

Influences of forest type and forest structure on bird communities in oak and pine woodlands in Spain

Leticia Díaz*

*Dpto. Biología Evolutiva y Biodiversidad, Museo Nacional de Ciencias Naturales de Madrid,
C/José Gutiérrez Abascal, No. 2, Apdo. 28006, Madrid, Spain*

Received 15 February 2005; received in revised form 18 October 2005; accepted 24 October 2005

Abstract

Complex vegetation structure and floristic composition heterogeneity increase niche diversity, which is thought to also increase avian diversity. Woodland avifauna from the Sierra de Guadarrama, Madrid, was studied during spring 2003 to test whether floristic composition and structure of mixed oak-pine forests provided a suitable environment to sustain a specialized avian community that differed in species composition from those of pure pinewoods and oak woodlands. Habitat selection patterns of each species, as well as the intensity with which they selected their preferred habitat were also studied.

Bird species richness was significantly higher in mixed oak-pine forests than in pinewoods, whereas differences in avian abundance among the three forest types were not clear. No species preferred or exclusively used mixed transitions. Therefore, slight increases in avian abundance and species richness within mixed forests were explained through the assemblage of both typical oakwood and pinewood avifauna. The results are discussed in the context of the general impoverishment of Nearctic-Palaearctic bird species in the southwestern Palaearctic margin, and the high spatiotemporal fluctuations that mixed transitions have suffered since the Quaternary period.

The results highlighted the importance of forest maturity, low altitudinal position of forests and, diversity and development (cover and height) of the shrub layer for forest birds in the region.

© 2005 Elsevier B.V. All rights reserved.

Keywords: Vegetation structure; Shrub diversity; Mixed forest; Bird species richness; Habitat selection; Forest transition

1. Introduction

Contact areas between habitat types have constituted the premise of numerous studies in the field of ecology (Bonham et al., 2002; Carignan and Villard, 2002; Arnold, 2003), because structural characteristics derived from different vegetal compositions in such discontinuities might cause remarkable changes in their animal community assemblages (Odum, 1958). In this context, two similar concepts can be distinguished, ecotone and habitat edge. The ecotone concept refers to an area variable in size, in which a floristic composition gradient is established between two habitats (Blondel and Farré, 1988; Blake and Loiselle, 2000; Grytnes and Vetaas, 2002). Habitat edge is restricted to the narrow band where two very different and easily distinctive habitats come into contact (Dover and Sparks, 2000; Berry, 2001; Backer et al., 2002).

Research on the influence of ecotones and habitat edges on their associated animal communities has been widely carried out, mainly in the context of fragmentation, although both the nature and the intensity of its effects are still to be defined (see Murcia, 1995 for a review). Effects of ecotones and habitat edges are species dependent, since, for example, body size or dispersal capabilities frequently determines the spatial scale used. This prevents agreement on a single conclusion regarding the effects of ecotones (e.g., Donald et al., 1998; Dover and Sparks, 2000; Blouin-Demers and Weatherhead, 2001; Pryke and Samways, 2001; Backer et al., 2002; Bailey et al., 2002; Estrada and Coates-Estrada, 2002; Lindenmayer and Lacy, 2002; Sawchik et al., 2002; Van Lien and Yuan, 2003). Moreover, the research outcome depends in part on the ecological aspect to be analysed, since structural and floristic changes are far more intense when forests contact with open gaps, shrublands, crops and prairies (Wardell-Johnson and Williams, 2000; Berry, 2001; Blouin-Demers and Weatherhead, 2001; Rodewald and Yahner, 2001; Backer et al., 2002; Herrando and Brotons, 2002; Van Lien and Yuan, 2003), than

* Tel.: +34 91 4111328; fax: +34 1 5645078.

E-mail address: menld661@mncn.csic.es.

when two kinds of forests come into contact (Donald et al., 1998; Hobson and Bayne, 2000a; Carignan and Villard, 2002; Lindenmayer and Lacy, 2002; Machtans and Latour, 2003). Finally, due to increases in structural heterogeneity, the effect of ecotones on a variety of organisms are illustrated by sinecological parameters (e.g., Rodewald and Yahner, 2001; Backer et al., 2002; Herrando and Brotons, 2002), predation rates and parasitism rates (Donovan et al., 1995; Bayne and Hobson, 1997; Friesen et al., 1999; Carlson and Hartman, 2001; Forsman et al., 2001; Carignan and Villard, 2002).

Despite the range of situations and parameters studied, there is currently a lack of research on variation in avian communities across natural vegetation gradients between two types of forests. Because of difficulties in defining the spatial demarcation of such ecotones, studies exploring the main environmental factors that affect their avifauna are scarce. However, in the Mediterranean region of the Iberian Peninsula, unmanaged oak-pine woods transitions are rare and restricted to areas where two bioclimatic plateaus come in contact. Thus, they are relatively easy to locate and are particularly suitable to studying effects of ecotones on animal communities.

The objectives of this study are to: (1) explore the effects of the structure and floristic composition of mixed forests (oak woodlands and pinewoods) on woodland avifauna, by studying sinecological parameters (abundance and species richness); (2) identify factors determining the preferred distribution habitat of the species comprising avian communities in these three ecosystems; (3) determine the intensity of selection of each species by their preferred habitat; and (4) provide management recommendations for encouraging forest avifauna in oak woodlands, pinewoods, and mixed transitions.

2. Methods

2.1. Study area

This study was carried out in forests in the southern part of the Sierra de Guadarrama, a portion of the Sistema Central (Madrid: 40°47'35"N, 04°00'40"). The main orientation of the Sistema Central is northeast-southwest and it comprises seven mountainous systems. The survey area comprised 14 forest areas spanned over 900 km². The climate of the area is Mediterranean, with hot, dry summers and cool, wet winters, since the decrease in precipitation corresponds with increased temperature in the summer (Izco, 1984 and Costa et al., 1998). Its continental placement and mountainous topography determine large thermal variations throughout the day and year. Hence, growing period for vegetation in this landscape is quite short.

Forests from the study area are dominated by two tree species, Pyrenean Oak *Quercus pyrenaica* and Scots Pine *Pinus sylvestris*. Oak woodlands of *Q. pyrenaica* are found from 1000 to 1700 m in the Sistema Central, while pine woodlands occupy the 1600–2100 m band. As they usually are distributed across different plateaus, it is rare that they are found in the same location. However, the mountainous topography of this region

provides suitable environments for their interaction that are rarely found elsewhere. Mixed oak-pine forests comprising such transitions vary in their distribution according to the orientation and steepness of the terrain. Therefore, in wet and warm areas (e.g., southern and riparian areas) oaks spread upward into pine-dominated areas, while in dry and cool areas pines spread down into oak-dominated areas (see Costa et al., 1998 for detailed information).

2.2. Survey design

Data of bird abundance was gathered using point counts of 50 m radius (0.8 ha). Each point was separated by at least 250 m from the all other points to minimize the probability of sampling the same bird more than once. Survey plots were established along an altitudinal gradient from 960 to 1850 m.a.s.l. An average of 5–6 elevational tracks of census plots were established in each of the 14 forest sites. Within each forest site, plots of different tracks were separated at least 300 m. Within each altitudinal track, census plots were arranged from oak woodlands (lowland areas) to pine woodlands (upland areas) in a way that at least one plot fell within each forest type, including the transition areas. As census plots belonging to the same elevational track were sampled the same day, the three forest types were surveyed throughout the whole sampling. Each track was surveyed twice a day, one in the morning (from dawn to three hours later) and one in the afternoon (beginning three hours before sunset), to accomplish for possible differences in detectability due to time. Moreover, the visit order to the tracks and to the plots within each track, changed between the morning and the afternoon period, ensuring that all plots were visited once within the span-time where birds were more active. Listening time in each plot was 10 min/visit, so each sample point had an accumulated listening time of 20 min, which was later averaged to obtain mean abundance data of the bird species (birds/0.8 ha/10 min). Surveys were carried out from the first fortnight of May to the second fortnight of June 2003, ensuring the arrival of all the migrant bird species. I avoided sampling in days with bad weather (hard wind, storms, etc.), to reduce problems of detectability (Tellería, 1986 and references therein). Also, only continuous patch forests were surveyed, avoiding clear cuts or open borders, to reduce the probability of including species from other environments. We obtained a total of 262 point counts: 77 in oak woodlands, 86 in pine woodlands and 99 in oak-pine transitions.

A 25-m radius plot was placed within each census point to sample vegetation structure and measure those variables indicating its position and cardinal orientation (see Table 1 for a synthesis). Factors representing vegetation structure were: percent ground cover of stones (CSTO), herbs (CHER), litter (CLIT) and shrubs (CSHR); mean height of shrubs (HSHR) and overstory trees (HTREE); mean diameter of the five largest trees (DIAM); number of trunks of pines (NT P) and oaks (NT O) when surpassed 4 cm diameter at breast height (DBH) and 2 m height; number of trunks of four diameter classes: thin (TREE t; 5–9 cm DBH), medium (TREE m; 10–29 cm DBH),

Table 1
Results of PCA showing variables describing forest habitat heterogeneity (a); and degree of exposure of forest parcels (b) to each principal component

(a) Variables	VG1	VG2	VG3	VG4
CSTO (stone cover)	0.08	0.07	0.09	0.02
CHER (herb cover)	0.05	−0.11	0.86	0.15
CLIT (litter cover)	−0.03	0.74	−0.08	0.02
CSHR (shrub cover)	−0.09	−0.24	−0.88	−0.14
HSHR (shrub height)	0.07	−0.03	−0.66	0.18
HTREE (tree height)	0.37	0.12	0.19	0.62
DIAM (average five thickest trunks)	0.42	−0.15	0.11	0.74
TREE t (trees of thin trunk, 5–9 cm Ø)	−0.90	0.15	0	−0.1
TREE m (trees of medium trunk, 10–29 cm Ø)	−0.43	0.65	0.19	−0.26
TREE tk (trees of thick trunk, 30–59 cm Ø)	0.58	0.41	0.25	0.25
TREE vtk (trees of very thick trunk, Ø >60 cm)	−0.12	−0.05	−0.09	0.81
NT O (no. of oaks)	−0.93	−0.13	0.04	−0.05
NT P (no. of pines)	0.39	0.79	0.15	−0.04
NEBX (no. of nestboxes)	0.04	−0.01	0.01	0.1
NT CLIM (no. of trunks covered by lianas)	0.02	−0.01	−0.06	0.01
Eigenvalue	2.68	1.91	2.15	1.81
Explained variance (%)	17.8	12.7	14.3	12.1
(b) Variables	PS1	PS2		
ALT (average altitude)	0.87	0.02		
SLOPE (slope)	0.84	−0.18		
SENORI (sin of the orientation)	−0.01	0.69		
COSORI (cosin of the orientation)	−0.19	−0.75		
Eigenvalue	1.5	1.07		
Explained variance (%)	37.5	26.8		

Correlation coefficients in bold denote $p < 0.001$.

thick (TREE tk; 30–59 cm DBH) and very thick (TREE vtk; >60 cm DBH). More detailed information was recorded as well, to build synthetic variables including shrub stratum diversity (DSHR). Shrub diversity were calculated to explain how was the shrub cover of a census plot divided among shrub genus. For that purpose, I used the inverse of the Simpson index (1949):

$$D = \sum_{i=1}^n p_i^2;$$

being “ n ” the number of shrub species present in the study area and “ p_i ” the percentage of cover of the shrub genus “ i ” respect the total shrub cover in that census plot. This index was later divided by the number of shrub genus present in the survey area. Therefore, that new index went from 0 up to 1, being 0 when no shrub species was present in the census plot, and 1 when all the genus present in the study area were also present in the census plot and occupied the same surface. In a similar way, tree species diversity (DTREE) and tree diameter diversity (DDIAM) were calculated. Variables summarizing geographic location (altitude-ALT-, slope-SLOPE-) and orientation (that

were later sin and cosine transformed –SENORI- and –COSORI- to obtain an index of south-north and east-west orientation, respectively) were obtained from 1:25000 maps of the Centro Nacional de Información Geográfica de España. Distances to the nearest permanent water source (DISWAT) and to the nearest mixed parcel (DIST) also were gathered from these maps. I also recorded number of nestboxes (NEBOX), and number of trunks covered by lianas of *Hedera* spp. for at least in 20% of their surface (NT CLIM). These variables were included because it is known that nestboxes benefit birds such as Coal Tit (*Parus ater*), Crested Tit (*Parus cristatus*), Great Tit (*Parus major*), Blue Tit (*P. caeruleus*), Eurasian Nuthatch (*Sitta europaea*), European Pied Flycatcher (*Ficedula hypoleuca*), and other species that used them for breeding (Summers and Taylor, 1996; Pérez de Ana, 1997). In addition, lianas not only promote trophic diversity (arthropods, Coutin, 1997; Litt, 2000), but also increase number of breeding sites (e.g., for Common Blackbird *Turdus merula*, Northern Wren *Troglodytes troglodytes*, Firecrest *Regulus ignicapillus*, and others).

Vegetation structure variables were visually estimated and bird species visually and acoustically identified, excluding individuals that flew over the survey plot and did not stop within.

2.3. Statistical analyses

2.3.1. Forest type scale

Normality of variables was explored by testing for significant skewness and kurtosis with t -tests, and homoscedasticity was checked using univariate tests of the Hartley, Cochran and Bartlett’s family. It was not necessary to transform any variable as they conformed to normality. One-way analyses of variance were performed to assess differences in species richness and abundance of birds among forest types. Tukey a posteriori tests were later used to establish significance of pairwise comparisons among those forest types.

Differences in frequency of occurrence of each species among woodlands were accomplished by t -tests of independent samples and unequal sample sizes, using sequential Rice correction of p -level to mitigate for problems derived from multiple pairwise tests (Rice, 1989).

2.3.2. Habitat scale

To determine the factors undergoing bird abundance and species richness, stepwise regression analyses were conducted in whole survey plots. Both backward and forward procedures were used for each regression analysis, due to the influence that the order of introduction or exclusion of variables in the stepwise procedures may have on the results (chiefly if colinearity problems exist; see Sen and Srivastava, 1990; Quinn and Keough, 2002). As the models were consistent, regardless of the order of selection, it was not necessary to employ other types of analyses (e.g., cross-validation or best subsets regression analyses).

Influences of structure, geographic location and orientation of patches were evaluated using two principal component analyses (PCA). The first PCA only included structure and

floristic composition variables (VG), while the second only included orientation and geographic placement of plots (PS). In this way, their interpretation and subsequent use in multiple regression analyses were simplified. Vegetation principal components were rotated by the varimax normalized procedure to facilitate interpretation. In addition to the vegetation and position components, variables indicating proximity to the transition areas between oak woodlands and pine woodlands and those relating vegetation structure complexity were also included in the regression models (DIST, DTREE, DDIAM and DSHR). In the bird abundance model, the bird species richness (SBIRD) was included as an independent variable, due to its strong influence over bird abundance when small sample units are concerned (Wiens, 1989).

Regression trees were used to establish which variables were most strongly related to abundance and species richness distributions within the study territory and relationships among variables. Also, absence/occurrence of each bird species were analyzed using classification trees to determine habitat selection preferences. Regression and classification trees allow evaluation of hierarchy among variables as well as relationships among them. Moreover, biases derived from multicollinearity problems are avoided using such techniques (see Hastie and Tibshirani, 1990; Hayden and Hamilton, 1997; Breiman et al., 1984; and De'Ath and Fabricius, 2000 for more information), this is very useful when complex analytical situations are considered, like those describing species habitat selection patterns (e.g., Hayden and Hamilton, 1997; Rodewald and Smith, 1998; Clark et al., 1999; Robinson and Robinson, 1999; De'Ath and Fabricius, 2000; Drapeau et al., 2000). The process is based on iterative splitting of the original data into groups that relate through tree diagrams. In each branch splitting, the variable that maximizes the differences between the two groups of data is identified and represented by new emergent branches. Those differences are estimated through correct classification rates (classification trees) or deviance (classification or regression trees), and branch lengths are proportional to those differences (see Breiman et al., 1984 and De'Ath and Fabricius, 2000). In the splitting procedure, a minimum deviance of 0.01 and a minimum sample size of 10 were used to separate groups. Once the model was obtained, those variables whose influence were not significant were excluded. To accomplish for that requirement I used a χ^2 -test for checking whether the residual deviance obtained before applying a variable significantly differ from the residual deviance after applying that variable. Afterwards, the tree was reduced to 10 final leaves to facilitate interpretation.

Habitat selection patterns were only analyzed for species with more than 20 occurrences, since lower sizes produced unstable results.

2.3.3. Habitat selection intensity

Multidimensional graphic representation of structural components defined a volume that summarized the floristic and vegetation variability of the landscape. Therefore, the origin of coordinates of this multidimensional figure would represent the averaged available habitat. Euclidean distances

between the averaged location of a species in that volume and the zero coordinate defines the magnitude of the habitat selection intensity. *t*-tests were used to ascertain whether those selection intensities were significant and the species could be considered stenotic. For that purpose, the standard deviations of Euclidean distances were also calculated. In the same way, the average Euclidean distances between the location of each species and the origin of coordinates of each vegetation component were studied. This provides an index of habitat selection intensity for each species for the kind of vegetation defined by each component. Therefore, a species not considered stenotic in general terms may have a significant selection intensity for the landscape defined by some vegetation components, and vice versa. *t*-tests results were also corrected for multiple *p*-estimates by Rice.

3. Results

3.1. Characteristics influencing species richness and abundance of birds

Forty-two bird species were recorded during the survey, being 25 of them detected in either oak woodlands, pine woodlands or oak-pine transitions. In contrast, 3 bird species were detected only in oak woodlands, 2 were detected only in pine woodlands and 4 were encountered only in oak-pine transitions. The remaining 8 species were distributed in mixed transitions and either oak or pine woodlands. Average bird species richness was 9.1 spp/0.8 ha (± 2.6 spp/0.8 ha) in oak woodlands, 9.9 spp/0.8 ha (± 2.7 spp/0.8 ha) in mixed oak-pine forests, and 8.6 spp/0.8 ha (± 3.3 spp/0.8 ha) in pine woodlands. Also, average bird density was 8.4 birds/0.8 ha (± 2.9 birds/0.8 ha) in oak woodlands, 8.8 birds/0.8 ha (± 2.3 birds/0.8 ha) in mixed oak-pine forests and 7.9 birds/0.8 ha (± 2.2 birds/0.8 ha) in pine woodlands.

Bird species richness significantly differed among the three forest types ($F_{2,259} = 4.92$; $p = 0.008$; $R^2 = 3.7\%$), being higher in mixed oak-pine forests than in pure pine woodlands (Tukey a posteriori test: $p = 0.009$). There were no clear differences among the three forest types in total bird abundance ($F_{2,259} = 2.96$; $p = 0.053$; $R^2 = 2.2\%$). Therefore, differences among the main forest types in the study region are very subtle and only responsible for small variations in bird density and species richness.

The first four vegetation components accounted for 56.9% of original variation in habitat structure (see Table 1). The first component (VG1) differentiated young oak woodlands from mature pinewoods. The second component (VG2) defined a trend of increasing density of mature pines and litter cover. The third component (VG3) separated forests with a well-developed shrub layer from those with large herbaceous covers. The fourth component (VG4) related to tree maturity. The first two principal components for position accounted for 64.2% of variation in geographical location. The first component (PS1) was positively associated to altitude and steepness of forest patches, while the second (PS2) discriminated northwest to southeast oriented areas.

Table 2
Regression models explaining the increase in bird species richness and avian abundance

Variables	Species richness (S/0.8 ha.)			Bird abundance (A/0.8 ha.)		
	B	% Var	P	B	% Var	P
Intercept	5.966			2.409		
DIST (minimum distance)						
DTREE (tree species diversity)						
DDIAM (diameter diversity)						
DSHR (shrub species diversity)	7.963	8.43	0.0000			
PS1 (high and steep areas)	-0.590	7.15	0.0000			
PS2 (southeast facing areas)				0.259	1.06	0.0120
VG1 (mature pinewoods)	0.546	5.33	0.0000			
VG2 (semimature pinewoods with litter)						
VG3 (forests with ground of herbs)						
VG4 (forest maturity)	0.449	5.68	0.0003			
SBIRD (bird species richness)				0.828	56.06	0.0000
Total		26.6	0.0001		57.1	0.0001

Coefficients (B), variance explained (% Var) and *p*-level (*P*) of only the significant variables are provided. The meaning of the acronyms used for the PCs and for the independent variables are given between brackets.

Associations of the environmental gradients described by PCA with bird community parameters are shown in Table 2. Bird species richness increased with tree maturity (VG4), coniferous cover (VG1), and shrub species diversity (DSHR), and was inversely related to altitude and steepness (PS1). These relationships explained 26.6% of interplot variability in species ($F_{4,257} = 23.27$; $p < 0.0001$). Therefore, species richness was highest in mature lowland pinewoods provided with a diverse understory. Variation in bird density ($F_{2,259} = 172.39$; $R^2 = 0.571$; $p < 0.0001$) was mainly correlated with bird species richness, although it also was subtly associated with the second position component (PS2); bird abundance significantly increased from northwestern to southeastern facing areas.

Fig. 1 shows the results of regression trees identifying the habitat attributes that better explain the variations in bird abundance and species richness. Variables most influencing bird species richness were: positively, the floristic diversity of the understory layer; mainly negative, the average diameter of the five thickest trunks and, negatively, the amount of oaks. The highest bird species richness was recorded at forests with a shrub layer more diverse than 0.17, and a semimature canopy layer with at least 33 trees with DBH between 30 and 60 cm and lacking large trees (with more than 34 cm DBH). Bird abundance was mainly determined by the increase in shrub height, and was inversely associated with the density of thin trees (5–10 cm DBH) and steepness of the terrain. In fact, the largest bird abundance was recorded in forest patches with less than 27.5% grade, a shrub layer at least 0.55 m tall, and fewer than 313 thin trees/ha.

3.2. Forest characteristics determining individual bird species distribution

From the 42 bird species recorded during the survey, only 20 had adequate sample size for analyzing at habitat scale. Frequencies of occurrence of 13 species did not differ among forest types, showing the lack of discrimination by these species (Table 3). However, Coal Tits, Crested Tits and

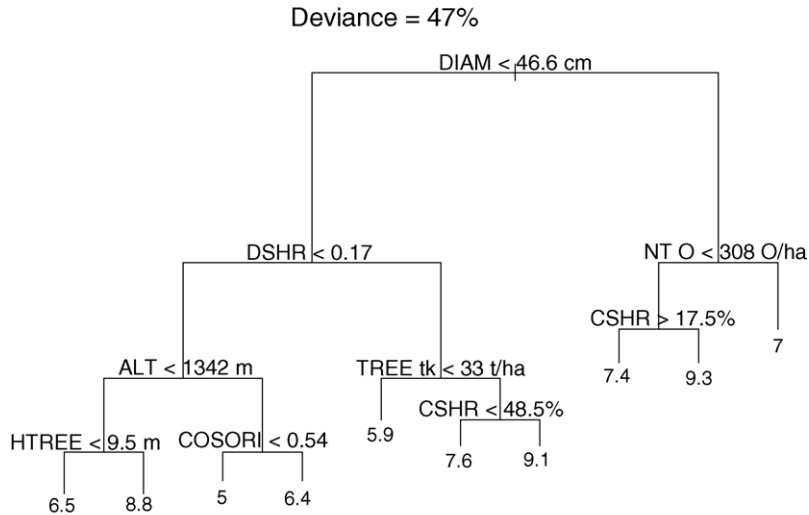
Firecrests were more frequent in pine woodlands and mixed forests than in oak woodlands. In contrast, Blue Tits, Great Tits and Bonelli's Warblers (*Phylloscopus bonelli*), were more frequent in oak woodlands and mixed forests than in pine

Table 3
Species distribution of frequency of occurrence across the three kinds of forests considered

Species	ACR	OC	Frequencies (%)		
			Oak	Mix	Pine
Non-selective species					
<i>Aegithalos caudatus</i>	AECA	26	7	15	6
<i>Dendrocopos major</i>	DEMA	35	9	18	12
<i>Emberiza hortulana</i>	EMHO	26	9	6	15
<i>Erithacus rubecula</i>	ERRU	177	66	76	59
<i>Ficedula hypoleuca</i>	FIHY	24	8	11	8
<i>Fringilla coelebs</i>	FRCO	247	95	97	91
<i>Garrulus glandarius</i>	GAGL	37	10	15	16
<i>Serinus serinus</i>	SESE	40	13	17	15
<i>Sitta europaea</i>	SIEU	43	15	14	20
<i>Sylvia atricapilla</i>	SYAT	33	19	11	8
<i>Troglodytes troglodytes</i>	TRTR	67	16	28	31
<i>Turdus merula</i>	TUME	184	84	66	63
<i>Turdus viscivorus</i>	TUVI	31	9	11	15
Species preferring oak woodlands and mixed forests					
<i>Parus caeruleus</i>	PACA	59	58*	13	1
<i>Parus major</i>	PAMA	102	74**	37*	9
<i>Phylloscopus bonelli</i>	PHBO	137	78*	57	24
Species preferring pine woodlands and mixed forests					
<i>Certhia brachydactyla</i>	CEBR	150	42	69*	57
<i>Parus ater</i>	PAAT	185	17	92*	94*
<i>Parus cristatus</i>	PACR	72	0	30*	49*
<i>Regulus ignicapillus</i>	REIG	88	9	49*	38*

Acronyms (ACR) and number of occurrences among the 262 census plots (OC) of each species are also provided. Species are grouped according to their maximum density in non-selective species, species preferring oak woodlands, and species preferring pinewoods and/or mixed forests. (*) Denotes forest with a frequency value only significantly higher than the forest with the lowest frequency. (**) Denotes forest with a frequency significantly higher than the two remaining forests (following the sequential Rice correction, a *p*-value of $p < 0.0006$ was considered critical for both * and **).

(b) REGRESSION TREE OF BIRD SPECIES RICHNESS (S / 0.8 ha)



(a) REGRESSION TREE OF BIRD ABUNDANCE (birds / 0.8 ha):

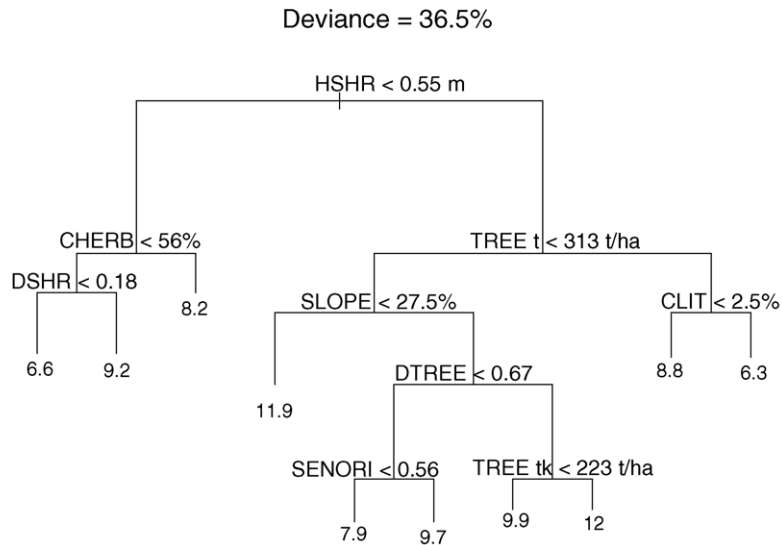


Fig. 1. Regression trees of bird abundance (birds/0.8 ha) and species richness (S/0.8 ha). The threshold defined by each variable corresponds to the left hand branch. The percentage of deviance retained by each model is also provided (see Section 2 for the meaning of variable’s acronyms).

woodlands, and Great Tits were present significantly more often in oak woodlands than in mixed forests. Finally, the Short-toed Treecreeper (*Certhia brachydactyla*), was the only species more frequent in mixed forests than in oak woodlands. Although, it also had large occurrences in both oak and pine woodlands.

Distances of each species to the centre of the space defined by the VG components were compared to species habitat selection intensity (Table 4). Five bird species (Ortolan Bunting, *Emberiza hortulana*; Robin, *Erithacus rubecula*; European Pied Flycatcher; Common Chaffinch, *Fringilla coelebs* and Common Blackbird) were considered ubiquitous, showing selection intensities that did not significantly differ from the null selection model. All other species had habitat preferences significantly different from what is available, on average, in their environment (Fig. 2). However, it did not mean that all the species but those five showed a significant selection

intensity for all the VG components. Accordingly, of those species preferring oak woodlands, only Blue Tits and Great Tits showed significant selection intensity for the negative extreme of VG1. Conversely, Crested Tits, Coal Tits, Northern Wrens, Short-toed Treecreepers, Firecrests and European Serins (*Serinus serinus*) had the highest selection intensities for pine woodlands. When pines are mature, Crested Tits showed the highest selection intensity for pine woodlands, since it significantly related to the positive extreme of VG2. No species was significantly associated with the space defined by a mixed oak-pine composition. Great Spotted Woodpecker (*Dendrocopos major*), and Bonelli’s Warbler showed significantly high selection intensity for forest patches with a well-developed shrub layer. Whereas no species had a significantly high intensity of selection for woodlands with large herbaceous cover. Finally, Northern Wren, Short-toed Treecreeper and

Table 4
Variables predicting each species preferred habitat

Species	%D	Species preferred habitat	N	P(1)%	ORTO	sd ORTO
AECA	45	TREE tk < 246 t/0.8 ha; DTREE > 0.51/0.2 ha; DIAM > 0.49 cm	88	0	0.33*	0.60
CEBR	47	DIAM > 46.3 cm; CHER > 47%	9	79	0.39*	1.01
DEMA	61	ALT < 1580 m; HTREE > 10.5 m; CSHR > 22.5%; SENORI > -0.87; TREE tk > 254 t/0.8 ha	5	1	1.00*	1.75
EMHO	53	HSR < 0.65 m; CSTO > 4%; CLIT > 8.5%; COSORI > -0.39; TREE tk < 250 t/0.8 ha; CHER > 41.5 %; SLOPE < 62.5%	6	0	0.27	1.25
ERRU	43	ALT < 1793 m; CSHR > 38.5%; HTREE > 11.5 m;	17	55	0.16	0.95
FIHY	48	ALT > 1397 m; SENORI > 0.93; COSORI < 0.07; NT P < 268 p/0.8 ha	5	3	0.29	0.65
FRCO	71	DISWAT > 44.3 m; ALT > 1296 m	150	98	0.04	0.96
GAGL	44	DIST > 1242 m	5	80	0.23*	0.66
PAAT	77	DIST > -195 m; ALT > 1313 m; NT P > 230 p/0.8 ha	100	90	0.37*	0.99
PACA	61	NT P < 38 p/0.8 ha; DIST < -963 m	13	57	0.79*	0.87
PACR	57	DIST > -92 m; DSHR > 0.12/0.2 ha; DSHR > 0.08/0.2 ha	21	17	0.73*	0.72
PAMA	45	DIST < 207 m; DIST < -210 m; TREE tk < 114 t/0.8 ha	62	34	0.56*	0.81
PHBO	47	NT P < 282 p/0.8 ha; CSTO < 16%; ALT < 1397 m; ALT > 1239 m	47	45	0.48*	0.73
REIG	37	NT P > 62 p/0.8 ha; ALT < 1549 m; CHER > 76.5%	8	27	0.54*	1.01
SESE	49	ALT < 1295 m; NT O < 22 o/0.8 ha; CSTO < 12.5%	12	25	0.61*	0.72
SIEU	55	DIAM > 46 cm; NT O < 14 o/0.8 ha; COSRI > -0.75	27	10	0.48*	0.60
SYAT	50	ALT < 1299 m; CSHR > 22.5%; DISWAT > 556 m	9	7	0.76*	1.41
TRTR	34	DIAM > 42 cm; HSR > 0.65 m; SLOPE > 39%; DSHR > 0.17/0.2 ha; DIAM > 48 cm	19	7	0.44*	0.67
TUME	44	ALT < 1424 m; TREE t < 70 t/0.8 ha	49	89	0.15	0.91
TUVI	47	CHER > 60.5%; DIAM < 43 cm	8	21	0.74*	1.21

Classification trees provided deviance retained by the whole tree (%D), influence and boundaries of each variable, sample size at last split (N), and probability of contacting each species following the given clues (P(1)%). Results of analysis of distances indicating selection intensity of each species preferred habitat (ORTO) and accuracy of those estimates (sd ORTO) are also provided. Differences between species selection intensities and the null selection intensity are denoted by * if $p < 0.004$, according to sequential Rice corrections of multiple p -estimates. Note that DIST (distance to the nearest mixed parcel) may have positive or negative values, depending on whether oak woodlands or pinewoods are concerned, respectively. Meaning of each of the variables' acronyms are supplied in Section 2.

Eurasian Nuthatch were the only species having significant preferences for mature woodland patches. The most ubiquitous species (according to ORTO values), were located near the centre of the planes in both PCAs.

Table 4 shows variables describing the preferred habitat of each species based on their occurrences. All classification tree models accounted for high proportion of deviance (mean deviance of 51%; range: 34–77%), so species habitat distribution was highly explainable. Variables most implicated in bird habitat preferences were altitude (present in the classification tree models of 10 species) and average diameter of the largest trees (appearing in 6 classification tree models). Diversity of tree species in the canopy, which was associated with mixed transitions, only appeared once. However, distance to the nearest transition patch was present in five classification trees.

4. Discussion

4.1. Effects of oak-pine mixed woodlands on avian communities

Increases in vegetation structure complexity and floristic composition quite often are related to enrichment of associated

bird communities (see Wiens, 1989; Mönkkönen, 1994; Hobson and Bayne, 2000a,b; Shochat et al., 2001; Laiolo, 2002; Machtans and Latour, 2003). However, only a subtle increase in bird species richness in mixed oak-pine forests in comparison to pine woodlands were found in this study, while no differences in total avian abundance among the three forest types could be clearly asserted. In addition, none of the 20 species investigated was recorded exclusively using mixed transitions, and only one (Short-toed Treeceeper) showed a significantly higher frequency of occurrence in such environments than in either pine or oak woodlands. Consequently, the slight increase in bird species richness in mixed oak-pine transitions should be the result of the assemblage of bird species from pine and oak woodlands (see Donald et al., 1998; Hobson and Bayne, 2000a; Backer et al., 2002; Machtans and Latour, 2003; for similar results). This lack of a specialized bird fauna of mixed oak-pine forests may be due to: (1) the general impoverishment of avifauna towards the southwestern Palaearctic, which also implies the reduction of stenoic species; and (2), present and past distribution area of mixed oak-pine transitions.

Although only 5 out of 20 bird species were distinctly ubiquitous respect to habitat preferences defined by Euclidean

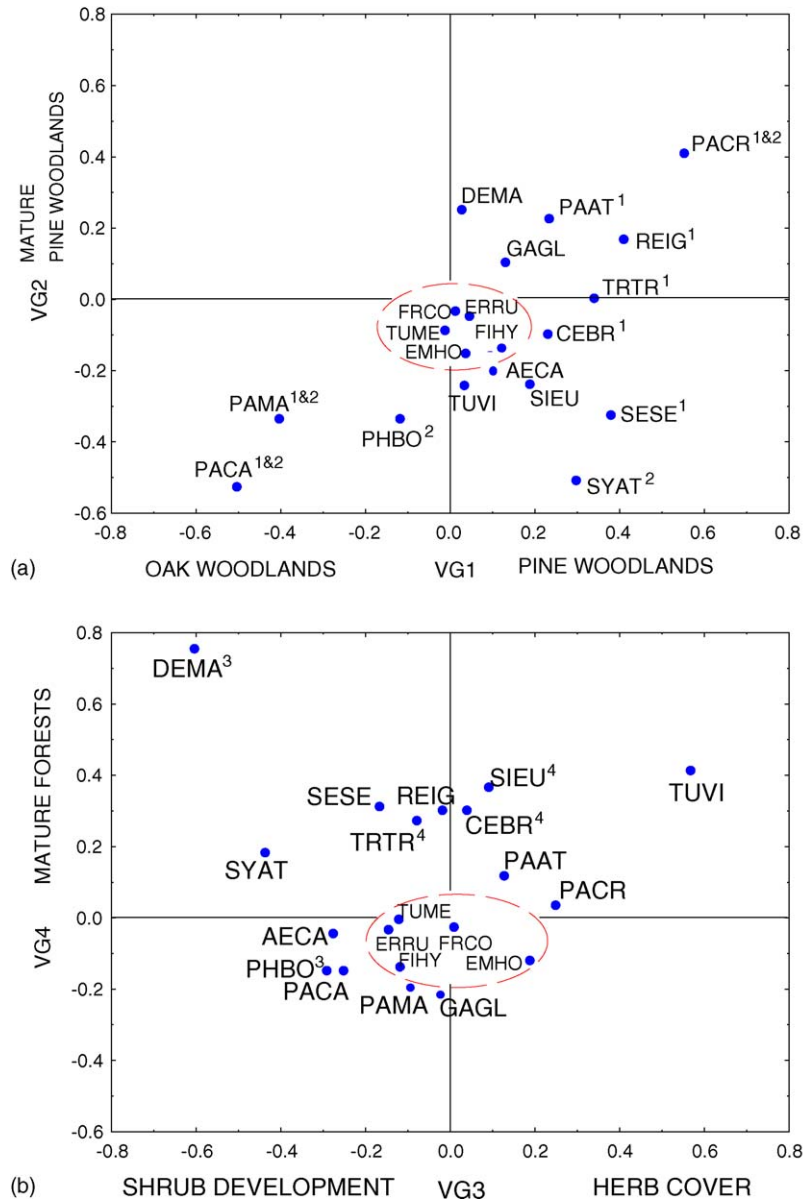


Fig. 2. Species distribution in the planes spanned by VG1 vs. VG2 (a); and VG3 vs. VG4 (b). Plane VG1-VG2 defines species habitat selection according to the floristic composition of the tree canopy layer. The space spanned by VG3-VG4 locates species within the structural gradients associated with shrub layer development and tree maturity. Species showing significant selection intensity for some vegetation components are marked with the number of those components. Species considered ubiquitous in the analysis of Euclidean distances to all of the vegetation components together are encircled in both graphs (see ORTO values in Table 4). Meaning of each species' acronym is provided in Table 3.

distances, all species but Crested Tit were detected at least once in each of the three forest types. Moreover, frequency of occurrence for most of the species analyzed were not significantly different across the three forest types (65% of species), meaning that habitat selection constraints were subtle or acted at site-scale for most species. Some studies have described decreases in bird species richness from eastern to western Palearctic forests, and towards both the north and south of the Eurasian continent (Mönkkönen, 1994; Mönkkönen and Viro, 1997; Covas and Blondel, 1997), suggesting that forest bird faunas of the Iberian Peninsula are somewhat impoverished with respect to other central and northern European latitudes (Blondel and Farré, 1988). Moreover,

Carrascal and Lobo (2003; see also Tellería and Santos, 1993, 1994; Carrascal and Díaz, 2003), recorded impoverishment of forest bird species richness from the Pyrenees to the southwestern region of the Iberian Peninsula, chiefly for species of European or Nearctic-Palaeartic distribution (see Voous, 1960; for faunal types). Consequently, fewer species of restricted requirements were expected in the Sistema Central, located in the middle of the Iberian Peninsula, at the southwestern limit of the Palaeartic region. Firstly, species with restricted requirements are the most vulnerable to the habitat variations that should impose distribution limits, and should thus be the first to disappear of such areas (see Brown and Lomolino, 1998; for such a general pattern). But, also,

some species considered specialist at middle latitudes may shift their habitat preferences at their southern limit of distribution, becoming more ubiquitous (see Fuller, 2002; for a general review).

Furthermore, the low extension that mixed oak-pine forests occupy, together with the high spatio-temporal fluctuations in ranges during the Quaternary (Izco, 1984; Costa et al., 1998), may have resulted in the absence of a specialized bird community from mixed oak-pine forests.

Mixed Scots Pine-Pyrenean Oak forests are very scarce, and are restricted to elevational belts where both tree species come into contact. In fact, mixed oak-pine forests are not analogous to the extensive European mixed forests, since transitions do not usually occupy large areas. If pine woodlands are managed, as in the study area, transitions may become even narrower, since habitat margins are more strictly established. Therefore, although mixed transitions provide more types of breeding sites than either pure oak woodlands or pure pine woodlands, their reduced extension have determined the low representation of each site type. Consequently, although more species may use mixedwoods compared to pure oak or pine forests, quite few individuals of each bird species may establish within them, so no bird speciation process is expected to have occurred.

As mentioned before, the distribution of Scots Pinewoods and Pyrenean Oakwoods follows the altitudinal gradient in a way that, each forest type occupies the elevation range which provides the precipitation and temperature regimes they require. Therefore, the long-lasting climatic variations (i.e. glaciations) have been changing their distribution ranges until now (see Izco, 1984; Costa et al., 1998). As a result, mixed transition areas between both forest types have been subjected to the same latitudinal and/or altitudinal range fluctuations. Such variability in distribution ranges, extension and, probably, degree of tree species mixture, should not have allowed the specialization of bird species comprising their avian communities.

4.2. Advice for the woodland management

The results highlight the importance of shrub layer development in explaining bird community parameters. Shrubs not only promote structural heterogeneity, increasing the diversity of different breeding sites and refuges, but also increase food diversity and availability during the breeding season through the associated arthropod fauna (Golet et al., 2001; Bonham et al., 2002; Johnson and Freedman, 2002; Sánchez and Parmenter, 2002). Positive influence of understory over forest avifauna has been determined in other studies. Often those studies involve places where natural refuges are scarce, such as pastures or croplands (Bradbury et al., 2000; Illera, 2001; Jansen and Robertson, 2001; Ribic and Sample, 2001; Södesrtröm et al., 2001 and Pere et al., 2003), but others have also emphasized the positive effects of developed shrub layering in wooded areas (Alvarez and Santos, 1992; Turchi et al., 1995; López and Moro, 1997; Diaz et al., 1998; Marsden et al., 2001; Johnson and Freedman, 2002; Arnold, 2003). All of these studies have highlighted the importance of shrub layer

where impoverished environments are concerned. The present study also supports this premise, since a complex understory benefited bird species richness when the canopy layer was not mature.

Most of the studies that have focused on the effect of shrub layer on birds focussed on structural characteristics such as cover (Golet et al., 2001; Kirk and Hobson, 2001; Ross et al., 2001; Herrando and Brotons, 2002; Liebezeit and George, 2002; Bombay et al., 2003) or height (Kirk and Hobson, 2001; Fernández-Juricic et al., 2002), frequently disregarding floristic composition (however see, Holmes and Robinson, 1981; Robinson and Holmes, 1984; Gillespie and Walter, 2001). In this study, diversity of understory markedly affected bird species richness and bird abundance. However, this study also demonstrates that structural characteristics of shrub layer, such as cover or height, were also important determinants of abundance and richness. Therefore, understory diversity, covers and height should be considered jointly when managing Mediterranean forests.

Geographical location of forest patches should also be considered. In this survey, the highest areas, over 1740 m, have only pine woodlands of more open structure that shelter particular species such as European Serin, Goldcrest (*Regulus regulus*), and Common Crossbill (*Loxia curvirostra*). However, a global pattern of decreasing bird abundance and species richness is frequently established in forests of mountainous environments, since upper elevations often behave as ecological islands (Rahbek, 1995, 1997; Hawkins, 1999; Blake and Loiselle, 2000; Lomolino, 2001; Grytnes and Vetaas, 2002; Prodon et al., 2002; Kattan and Franco, 2004). This pattern is also recorded in this study, since altitude was positively associated with slope, and both negatively affected bird species richness and abundance.

Forest maturity enhances bird communities in many forest types, since mature forests have a more diverse strata composition than younger ones (Shochat et al., 2001; Laiolo, 2002). Besides, older trees provide more food availability for foliage- and trunk-gleaners than younger trees, as well as more breeding sites for birds nesting in tree holes (Hobson and Bayne, 2000b; Laiolo, 2002; Machtans and Latour, 2003; but see Thompson et al., 1999; Keller et al., 2003). The present study supports this view, as characteristics typical of mature forests, including height of trees, average diameter of the thickest trunks and number of trees of thick or medium trunks, favoured bird species richness and abundance.

Avian abundance was lower in stands with densities greater than 308 oaks/ha. In the study area, oak woodlands have been subjected to management for centuries (timber extraction, pastures for cattle grazing, etc.), although they are now recovering (Izco, 1984). Regrowth of such forests usually results in development of a thick undergrowth layer of oaks sprouting from the root system of existing oaks (see Costa et al., 1998). Therefore, there are oak woodlands with high densities of predominantly young trees. Such areas generally have fewer birds because of the youth of the trees, as high density of thin trunks negatively influenced bird species richness when it is greater than 313 trees/ha.

Thinning may negatively affect foliage gleaners and troglodyte birds, since they reduce nesting sites and food supplies, also increasing bird conspicuousness (Hake, 1991; Christian et al., 1996; Tubelis and Cavalcanti, 2000; Hayes et al., 2003). However, most of the studies examining such topics emphasized the benefit that thinned patches usually involve for bird communities (DeGraaf et al., 1991; Dellasala et al., 1996; Easton and Martin, 2002; Haveri and Carey, 2000; Hayes et al., 2003; Hagar et al., 2004). When monotonous forests are considered, thinning provides for a more heterogeneous vegetation structure, allowing the entrance of bird species of more open wooded areas, and ground gleaners. In this study, undergrowth specialists were not recorded. Consequently, management of highly dense immature oak woodlands can involve the removal of trees, maintaining densities under 308 oaks/ha to enhance maturation of the remaining trees, and the establishment of a diverse and well-developed shrub layer.

5. Conclusion

This work concludes that, mixed oak-pine transitions increase bird species richness, but do not contribute to significantly increase bird abundance, respect to either pure oak woodlands or pure pine woodlands. Mixed oak-pine transitions neither favour the establishment of a distinctive avian community, since they are composed of birds of pine and oak woodlands that are also able to exploit the surrounding mixed environments. The strong influence of understory features (species diversity, cover and height), increasing not only bird species richness, but also bird abundance, has to be considered when managing forests. Other vegetation characteristics, like maturity of trees or undergrowth density, may also play very important roles.

Acknowledgements

I am very grateful to Luis M. Carrascal for his constructive comments on the manuscript. Javier Seoane also provided valuable comments, and Kevin Pilz and Jorge Cassinello who read the final work and provided good advice for the English version. I was supported by a predoctoral grant (BOE: 05/06/02) from the Ministerio Español de Ciencia y Tecnología within the Comunidad de Madrid project: 07M/0137/2000.

References

Alvarez, G., Santos, T., 1992. Efectos de la gestión del monte sobre la avifauna de una localidad mediterránea (Quintos de Mora Montes de Toledo). *Ecología* 6, 187–198.

Arnold, G.W., 2003. Bird species richness and abundance in wandoo woodland and in tree plantations on farmland at Baker's Hill, Western Australia. *Emu* 103, 259–269.

Backer, J., French, K., Whelan, R., 2002. The edge effect and ecotonal species: bird communities across a natural edge in southeastern Australia. *Ecology* 83, 3048–3059.

Bailey, S.A., Haines-Young, R.H., Watkins, C., 2002. Species presence in fragmented landscapes: modelling of species requirements at the national level. *Biol. Conserv.* 108, 307–316.

Bayne, E., Hobson, K., 1997. Comparing the effects of landscape fragmentation by forestry and agriculture on predation of artificial nests. *Conserv. Biol.* 11, 1418–1429.

Berry, L., 2001. Edge effects on the distribution and abundance of birds in a southern Victorian forest. *Wildl. Res.* 28, 239–245.

Blake, J.G., Loiselle, B.A., 2000. Diversity of birds along an elevational gradient in the Cordillera Central Costa Rica. *Auk* 117, 663–686.

Blondel, J., Farré, H., 1988. The convergent trajectories of bird communities along ecological successions in European forests. *Oecologia (Berl.)* 75, 83–93.

Blouin-Demers, G., Weatherhead, P., 2001. Habitat use by black rat snakes (*Elaphe obsoleta obsoleta*) in fragmented forests. *Ecology* 82, 2882–2896.

Bombay, H., Morrison, M., Hall, L., 2003. Scale perspectives in habitat selection and animal performance for willow flycatchers (*Empidonax traillii*) in the central Sierra Nevada, California. *Studies Avian Biol.* 26, 60–72.

Bonham, K., Mesibov, R., Bashford, R., 2002. Diversity and abundance of some ground-dwelling invertebrates in plantation vs. native forests in Tasmania, Australia. *For. Ecol. Manag.* 158, 237–247.

Bradbury, R., Kyrkos, A., Morris, A., Clark, S., Perkins, A., Wilson, J., 2000. Habitat associations and breeding success of yellowhammers on lowland farmland. *J Appl. Ecol.* 37, 789–805.

Breiman, L., Friedman, J., Olshen, R., Stone, C., 1984. *Classification and Regression Trees*. Chapman & Hall/CRC, Boca Raton, London, New York, Washington, D.C., 358 pp.

Brown, J., Lomolino, M., 1998. *Biogeography*. Sinauer Associates, Sunderland, Massachusetts, 691 pp.

Carignan, V., Villard, M.-A., 2002. Effects of variations in micro-mammal abundance on artificial nest predation in conifer plantations and adjoining deciduous forests. *For. Ecol. Manag.* 157, 255–265.

Carlson, A., Hartman, G., 2001. Tropical forest fragmentation and nest predation—an experimental study in an Eastern Arc montane forest, Tanzania. *Biodivers. Conserv.* 10, 1077–1085.

Carrascal, L.M., Lobo, J., 2003. Respuestas a viejas preguntas con nuevos datos: estudio de los patrones de distribución de la avifauna española y su aplicación en conservación. In: Martí, R. y Del Moral, J.C., Atlas de las aves nificantes de España. Sociedad Española de Ornitología, Madrid, pp. 651–668.

Carrascal, L.M., Díaz, L., 2003. Asociación entre distribución continental y regional. análisis con la avifauna forestal y de medios arbolados de la península ibérica. *Graellsia* 59, 179–207.

Christian, D.P., Hanowski, J.M., ReuversHouse, M., Niemi, G.J., Blake, J.G., Berguson, W.E., 1996. Effects of mechanical strip thinning of aspen on small mammals and breeding birds in northern Minnesota, USA. *Can. J. For. Res.* 26, 1284–1294.

Clark, W., Schimtz, R., Rogenschutz, T., 1999. Site selection and nest success of Ring-necked Pheasant as a function of location in Iowa landscapes. *J Wildl. Manag.* 63, 976–989.

Costa, M., Morla, C., Sainz, H., 1998. Los bosques ibéricos. Una interpretación geobotánica. Ed Geoplaneta, Barcelona, 597 pp.

Coutin, R., 1997. Insectes et acarien du Lierre. *Insectes* 104, 15–18.

Covas, R., Blondel, J., 1997. Biogeography and history of the mediterranean bird fauna. *Ibis* 140, 395–407.

De'Ath, G., Fabricius, K., 2000. Classification and regression trees: a powerful yet simple technique for ecological data analysis. *Ecology* 81 pp. 3192–3198.

DeGraaf, R.M., Healy, W.M., Brooks, R.T., 1991. Effects of thinning and deer browsing on breeding birds in New-England oak woodlands. *For. Ecol. Manag.* 41, 179–191.

Dellasala, D.A., Hagar, J.C., Engel, K.A., McComb, W.C., Fairbanks, R.L., Campbell, E.G., 1996. Effects of silvicultural modifications of temperate rainforest on breeding and wintering bird communities, Prince of Wales Island, southeast Alaska. *Condor* 98, 706–721.

Diaz, M., Carbonell, R., Santos, T., Telleria, J.L., 1998. Breeding bird communities in pine plantations of the Spanish plateaux: biogeography, landscape and vegetation effects. *J. Appl. Ecol.* 35, 562–574.

Donald, P., Fuller, R., Evans, A., Gough, S., 1998. Effects of forest management and grazing on breeding bird communities in plantations of broadleaved and coniferous trees in western England. *Biol. Conserv.* 85, 183–197.

- Donovan, T., Lamberson, R.H., Kimber, A., Thompson, F.R., Faaborg, J.F., 1995. Modeling the effects of habitat fragmentation on source and sink demography of Neotropical migrant birds. *Conserv. Biol.* 9, 1396–1407.
- Dover, J., Sparks, T., 2000. A review of the ecology of butterflies in British hedgerows. *J. Environ. Manag.* 60, 51–63.
- Drapeau, P., Leduc, A., Giroux, J.-F., Savard, J.-P., Bergeron, Y., Vickery, W., 2000. Landscape-scale disturbances and changes in bird communities of boreal mixed-wood forests. *Ecol. Monogr.* 70, 423–444.
- Easton, W.E., Martin, K., 2002. Effects of thinning and herbicide treatments on nest-site selection by songbirds in young, managed forests. *Auk* 119, 685–694.
- Estrada, A., Coates-Estrada, R., 2002. Bats in continuous forest, forest fragments and in an agricultural mosaic habitat-island at Los Tuxtlas, México. *Biol. Conserv.* 103, 237–245.
- Fernández-Juricic, E., Jiménez, M.D., Lucas, E., 2002. Factors affecting intra- and inter-specific variations in the difference between alert distances and flight distances for birds in forested habitats. *Can. J. Zool.* 80, 1212–1220.
- Forsman, J., Mönkkönen, M., Hukkanen, M., 2001. Effects of predation on community assembly and spatial dispersion of breeding forest birds. *Ecology* 82, 232–244.
- Friessen, L., Cadman, M.D., MacKay, R.J., 1999. Nesting success of Neotropical migrant songbirds in a highly fragmented landscape. *Conserv. Biol.* 13, 338–346.
- Fuller, R.J., 2002. Spatial differences in habitat selection and occupancy by woodland bird species in Europe: a neglected aspect of bird-habitat relationships. *Avi. Landsc. Ecol. IALE (UK)*.
- Gillespie, T., Walter, H., 2001. Distribution of bird species richness at a regional scale in tropical dry forest of Central America. *J. Biogeogr.* 28, 651–662.
- Golet, F., Wang, Y., Mellow, J., DeRagon, W., 2001. Relationship between habitat and landscape features and the avian community of red maple swamps in southern Rhode Island. *Wilson Bull.* 113, 217–227.
- Grytnes, J.A., Vetaas, O.R., 2002. Species richness and altitude: A comparison between null models and interpolated plant species richness along the Himalayan altitudinal gradient, Nepal. *Am. Nat.* 159, 294–304.
- Hagar, J., Howlin, S., Ganio, L., 2004. Short-term response of songbirds to experimental thinning of young Douglas-fir forests in the Oregon Cascades. *For. Ecol. Manag.* 199, 333–347.
- Hake, M., 1991. The effects of needle loss in coniferous forests in south-west Sweden on the winter foraging behavior of Willow Tits *Parus montanus*. *Biol. Conserv.* 58, 357–366.
- Hastie, T.J., Tibshirani, R.J., 1990. Generalized additive models. *Monographs of statistics and applied probability*, 43. Chapman & Hall, 335 pp.
- Haveri, B.A., Carey, A.B., 2000. Forest management strategy, spatial heterogeneity, and winter birds in Washington. *Wildl. Soc. Bull.* 28, 643–652.
- Hawkins, A.F.A., 1999. Altitudinal and latitudinal distribution of east Malagasy forest bird communities. *J. Biogeogr.* 26, 447–458.
- Hayden, S., Hamilton, C., 1997. Predicting invasions of woody plants introduced into North America. *Conserv. Biol.* 1, 193–203.
- Hayes, J.P., Weikel, J.M., Huso, M.M.P., 2003. Response of birds to thinning young Douglas-fir forests. *Ecol. Appl.* 13, 1222–1232.
- Herrando, S., Brotons, L., 2002. Forest bird diversity in Mediterranean areas affected by wildfires: a multiscale approach. *Ecography* 25, 161–172.
- Hobson, K., Bayne, E., 2000a. Breeding bird communities in boreal forest or western Canada: consequences of unmixing the mixedwoods. *Condor* 102, 759–769.
- Hobson, K., Bayne, E., 2000b. The effects of stand age on avian communities in aspen dominated forests of central Saskatchewan, Canada. *For. Ecol. Manag.* 136, 121–134.
- Holmes, R.T., Robinson, S.K., 1981. Tree species preferences of foraging insectivorous birds in a northern hardwood forest. *Oecologia* 48, 31–35.
- Illera, J.C., 2001. Habitat selection by the Canary Islands stonechat (*Saxicola dacotiae*) (Meade-Waldo, 1889) in Fuerteventura Island: a two-tier habitat approach with implications for its conservation. *Biol. Conserv.* 97, 339–345.
- Izco, J., 1984. Madrid verde. Jesús Izco-Madrid: Instituto de Estudios Agrarios, Pesqueros y Alimentarios, D.L., 517 pp.
- Jansen, A., Robertson, A., 2001. Riparian bird communities in relation to land management practices in floodplain woodlands of south-eastern Australia. *Biol. Conserv.* 100, 173–185.
- Johnson, G., Freedman, B., 2002. Breeding birds in forestry plantations and natural forest in the vicinity of Fundy National Park, New Brunswick. *Can. Field Nat.* 116, 475–486.
- Kattan, G.H., Franco, P., 2004. Bird diversity along elevational gradients in the Andes of Colombia: area and mass effects. *Global Ecol. Biogeogr.* 13, 451–458.
- Keller, J.K., Ritchmond, M.E., Smith, C.R., 2003. An explanation of patterns of breeding bird species richness and density following clearcutting in north-eastern USA forests. *For. Ecol. Manag.* 174, 541–564.
- Kirk, D., Hobson, K., 2001. Bird-habitat relationships in jack pine boreal forests. *For. Ecol. Manag.* 147, 217–243.
- Laiolo, P., 2002. Effects of habitat structure, floral composition and diversity on a forest bird community in north-western Italy. *Folia Zool.* 51, 121–128.
- Liebezeit, J., George, L., 2002. Nest predators, nest-site selection, and nesting success of the Dusky Flycatcher in a managed ponderosa pine forest. *Condor* 104, 507–517.
- Lindenmayer, B.D., Lacy, R.C., 2002. Small mammals, habitat patches and PVA models: a field test of model predictive ability. *Biol. Conserv.* 103, 247–265.
- Litt, R., 2000. Insectes observes sur le lierre (*Hedera helix*) a Saint Hippolyte du Fort dans le département du Gard (France). *Lambillionea* 100, 266–268.
- Lomolino, M.V., 2001. Elevation gradients of species-density: historical and prospective views. *Global Ecol. Biogeogr.* 10, 3–13.
- López, G., Moro, M.J., 1997. Birds of Aleppo pine plantations in south-east Spain in relation to vegetation composition and structure. *J. Appl. Ecol.* 34, 1257–1272.
- Machtans, C., Latour, P., 2003. Boreal forest songbird communities of the liard valley, northeast territories, Canada. *Condor* 105, 27–44.
- Marsden, S.J., Whiffin, M., Galetti, M., 2001. Bird diversity and abundance in forest fragments and Eucalyptus plantations around an Atlantic forest reserve, Brazil. *Biodivers. Conserv.* 10, 737–751.
- Mönkkönen, M., 1994. Diversity patterns in Palearctic and Nearctic forest bird assemblages. *J. Biogeogr.* 21, 183–195.
- Mönkkönen, M., Viro, P., 1997. Taxonomic diversity of the terrestrial bird and mammal fauna in temperate and boreal biomes of the northern hemisphere. *J. Biogeogr.* 24, 603–612.
- Murcia, C., 1995. Edge effects in fragmented forests: implications for conservation. *Trends Ecol. Evol.* 10, 58–62.
- Odum, E.P., 1958. *Fundamentals of Ecology*, second ed. Saunders, Philadelphia, Pennsylvania, USA, 546 pp.
- Pere, P., Lambert, B., Rigolot, E., Prodon, R., 2003. The effects of grassland management using fire on habitat occupancy and conservation of birds in a mosaic landscape. *Biodivers. Conserv.* 12, 1843–1860.
- Pérez de Ana, J.M., 1997. Nidificación de aves en diferentes tipos de cajas anidaderas en la vertiente cantábrica del País Vasco. *Estudios del Museo de Ciencias Naturales de Álava* 12, 227–232.
- Prodon, R., Thibault, J.C., Dejaife, P.A., 2002. Expansion vs. compression of bird altitudinal ranges on a Mediterranean island. *Ecology* 83, 1294–1306.
- Pryke, S., Samways, M., 2001. Width of grassland linkages for the conservation of butterflies in South African afforested areas. *Biol. Conserv.* 101, 85–96.
- Quinn, G., Keough, M., 2002. *Experimental Design and Data Analysis for Biologists*. Cambridge University Press, 537 pp.
- Rahbek, C., 1995. The elevational gradient of species richness: a uniform pattern? *Ecography* 18, 200–205.
- Rahbek, C., 1997. The relationship among area, elevation, and regional species richness in neotropical birds. *Am. Nat.* 149, 875–902.
- Ribic, C., Sample, D., 2001. Associations of grassland birds with landscape factors in southern Wisconsin. *Am. Midl. Nat.* 146, 105–121.
- Rice, W.R., 1989. Analyzing tables of statistical tests. *Evolution* 43, 223–225.
- Robinson, S., Holmes, R.T., 1984. Effects of plant and foliage structure on the foraging behaviour of forest birds. *Auk* 101, 672–684.
- Robinson, D., Robinson, S., 1999. Effects of selective logging on forest bird populations in a fragmented landscape. *Conserv. Biol.* 13, 58–66.
- Rodewald, P., Smith, K., 1998. Short-term effects of understory and overstory management on breeding birds in Arkansas oak-hickory forests. *J. Wildl. Manag.* 62, 1411–1417.
- Rodewald, A., Yahner, R., 2001. Influence of landscape composition on avian community structure and associated mechanisms. *Ecology* 82, 3493–3504.

- Ross, B., Morrison, M., Hoffman, W., Fredericksen, T., Sawicki, R., Ross, E., Lester, M., Beyea, J., Johnson, B., 2001. Bird relationships to habitat characteristics created by timber harvesting in Pennsylvania. *J. Pennsylv. Acad. Sci.* 74, 71–84.
- Sánchez, B., Parmenter, R., 2002. Patterns of shrub-dwelling arthropod diversity across a desert shrubland-grassland ecotone: a test of Island Biogeographic Theory. *J. Arid Environ.* 50, 247–265.
- Sawchik, J., Dufrêne, M., Lebrun, P., Schtickzelle, N., Baguette, M., 2002. Metapopulation dynamics of the bog fritillary butterfly: modelling the effect of habitat fragmentation. *Acta Oecol.* 23, 287–296.
- Shochat, E., Abramsky, Z., Pinshow, B., 2001. Breeding bird species diversity in the Negev: effects of scrub fragmentation by planted forests. *J. Appl. Ecol.* 38, 1135–1147.
- Sen, A., Srivastava, M., 1990. Regression analysis. In: *Theory, Methods and Applications*, Springer-Verlag, 347 pp.
- Södesröm, B., Svensson, B., Vessby, K., Glimskar, A., 2001. Plants, insects and birds in semi-natural pastures in relation to local habitat and landscape factors. *Biodivers. Conserv.* 10, 1839–1863.
- Summers, R.W., Taylor, W.G., 1996. Use by tits of nest boxes of different designs in pinewoods. *Bird Study* 43, 138–141.
- Tellería, J.L., 1986. Manual para el censo de los vertebrados terrestres. Raíces, 278 pp.
- Tellería, J.L., Santos, T., 1993. Distributional patterns of insectivorous passerines in the Iberian forests: does abundance decrease near the border? *J. Biogeogr.* 20, 235–240.
- Tellería, J.L., Santos, T., 1994. Factors involved in the distribution of forest birds in the Iberian Peninsula. *Bird Study* 41, 161–169.
- Thompson, I.D., Hogan, H.A., Montevecchi, W.A., 1999. Avian communities of mature balsam fir forests in Newfoundland: age-dependence and implications for timber harvesting. *Condor* 101, 311–323.
- Tubelis, D.P., Cavalcanti, R.B., 2000. A comparison of bird communities in natural and disturbed non-wetland open habitats in the Cerrado's central region, Brazil. *Bird Conserv. Int.* 10, 331–350.
- Turchi, G.M., Kennedy, P.L., Urban, D., Hein, D., 1995. Bird species richness in relation to isolation of Aspen habitats. *Wilson Bull.* 107, 463–474.
- Van Lien, V., Yuan, D., 2003. The differences of butterfly (*Lepidoptera Papilionoidea*) communities in habitats with various degrees of disturbance and altitudes in tropical forests of Vietnam. *Biodivers. Conserv.* 12, 1099–1111.
- Voous, K., 1960. *Atlas of European Birds*. Nelson, Amsterdam, 284 pp.
- Wardell-Johnson, G., Williams, M., 2000. Edges and gaps in mature karri forest, south-western Australia: logging effects on bird species abundance and diversity. *For. Ecol. Manag.* 131, 1–21.
- Wiens, J., 1989. *The ecology of bird community. Foundations and Patterns*, vol. 1. Cambridge University Press, 539 pp.