composition being closer together on both axes. Plots (coloured circles) were also tagged according to forest type. Crosses represent the position of each bird species within the two-dimensional axes.

## Discussion

In this work, we studied a bird community in the forests of the northern Iberian Peninsula to ascertain whether mature non-native plantations are able to maintain a similar bird species composition to that of native forests and, if not, whether any differences were the consequence of species-specific associations for habitat composition. We found that mature non-native plantations (especially conifer plantations) presented complementary habitat properties to those of native forest types (i.e. oak and beech). Despite these differences in habitat composition, we found bird species composition to be similar between native forests and non-native plantations. We also found that community assembly was a consequence of species-specific associations for habitat composition, both at the canopy and at the understory level. This latter result suggests that no one single set of indicators of habitat quality captures the complexity of the entire bird community.

The production of mature and old-growth forests is usually dependent on long periods of forest maturation without any human disturbances (Moning and Müller, 2009). For our study site, we found strong differences in habitat composition measured at the understory level that were not explained simply by differences in forest type (Winter and Möller, 2008). Specifically, tree cavities were abundant in beech forests, moderately so in oak forest types, but not common in mature conifer plantations; deadwood values were low in beech forests and high in mature conifer plantations; and structural complexity was low in beech forests but high in conifer plantations and oak forests. Beech forest is the major forest type in our study area and essentially provides resources for both breeding and roosting for cavity-dwelling species (e.g. Winter and Möller, 2008; Bauhus et al., 2009). In contrast, mature conifer plantations, while comprising a small percentage of the forested area, provide a complementary source of forest resources in terms of deadwood that ensured an abundant food supply (e.g. Bauhus et al., 2009; Rosenvald et al., 2011). Finally, oak forests are relatively abundant in the study area and provide a range of habitat resources (Halaj et al., 2000; Bauhus et al., 2009; Burrascano et al., 2013),



**Figure 4** Principal components analysis (PCA) relating the occurrence of bird species to habitat variables at the canopy (a) and understory (b) level, based on six and eight variables of habitat composition, respectively. For canopy and for understory level, species are positioned on two-dimensional axes based on the model estimates relating species occurrence to habitat composition (see Tables S2 and S3). Bird species (coloured names) are positioned on the two axes, whereas arrows indicate the habitat variables shown in the biplot.

while in broad-leaf plantations, habitat complexity and resources were variable and values fell somewhere between those of oak and beech forests. Overall, these results suggest that the presence of mature conifer plantations increases the breadth of habitat attributes associated with deadwood availability, at least in areas like ours with abundant beech forests.

Bird communities are structured according to species-specific requirements that are critical for species life-histories (Fuller *et al.*, 2012). In this work, we provide data of habitat quality and resources for the breeding period of majority of forest birds found in Europe in general, and in the Iberian peninsula in particular. Rarefaction curves demonstrated that we did not capture the full bird richness in our study area. Despite this, however, the results suggest that bird species composition in each plot is highly variable and is not explained by forest type alone (i.e. beech or oak forest or conifer or broad-leaf plantation). Thus, the habitat properties of different forest types are insufficient to describe our bird community, as we found that the differences at the understory level translated into an unstructured species composition not explained by the habitat composition in either native forest or non-native plantations. We additionally found higher variability when a species-based rather than a habitat-based classification was used, meaning that the plots with species in common are spread more widely across the study area than plots of the same forest type. Our sampling design could additionally be constrained by the relatively lower abundance of non-native plantations compared to native forests (see Figure S1), which may have influenced our finding of an unstructured bird community. A detailed analysis of the species composition between plots showed that oak forests and broad-leaf plantations were proportionally more homogeneous than were beech forests and mature conifer plantations, suggesting that the more varied resources available in the latter forest types led to the generation of a less homogenized bird community. That said, future works that provide detailed analyses of species preferences for habitat composition would shed light on the main process structuring our bird community.

Across fragmented and heterogeneous landscapes, both the amount of native forest and the distance to forest edge usually favour the occurrence of richer bird communities (e.g. Lindenmayer and Franklin, 2002; Barbaro *et al.*, 2007; Fuller *et al.*, 2012). As in the majority of studies on the effect of species distribution on fragmented landscapes, we found that most bird species had both a negative preference for altitude and a positive preference for distance to forest edge. However, these two environmental variables covary in our study site, suggesting that the negative effect of high altitude and short distance to forest edge were additive in explaining species occurrences. In addition, we found that bird species were positively associated with beech forests, conifer plantations and oak forests, but negatively with broad-leaf plantations. Even though beech and oak forests and conifer plantations presented a large suite of habitat properties across our study site (see above), we found no differences in the responses of individual species to habitat composition, which could be a sign of the richness of the suite of resources in the study area (independent of the forest type) for our bird community, as has been found in other mature woodlands (Fuller *et al.*, 2012 and references therein).

In Europe, stand age and structure are the most important explanatory variables for predicting bird richness and composition,

rather than forest type or the dominant tree species (e.g. Wilson *et al.*, 2006; Torras *et al.*, 2008; Balestrieri *et al.*, 2015; Bergner *et al.*, 2015). According to our data, bird species were positioned along increasing gradients of preference to the understory parameters related to tree cavity (i.e. CavityStem and Cavity5cm), tree structural complexity (i.e. positive relationship with Crownbrock and RichUndTree), and increasing volume of deadwood (i.e. Snag) – resources associated with mature conifer plantations and oak forests (see above). In contrast, Martínez-Jauregui *et al.* (2016) used field data to describe habitat composition found greater bird richness in native forests than mature plantations of conifers, after controlling for the potential effect of environmental factors, forest cover and vegetation structure. Although a combination of below-canopy field and landscape data (based on remote sensing data) are potentially more time consuming and expensive to collect, such measures do better represent the habitat attributes at which bird species respond (Niemi and McDonald, 2004). In summary, a finer analysis of the species-habitat relationships at the understory level helps to better explain bird species composition, and provides a clearer picture of how bird communities are assembled.

## Conclusion

In Western Europe, many species of forest birds have expanded their distribution in the last few decades, presumably due to afforestation, reforestation and/or forest maturation (Martin *et al.*, 2012). Under this scenario, the question remains though as to whether mature non-native plantations might provide additional forest resources that are not available in native forests, and thus contribute to enriching the species of forest birds. We studied a bird community and forest resources and we found that bird community was clearly structured on the basis of species-specific preferences at the understory level. Our results suggest that mature non-native plantations embedded within mosaics of native forests could provide a complementary source of resources to support a rich bird community (Bauhus *et al.*, 2009). Birds have been widely acknowledged as biological indicators since they are usually associated with forest attributes and habitat-based composition within forests (Canterbury *et al.*, 2000) and their presence (or absence) may indicate the status of the resources that are important for biodiversity conservation (Balestrieri *et al.*, 2015; Bergner *et al.*, 2015).

## Supplementary data

Supplementary data are available at *Forestry* online.

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## Conflict of interest statement

None declared.

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