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Bird conservation in fragmented Mediterranean forests of Spain: effects of geographical location, habitat and landscape degradation

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Abstract

The effects of habitat fragmentation on forest bird assemblages were analysed in 214 holm oak (*Quercus ilex*) remnants spread across the northern and southern plateaux of central Spain. Bird richness was highly dependent on fragment area for all species regardless of isolation, and barely affected by habitat traits. Geographical location was associated with high differences in richness of bird assemblages, which included 17 species exclusive to northern remnants and one exclusive to southern remnants. This supports the hypothesis that habitat suitability deteriorates sharply from north to south for forest birds in Spain. The species-area relationships of bird assemblages sampled in fragmented forests along a broad continental gradient (from Norway to southern Spain) showed that true forest birds only nest in woodlands >100 ha in southern Spain, whereas the full complement of forest species occurs in much smaller fragments in central-western Europe. Loss of species that are particularly sensitive to habitat fragmentation accounts for these differences between dry Spanish and mesic European woodlands. These results are explained by the low habitat suitability of Spanish woodlands, associated with the restrictive conditions for plant regeneration in the Mediterranean climate and long-standing human usage. There is, therefore, a particular need to develop management strategies that conserve birds, and probably other forest organisms, in Mediterranean regions by preventing habitat deterioration and decreases in fragment size, and by conserving all woods >100 ha. © 2002 Elsevier Science Ltd. All rights reserved.

Keywords: Bird richness; Forest birds; Habitat fragmentation; Habitat suitability; Mediterranean Spain; Western–Central Europe; Landscape degradation

1. Introduction

The effects of habitat fragmentation on animal communities have been studied mostly in reference to avian species in temperate forests (Opdam, 1991; Bender et al., 1998; Hinsley et al., 1998). In Europe, most studies have focused on highlighting species loss in forest fragments and examining the effects of factors operating on local scales, such as connectivity, shape and habitat structure within fragments (Ciéslak, 1985; Ford, 1987; Opdam, 1991; Ciéslak and Dombrowski, 1993; McCollin, 1993; Bellamy et al., 1996). However, analyses on broader regional scales are rarer (Van Dorp and Opdam, 1987) despite their potential in determining local patterns of species richness (Caley and Schluter, 1997).

In a recent review of the effects of regional forest cover and geographical location on bird richness of fragment archipelagos across central and northern Europe (from 52° N to 60° N), Hinsley et al. (1998) found a sharp decrease northwards in the number of species retained by similar size forest fragments. Studies undertaken in Mediterranean European woodlands are scarcer (Baz and García-Boyero, 1995; Santos and Tellería, 1998; Díaz et al., 1998), and suggest that the negative effects of fragmentation on forest birds might be greater than in central European regions (Santos and Tellería, 1995, 1997). Mediterranean countries are arranged as peninsulas in the south-western Palearctic, isolated from the mesic conditions suitable for forest habitats that are widespread over most of Europe (Blondel and Aronson, 1999). Many forest species tend, in fact, to show restricted distributions in this area (Hagemeijer and Blair, 1997). On the Iberian Peninsula, for instance, such peninsular arrangement has been correlated with southern decreases in the species richness of butterflies (Martín and Gurrea, 1990) and forest birds (Tellería and Santos, 1993, 1999; Santos and Tellería, 1995).

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In this paper, we study the birds breeding in a broad sample of forest fragments distributed across the farming landscapes of the northern and southern plateaux of central Spain, two contrasting regions in which the conditions for forest growth deteriorate from north to south (Rivas-Martínez, 1981). Our main aim is to analyse factors affecting the distribution of bird fauna on several geographical scales and to compare our results with those obtained in other European studies. To do so, we first analyse the effects of patch size, habitat structure and isolation among patches on species richness in Spanish holm oak woodlands (*local scale*), searching for the effects of regional location of forests (northern vs. southern plateaux) on the ability of species to occupy fragments (*regional scale*). Secondly, we compare the differences in forest bird richness in similar size fragments between the bird communities of our study area and those inhabiting forest patches in central Europe (*continental scale*). Given the difficulty of devising local conservation strategies aimed at improving conditions resulting from large-scale temporal and spatial events (Landres, 1992), our approach seeks to obtain a multi-scale perspective on the current problems involved in conserving forest birds in Spanish agricultural landscapes.

2. Study area

The study was carried out on the agricultural plateaux of central Spain, a huge region in which intensive farming has reduced the original holm oak (*Quercus ilex*) woodlands (Blanco et al., 1998) to dispersed archipelagos with a predominance of small woodlots. The study forests are located north and south of the Sistema Central, a long east–west mountain range dividing the plateaux into two recognisable climatological regions within Spain's Mediterranean region (Table 1). The northern side is cooler and wetter, mainly during the hot season (Font, 1983; Table 1). These climatic differences are accompanied by a higher potential for forest growth and regeneration on the northern plateau (Rivas-Martínez, 1981). In fact, development of the tree and shrub layers and plant diversity are higher in the northern oak woodlands (Carbonell et al., 1998; Table 1). However, any evaluation of these differences must take into consideration that the forest vegetation in the study areas is quite degraded (mean tree height is 4.5–5 m) due to long-standing intensive use (grazing sheep and gathering firewood).

The study areas cover 190×35 km and 60×20 km on the northern and southern plateaux, respectively, and the distance between them ranges from 240 to 300 km. More than 90% of the land in the two study areas (Table 1) is given over to livestock farming (mainly sheep) and intensive agriculture (mainly cereals in the north, and cereals alternating with vineyards and olive groves in the south). Here, 65% of woodlands exists as patches <2 ha (Table 2), which are very isolated from large wooded patches (distance to nearest wood >100 ha ranges from 1 to 7 km; see Carbonell et al., 1998). Moreover, agricultural usage has intensified over the last 30 years, involving the removal of all corridors (hedges, tree lines) between forest patches. Most small forest fragments and medium-sized (up to 100 ha) patches have been isolated for at least 50–60 years.

We recorded bird species and habitat and landscape features in 214 holm oak fragments distributed across both study areas (Table 1). We selected the fragments to be representative of a wide size range, so larger sizes (>2 ha) were sampled more frequently than their relative availability (see Table 2 for the distribution of available and study forests among size classes). We considered forests >100 ha as control forests representative of the bird fauna potentially breeding in the adjacent region; most range from 100 to 300 ha (8 out of 12), and the remaining four cover over 350, 605, 1768 and 2450 ha. We selected these forests so that they were roughly interspersed among the rest of the study fragments.

3. Methods

3.1. Bird censuses

We censused birds during the 1994 breeding season from mid-April to mid-June. Given the problems associated with density estimates in very small areas (Haila,

Table 1
Climatic traits, and average degree of forest development (tree cover) of the holm oak fragments studied in central Spain[a]

Plateau	N	T	Ts	P	Ps	IHs	Tree cover (%)	Forest cover (%)
Northern	133 (9)	11.0–12.8	15.5–16.8	410–498	72–83	0.91–0.95	47.9	7.6
Southern	81 (3)	13.5–14.0	18.5–19.0	393–459	50–64	0.71–0.84	37.4	7.2

[a] N, number of forests (number of tracts >100 ha in brackets). Climatic variables give the range for 4 and 2 representative localities from the northern and southern plateaux, respectively (data taken from Elías and Ruiz, 1977). T, mean annual temperature; Ts, mean temperature in May–June; P, mean annual precipitation in mm; Ps, mean precipitation in May–June; IHs, mean moisture index in May–June. Tree cover within fragments and regional cover of forested habitat are mean values; see Section 3 for details of the calculation of average tree cover and Tellería and Santos (1999) for regional cover.

Table 2
Size-class distribution of forest oak fragments studied and % of forest bird species (F + FF) found occupying at least 20% of the fragments in each size class[a]

Fragment size (ha)	⩽2	>2–10	>10–100	>100
Northern plateau				
% of available fragments	65.8	15.9	13.0	5.3
% of fragments sampled	56.4	16.5	20.3	6.8
% of species present ⩾20%	11.1	33.3	55.5	85.2
Southern plateau				
% of available fragments	63.0	19.7	15.6	1.7
% of fragments sampled	50.6	24.7	21.0	3.7
% of species present ⩾20%	12.5	50.0	55.6	81.3

[a] Availability of fragment sizes was estimated from a random sample of 207 and 173 fragments on the northern and southern plateaux, respectively.

1988; Opdam, 1991), we only recorded the presence/absence of breeding birds in each fragment. We sampled bird assemblages in fragments by means of routes divided into 3-min sampling units, in which we recorded all evidence of breeding for each bird species: territorial signs (persistent singing, defence) and nesting behaviour (nest building, nest, food carrying, feeding young, etc.), or merely continuous presence in the fragment during successive visits. We applied a sampling effort that was proportional to fragment size following a roughly logarithmic scale and monitored the effort by constructing a species accumulation curve for each fragment. We therefore made several visits (2–7) to each fragment to achieve the planned sampling effort and/or stabilisation of the accumulation curve. The control forests were censused by means of 50 m-wide line transects (Järvinen and Väisänen, 1975), obtaining both presence/absence data and reference densities for unfragmented holm oak habitat.

Our search centred on forest species (in a broad sense), excluding birds with large territories and game species. Thus, eight out of 67 recorded species were excluded from the analyses [four raptors, three owls and the red-legged partridge (*Alectoris rufa*)]. The 59 remaining species were classified into three groups according to their nesting and feeding dependence on forest habitats (Appendix A; see Díaz et al., 1998 for more details): (1) Ubiquitous (U), a diverse group of 31 species with the ability to feed and nest in habitat patches other than forest fragments (isolated trees, shrubs in set-aside); some of these, such as wheatears, crested larks and Thekla larks, were only recorded at the edges of very degraded patches. (2) Forest generalists (F), a group of 14 forest breeders, most of which are tree- or shrub-nesters and ground feeders, although they may also feed in set-asides and grassland patches. (3) Forest specialists (FF) comprised 14 species, such as tits and warblers, restricted to wooded patches for feeding and nesting.

3.2. Habitat structure

Vegetation structure was assessed in each fragment by means of 12 variables that measured plant development and diversity (Table 3). All variables were recorded on circular sampling units with a 25-m radius, or over the entire patch area in the case of the smallest fragments (<0.2 ha). We applied a decreasing sampling effort in relation to increasing fragment size; thus, sampling included 40% of the area in 1 ha fragments (two samples), 22% (11 samples) in 10-ha fragments, and 5.6% (28 samples) in 100-ha forests (see Carbonell et al., 1998 for more details). Cover variables (Table 3) were estimated following Prodon and Lebreton (1981); cover and height estimates were recorded by a single observer to control for inter-observer variability (Morrison et al., 1992).

3.3. Landscape structure

We recorded four measures of landscape structure: fragment size (SIZE), two variables of habitat isolation (inter-patch distances), and a measure of fragment shape. Connectivity measures were not used since structures interconnecting forest patches are absent from the study landscapes. We used aerial photographs (1983–1986, 1:18.000) and satellite images (Landsat 1987, 1:100.000) to estimate landscape structure. Isolation variables were estimated for each fragment as the minimum distance to the nearest wooded patch (DISTNEIGHB) and to the nearest forest >100 ha (DISTSOURCE); we consider these extensive wooded patches not only as controls but as source populations for the fragments isolated. Finally, we estimated a shape index (SHAPE) for each fragment as the perimeter measured on aerial photographs divided by the perimeter of a circular fragment of the same area (Hinsley et al., 1995a).

3.4. Analyses

Species–area relationships were analysed for each plateau by means of regression analysis. We conducted separate analyses for total species richness (STOT), ubiquitous (SU), forest generalists (SF), forest specialists (SFF) and the two groups of forest species (SFTOT). Fragment size (SIZE) was logarithmically transformed prior to analyses. Stepwise regression analysis was used to explore the relationships of species richness (dependent variable) with the 16 vegetation and landscape variables recorded for each fragment (independent variables) in order to build the best predictive model for each richness value. We excluded the 12 control forests (forests >100 ha) from these analyses since one of the landscape variables was distance to such forests (DISTSOURCE). Relationships among vegetation

Table 3
Variables measured to characterise vegetation structure and tree and shrub composition in the study forest fragments[a]

1. GRCOVER: cover of bare ground.
2. HERBCOVER: cover of herbaceous plants.
3. SSHCOVER: cover of small shrubs (<50 cm tall).
4. LSHCOVER: cover of large shrubs (>50 cm tall).
5. LSHHEIGHT: average height of large shrubs (cm).
6. TREECOVER: cover of trees (vegetation layer >2 m tall).
7. TREEHEIGHT: average height of tree layer (m).
8. SMALLTREE: mean number of small trunks ($\leqslant 10$ cm d.b.h.).
9. MEDIUMTREE: mean number of medium-sized trunks (>10 $\leqslant 30$ cm d.b.h.).
10. LARGETREE: mean number of large trunks (>30 cm d.b.h.).
11. TREESP: number of tree species.
12. SHRUBSP: number of shrub species.

[a] Cover variables were recorded as percentages of the fragment area.

traits were previously examined by means of principal component analysis to simplify the analyses and eliminate multicollinearity among independent variables. However, as the factors we obtained had little biological meaning, we used the original variables for the regression analyses (see Van Dorp and Opdam, 1987; Bellamy et al., 1996 for a similar approach).

The role of geographical location was explored in two ways: (1) Residuals of the step-wise regressions were regressed with a dummy variable indicating plateau location (1: northern, 0: southern); (2) Bird richness was compared between plateaux by conducting ANCOVAs in which the variables of the regression models explaining $>1\%$ of the variance were used as covariants.

Finally, we analysed the presence-absence of 37 bird species recorded in at least nine fragments according to the same landscape, geographical and habitat variables. The probability of fragment occupancy by these species was modelled using logistic regression analyses (Hosmer and Lemeshow, 1989) excluding extensive forest >100 ha ($n=202$). In these and previous analyses (step-wise regressions for species richness), non-normal variables were angular (cover variables; see Table 3) or logarithmically transformed (Sokal and Rohlf, 1981).

3.5. Continental comparisons

We evaluated the richness of woodland birds breeding in Spanish oak fragments relative to other fragmented woodlands studied in more northerly countries (from the Netherlands to Norway). We used the studies reviewed by Hinsley et al. (1998) and the data of Ciéslak and Dombrowski (1993) for two eastern Polish archipelagos of mixed forests; the Polish fragments ranged from 0.04 to 15.44 ha, being quite similar to those in the localities studied by Hinsley et al. (1998). Species lists were restricted to true forest birds, i.e. those nesting and feeding within woodland, in accordance with Hinsley et al. (1998). Thus, we excluded from Polish and Spanish data all bird species that Hinsley and co-workers had removed from their original lists, and other additional, exclusive species according to criteria given in McCollin's review (1998) or to the author's experience (Spanish data). This reduced the original Polish list from 50 to 27 woodland species, whereas in Spain the revised lists amounted to 14 and 13 woodland species (in forests up to 15 ha) in the northern and southern fragments, respectively.

4. Results

4.1. Species pools

Fifty-six out of 59 species were recorded in the oak woodlands of the northern plateau, but only 39 (66%) on the southern plateau. Forest species (F and FF) were the most affected; thus, 12 out of the 28 forest birds nested exclusively in the north (six forest generalists and six forest specialists; Appendix A), whereas the Sardinian warbler (*Sylvia melanocephala*) was the only bird recorded exclusively from southern woodlands. Three additional forest species widespread in the north (nightingale *Luscinia megarhynchos*, Bonelli's warbler *Phylloscopus bonelli* and greenfinch *Carduelis chloris*) appeared to be uncommon breeders in the south.

4.2. Local and regional effects on bird richness

Bird richness correlated significantly with fragment size ($n=214$, $P<0.001$ in the five analyses), ranging from $r=0.80$ (SF) to $r=0.90$ (STOT). Species–area relationships were also significant in all analyses on each plateau ($P<0.001$), but both slopes and intercepts were always higher on the northern plateau (Fig. 1; $\mathrm{SFTOT}=2.35+4.30\mathrm{LGSIZE}$, $r=0.90$ for the northern plateau, and $\mathrm{SFTOT}=2.00+2.84\mathrm{LGSIZE}$, $r=0.82$ for the southern). Therefore, bird richness was commonly higher in the northern fragments.

Fragment size was the variable with the greatest effects on bird richness, accounting for between 75.3% (STOT) and 57.3% (SF) of the variance explained by regression models (Table 4). Variance in species richness accounted for by isolation and vegetation variables ranged from 0.9% (SU) to 9.5% (SF), the vegetation explaining most of this additional variation (see Section 4.3 for details on habitat variables). The regressions conducted between the residuals of previous models and a dummy variable indicating geographical location (1: northern, 0: southern) barely accounted for additional variance, except for SF ($F_{1,200}=5.39$, $P=0.021$, $r^2=2.62$) and SFTOT ($F_{1,200}=5.59$, $P=0.019$, $r^2=2.23$). However, geographical location had a significant effect on all the ANCOVAs conducted to compare bird richness between plateaux using as covariates the variables

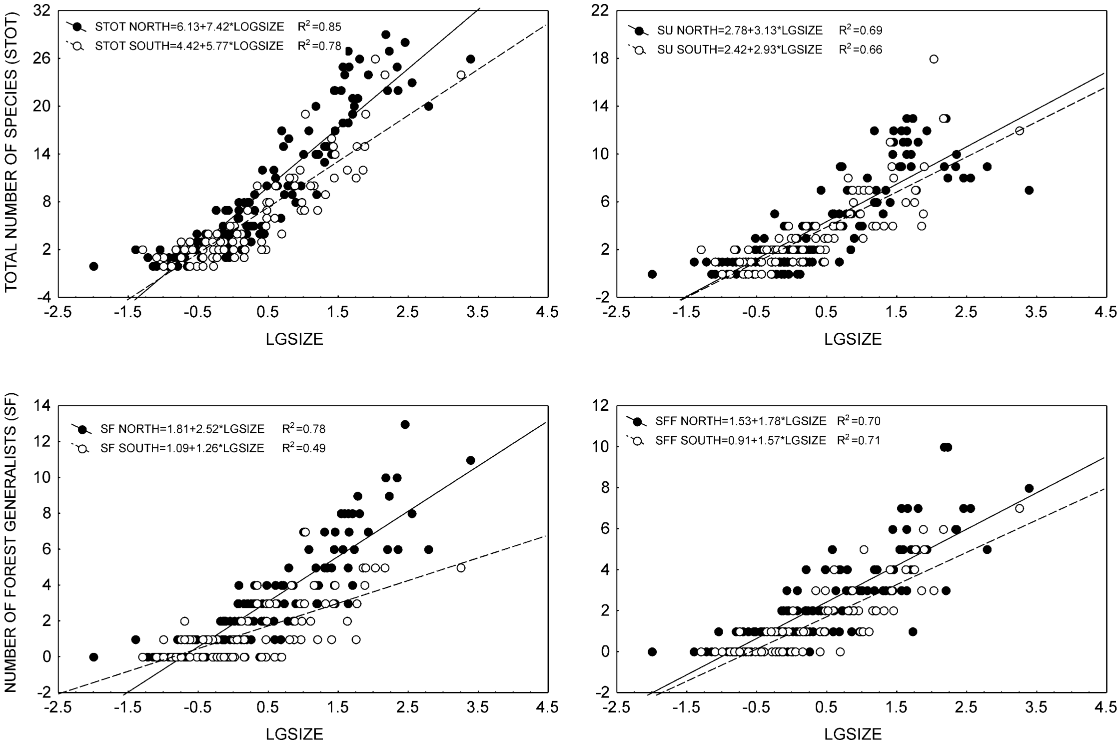

Fig. 1. Species–area relationships in holm oak (*Quercus ilex*) woodlands of Spanish plateaux (black dots: northern plateau; white dots: southern plateau) for total bird richness and for the three groups of bird species.

contributing to models >1% (STOT: $F_{1,197}=15.777$, $P=0.0001$; SU: $F_{1,199}=6.978$, $P=0.009$; SF: $F_{1,196}=22.757$, $P<0.0001$; SFF: $F_{1,196}=4.298$, $P=0.039$; see Table 4 for covariates).

4.3. Local and regional effects on individual species

The logistic analyses showed that, apart from fragment size (present in all the 37 logistic models; Appendix B), geographical location was the most frequent variable in models, indicating a general preference on the part of individual species for the northern plateau (11 out of 17 models). Isolation variables hardly appeared in the models, whereas the 12 habitat variables were significant in one to six models; the most outstanding pattern was the positive effect of variables indicating forest development (LSHCOVER, TREECOVER, TREEHEIGHT, MEDIUMTREE and TREESP; see Table 3).

4.4. Continental comparisons

The smallest pools of woodland species were those recorded in the fragments of both Spanish plateaux (Table 5); the rest ranged from very similar values (Sweden) to 2.5 times higher (the Netherlands). Pool size (number of breeding species in each group of fragments) was not related with the number of woods, which is an indirect measurement of the sampled area ($r=0.27$, $n=11$, $P=0.4$, and $r=0.38$, $n=9$, $P=0.3$ excluding the Spanish localities; the log of the number of woods yielded lower correlations), nor with the total area sampled in seven localities (Table 5; Fig. 2). Both the intercepts and slopes of Spanish localities were the lowest (Table 5) and their estimated richness was, consequently, the lowest for any fragment size (Fig. 3). These differences were greater than expected from species pools, so that the richness of non-Spanish localities was 1.7 to 6.5 times greater than in Spanish localities in 1 ha fragments and from 2.2 to 5.3 times greater in 15-ha fragments (Fig. 3; species pool was 1.7 to 1.8 times greater). Or, looked at another way, the Spanish 15-ha forests contained 31–43% of the total pool of forest species compared with 62–83% in the other countries (Fig. 3).

5. Discussion

The remarkable differences in richness of forest birds between the Spanish plateaux (regional scale), and the low influence of habitat suitability and isolation on richness and distribution of individual bird species in fragments (local scale) are two oustanding results of this study. The most conspicuous outcome related to bird conservation is, however, the distinctive lesser capability of small woodland patches to maintain forest birds in the Spanish Mediterranean compared with more mesic

Table 4
Coefficients of the step-wise multiple regression models (F to enter 4.0, F to remove 2.0) between species richness and 15 landscape and vegetation variables (see Table 3) estimated from 202 Oak forest fragments in central Spain[a]

	Species richness				
	STOT (Total species) b	SU (Ubiquitous species) b (R^2)	SF (Forest Generalists) b (R^2)	SFF (Forest Specialists) b (R^2)	SFTOT (Total Forest Species) b (R^2)
Model	$F_{5,196}=158.7$***	$F_{2,199}=205.5$***	$F_{7,194}=55.6$***	$F_{4,197}=102.8$***	$F_{6,195}=98.35$***
Intercept	4.17***	1.73***	0.90n.s.	0.20n.s.	3.37***
SIZE	**6.93*****(75.3)	**3.24*****(66.5)	**2.16*****(57.3)	**1.57*****(62.4)	3.78***(67.6)
TREECOVER	**0.05****	0.02*	**0.02****		0.03***
LSHCOVER	**0.08*****		0.27**	**0.02****	0.05***
TREEHEIGHT	−1.16***		−0.45**		−0.82***
GRCOVER	−0.08**		−0.03**	**−0.03*****	−0.06***
DISTNEIGHB			**−0.67****		−0.63*
DISTSOURCE			**0.41***		
TREESP				**2.88****	
% variance	80.2	67.4	66.7	67.6	75.2

[a] The variables used as covariants in the ANCOVAs performed to compare bird richness between plateaux are in bold type. Variance explained by fragment area (SIZE) is shown in brackets. n.s., non significant.; * $P \leqslant 0.05$; ** $P \leqslant 0.01$; *** $P \leqslant 0.001$.

Table 5
Pools of woodland species, and intercepts and slopes for exponential species-area relationships in 11 European localities (notations for localities 1–7 as in Hinsley et al., 1998)[a]

Locality[b]	% cover of woodland	No. of woods	Study area (ha)	Species pool	Intercept	Slope	Ref.[c]
NL 1	10	211		34	12.50	7.55	(1)
UK 2	9	20	48.21	24	10.20	7.68	(1)
UK 3 1990–1992	1	149	221.58	23	7.95	6.52	(1)
UK 3 1993–1995	–	56		23	9.62	7.69	(1)
UK 4	4	16	76.83	24	9.72	6.67	(1)
SW 5[d]	32	–		15	–	–	(1)
DM 6	15	39		19	6.59	5.11	(1)
NW 7[e]	25	200		19	3.27	2.01	(1)
PO 1 (Sieldce)	20	22	70.24	24	7.15	7.40	(2)
PO 2 (Luków)	20	28	39.11	19	5.67	6.82	(2)
SpN (Northern)	7.4	103	254.77	14	2.76	2.88	(3)
SpS (Southern)	7.2	66	181.54	13	1.62	1.76	(3)

[a] Slopes and intercepts (and mean number of species breeding in fragments of different sizes, in Fig. 3) were directly obtained from Hinsley et al. (1998), and from the exponential species–area relationships derived from the data in Ciéslak and Dombrowski (1993) for Poland and from our data (Spanish plateaux). The study area (ha) is the sum of areas of all study woods.

[b] NL, Holland; UK, England; SW, Sweden; DM, Denmark; NW, Norway; PO, Poland; SpN, northern Spain; SpS, southern Spain.

[c] (1): Hinsley et al. (1998); (2): Ciéslak and Dombrowski (1993); (3): this study.

[d] Species–area log/log relationships (intercept and slope omitted).

[e] Only forests up to 1.5 ha.

European localities (continental scale). This implies that Spanish woodlands are much poorer bird habitats than those of equivalent size in central Europe.

5.1. Bird richness variation on a local scale

The marked relationships between species richness and woodland size is quite a common feature of studies carried out on forest bird assemblages in temperate regions (e.g. Blake and Karr, 1987; Opdam, 1991; Bellamy et al., 1996; Díaz et al., 1998). Nevertheless, some studies carried out in British woodlots (McCollin, 1993; Bellamy et al., 1996) have recorded that variation in the number of edge species (equivalent to our group of ubiquitous species-SU) is mainly related to isolation and perimeter-shape features. This contrasts with the results of our study, in which fragment size is the major factor determining bird richness for ubiquitous species (98.7% of the total variance explained by the regression model). Since regional woodland cover is similarly low in the

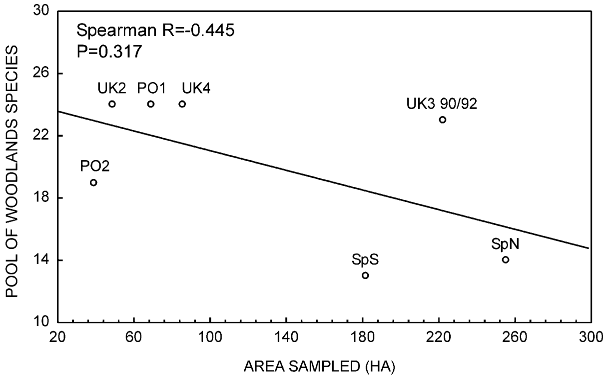

Fig. 2. Relationship between total area sampled and forest bird richness in 1–15 ha woodlands from seven localities included in three European countries (Fig. 3; Table 5).

British and Spanish localities (Table 5), the small influence of traits other than patch area in the latter (Table 4, Appendix B) might be related to the lack of radiating landscapes structures, such as shrubby hedges and tree lines, between woodland patches. However, these features, which are relatively numerous in British landscapes, would presumably provide border edge species with resources that complement those found in woodland patches.

Isolation had a negligible effect on richness in our study and was restricted to forest species groups (forest generalists and specialists-SF and SFF). In contrast, several British and Dutch studies (Van Dorp and Opdam, 1987; McCollin, 1993; Hinsley et al., 1995b) recorded a variable but important influence of isolation on both numbers and occurrence of forest species. Hence, the absence of effects recorded in our study might suggest that the species most sensitive to fragmentation have already been lost from Spanish woodlands (Soulé et al., 1988; Bellamy et al., 1996). In fact, many forest species absent (*Phoenicurus phoenicurus, Ficedula hypoleuca, Dendrocopos minor, Sitta europaea, Troglodytes troglodytes*) or extremely rare (*Muscicapa striata, Sylvia atricapilla, Phylloscopus collybita*; see Appendix A) in the study fragments are relatively frequent as breeders at a regional scale (Purroy, 1997). Moreover, these species are common in woodland patches from England and the Netherlands, where they are negatively affected by isolation (see above references and Verboom et al., 1991; Matthysen et al., 1995).

Vegetation structure had little effect on species richness (up to 7.1% of explained variance), coinciding, in this case, with results from northern European studies (Ford, 1987; Bellamy et al., 1996). Some authors (Van Dorp and Opdam, 1987; McCollin, 1993) have attributed this outcome to the low heterogeneity of the vegetation structure in the forests sampled. On the Spanish plateaux, this heterogeneity is also low due to the high level of degradation of the shrub and tree layers, which has given rise to poor development of oak woodlands (see Study Area and Table 1, and Carbonell et al., 1998).

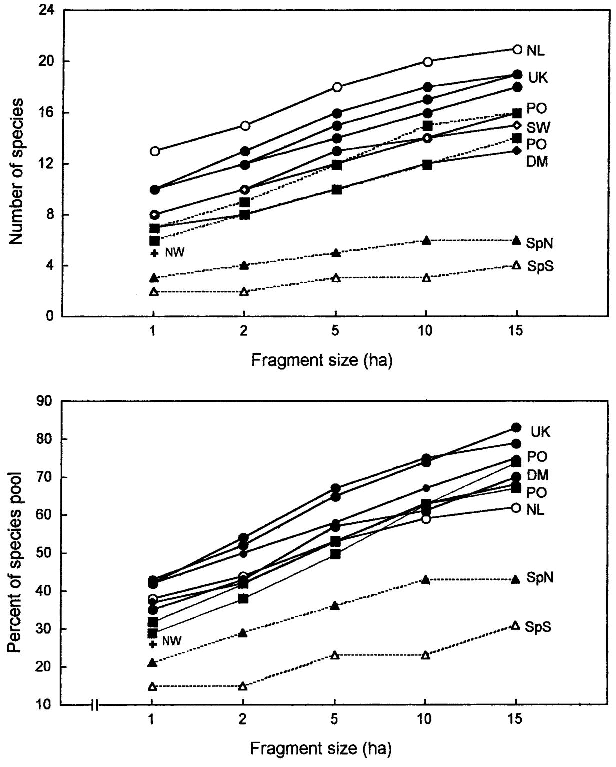

Fig. 3. Above: Species–area relationships for true forest species (according to Hinsley et al., 1998) in 1-15 ha woodlands sampled in 11 European farming localities (NL, Holland; UK, England; PO, Poland; SW, Sweden; DM, Denmark; NW, Norway; SpN, northern Spain; SpS, southern Spain). Given values are the mean number of species derived from regressions displayed in Table 5. Below: Species–area relationships expressed as percentage of the species pool recorded in all of the 1–15 ha woodlands sampled in each region (N.B. in no region do the largest forests hold 100% of the species pool).

5.2. Distribution of individual species

Logistic analyses corroborated the relative importance of different landscape and habitat variables on the distribution of individual species. Thus, the effects of area were seen in all 37 species considered, unlike the extensive studies carried out in northern Europe, in which the frequency of appearance of six out of 32 and 11 out of 31 forest species was independent of patch size (the Netherlands and eastern England, respectively; Van Dorp and Opdam, 1987; Hinsley et al., 1995b). Isolation variables, by contrast, influenced a lower percentage of species than in those countries, again suggesting the loss on the Spanish plateaux of many forest birds susceptible to isolation.

Habitat variables influenced the distribution of 27 species on the Spanish plateaux. There was a generally positive association between vegetation traits indicative of forest development and heterogeneity (tree cover and height, and number of tree species) and the frequency of appearance of forest species, as found in many similar studies (Howe, 1984; Lynch and Whigham, 1984; Opdam et al., 1985; Blake and Karr, 1987; Ford, 1987; Hinsley et al., 1995b). One striking outcome was the clear influence of bare ground, grass and small shrub cover, which negatively affected the distribution of some forest species (*Parus major* and *P. caeruleus*, *Sylvia undata*, and *Serinus serinus*). This result is probably related to the high degradation and the resulting low habitat suitability for forest birds of present oak woodlands (Santos and Tellería, 1995; Carbonell et al., 1998). It also explains the importance of patch size found in this study since the probability of tiny fragments remaining unoccupied will be greater in Spain than in other European countries where fragments have better habitat structure (e.g. Santos and Tellería, 1997; Tellería and Santos, 1999).

5.3. Variation in bird richness on a regional scale

In line with evidence obtained in fagaceous (Tellería and Santos, 1999) and pine woodlands (Díaz et al., 1998), forest species (F and FF) richness was much greater on the northern than on the southern plateau (27 vs. 16; Appendix A). Logistical analysis also showed the influence of geographical location on individual bird species, confirming that northern plateau woodlands are more likely to be occupied. However, the northern assemblage included nine species that are sparsely distributed over the northern forests (frequency of appearance up to 5%), of which five are restricted to intermediate-sized forests (>10 ha) and four to large forests (>100 ha); similar restricted forest species were uncommon on the southern plateau (two out of 16). Since such large forests are rare on the plateaux (Table 2) and the dynamics of fragmentation is toward increasing habitat loss and frequency of small fragments (sizes <10 ha and mainly 2 ha; see Santos and Tellería, 1998), oak woodlands of the northern plateau will inevitably undergo a dramatic impoverishment of these scarce forest species in the foreseeable future.

5.4. Bird richness variation on the continental scale

Our results corroborate previous although limited evidence of the lesser capacity of wooded patches immersed in farming habitat to maintain breeding birds in southern-Mediterranean localities compared with western and northern European localities (Santos and Tellería, 1997). The differences we recorded, which showed a dramatic impoverishment in forest species in the Spanish localities, are consistent with the north-south decrease in numbers in Spanish extensive woodlands (thousands of hectares) for many of these species (Tellería and Santos, 1993, 1994) and may be explained as the result of a concomitant loss of habitat suitability for species on the edges of their distribution ranges (Carbonell and Tellería, 1998; Pérez-Tris et al., 2000). From a biogeographical background, this loss may be attributed to the low climatic suitability for forest growth across the Spanish Mediterranean range (Rivas-Martínez, 1981; Santos and Tellería, 1995), an environmental trait that has probably been greatly accentuated by the dramatic impact of ancient and enduring human usage (Costa et al., 1990; Santos and Tellería, 1995). In fact, some variables indicative of marked habitat degradation negatively affected the distribution of individual forest species in this study. Furthermore, since forest regeneration is particularly slow in Mediterranean climates, the recovery of habitats impaired by human activity will be much slower than in mesic European localities, with climatic conditions that promote fast growth and regeneration responses in forest vegetation.

5.5. Implications for conservation

Our results suggest four conservation measures that could be undertaken to maintain and improve bird species in woodlands in central Spain:

1. Since only woodlands >100 ha retain percentages of $>80\%$ of the species pool in Spain, preserving the size and habitat suitability of large forests should be a priority. These woodlands are vital to maintain some species restricted to the northern plateau and representative of the European pool of forest birds (e.g. *Dendrocopos major, Prunella modularis*, *Muscicapa striata, Sylvia atricapilla, Phylloscopus collybita*, etc).
2. Even woods of 2–10 ha are worth trying to preserve since together they may contain between a third and a half of the full complement of woodland bird fauna.
3. Actions (1) and (2) should be strengthened in southern sectors, where climate and habitat suitability are less propitious for forest regeneration
4. Since habitat variables linked to forest development positively affect the presence in fragments of many common forest birds (*Oriolus oriolus*, *Phylloscopus bonelli*, *Aegithalos caudatus*, *Parus caeruleus*, *Parus major*), management of habitat suitability by preventing or reducing severe human impacts (grazing, firewood collection, etc.), should be regarded as a complementary measure with long-term effects on bird richness.

Finally, it is well worth noting that although the effects of forest fragmentation on birds in the Mediterranean basin have hardly been studied outside Spain, the conclusions and conservation implications obtained here are probably applicable to other areas and habitats (e.g. scrublands) of this region given the similar climatic stress and long-term human impacts found there.

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Appendix A. Breeding bird species recorded in the holm oak (*Quercus ilex*) forests of the Spanish plateaux classified according to their dependence on forest habitats as ubiquitous (U), forest generalists (F), and forest specialists (FF)[a]

	Northern plateau		Southern plateau	
	133 (%)	Sm. Fr.	81 (%)	Sm. Fr.
Stock dove *Columba oenas* (U)	5 (3.8)	6.16	0 (0.0)	–
Wood pigeon *C. palumbus* (U)	63 (47.4)	0.08	60 (74.1)	0.05
Turtle dove *Streptopelia turtur* (U)	18 (13.5)	0.7	16 (19.8)	0.08
Great spotted Cuckoo *Clamator glandarius* (U)	18 (13.5)	1.6	8 (9.9)	12.56
Cuckoo *Cuculus canorus* (U)	16 (12.0)	0.9	3 (3.7)	8.92
Nightjar *Caprimulgus europaeus* (U)	3 (2.3)	1.2	0 (0.0)	–
Red-necked nightjar *C. ruficollis* (U)	0 (0.0)	–	11 (13.6)	0.58
Hoopoe *Upupa epops* (U)	36 (27.1)	1.04	11 (13.6)	3
Green woodpecker *Picus viridis* (U)	36 (27.1)	0.78	18 (22.2)	6.28
Great Spotted woodpecker *Dendrocopos major* (FF)	6 (4.5)	36	0 (0.0)	–
Crested lark *Galerida cristata* (U)	2 (1.5)	15	8 (9.9)	7.2
Thekla lark *G. theklae* (U)	0 (0.0)	–	16 (19.8)	0.72
Wood lark *Lullula arborea* (F)	56 (42.1)	0.24	28 (34.6)	1.12
Dunnock *Prunella modularis* (F)	7 (5.3)	20	0 (0.0)	–
Robin *Erithacus rubecula* (F)	20 (15.0)	10	0 (0.0)	–
Nightingale *Luscinia megarhynchos* (F)	69 (51.9)	0.2	1 (1.2)	3.3
Black redstart *Phoenicurus ochruros* (U)	3 (2.3)	5.2	0 (0.0)	–
Stonechat *Saxicola torquata* (U)	3 (2.3)	1.4	0 (0.0)	–
Northern wheatear *Oenanthe oenanthe* (U)	1 (0.75)	1.56	0 (0.0)	–
Black-eared wheatear *O. hispanica* (U)	2 (1.5)	0.2	2 (2.5)	58
Blackbird *Turdus merula* (F)	44 (33.1)	1.4	6 (7.4)	3
Mistle thrush *T. viscivorus* (F)	2 (1.5)	63	6 (7.4)	2.2
Cetti's warbler *Cettia cetti* (U)	6 (4.5)	0.56	0 (0.0)	–
Melodious warbler *Hippolais polyglotta* (U)	20 (15.0)	0.7	0 (0.0)	–
Dartford warbler *Sylvia undata* (FF)	19 (14.3)	0.84	6 (7.4)	7.5
Subalpine warbler *S. cantillans* (FF)	104 (78.2)	0.09	25 (30.9)	0.5
Sardinian warbler *S. melanocephala* (FF)	0 (0.0)	–	16 (19.8)	3.3
Orphean warbler *S. hortensis* (FF)	18 (13.5)	3.74	7 (8.6)	2.2
Blackcap *S. atricapilla* (FF)	1 (0.75)	63	0 (0.0)	–
Bonelli's warbler *Phylloscopus bonelli* (FF)	38 (28.6)	0.7	3 (3.7)	10.64
Chiffchaff *P. collybita* (FF)	3 (2.3)	4	0 (0.0)	–
Firecrest *Regulus ignicapillus* (FF)	8 (6.0)	20	0 (0.0)	–
Spotted flycatcher *Muscicapa striata* (F)	1 (0.75)	280	0 (0.0)	–
Long-tailed tit *Aegithalos caudatus* (FF)	8 (6.0)	4.2	7 (8.6)	3
Crested tit *Parus cristatus* (FF)	2 (1.5)	150	0 (0.0)	–
Blue tit *P. caeruleus* (FF)	40 (30.1)	0.84	16 (19.8)	2.2
Great tit *P. major* (FF)	44 (33.1)	0.76	39 (48.1)	0.18
Short-toed treecreeper *Certhia brachydactyla* (FF)	3 (2.3)	150	0 (0.0)	–

(*Appendix A continued on next page*)

Appendix A (*continued*)

	Northern plateau		Southern plateau	
	133 (%)	Sm. Fr.	81 (%)	Sm. Fr.
Golden oriole *Oriolus oriolus* (F)	10 (7.5)	28	18 (22.2)	2.2
Great grey shrike *Lanius excubitor* (U)	7 (5.3)	0.36	4 (4.9)	6.28
Woodchat shrike *L. senator* (U)	8 (6.0)	2.95	7 (8.6)	1.44
Jay *Garrulus glandarius* (F)	15 (11.3)	4	0 (0.0)	–
Azure-winged magpie *Cyanopica cyana* (F)	3 (2.3)	150	0 (0.0)	–
Magpie *Pica pica* (U)	62 (46.6)	0.06	53 (65.4)	0.05
Jackdaw *Corvus monedula* (U)	2 (1.5)	4	2 (2.5)	0.9
Carrion crow *C. corone* (U)	36 (27.1)	0.3	2 (2.5)	41.8
Spotless starling *Sturnus unicolor* (U)	14 (10.5)	0.56	3 (3.7)	25.24
House sparrow *Passer domesticus* (U)	5 (3.8)	0.78	2 (2.5)	28.3
Tree sparrow *P. montanus* (U)	8 (6.0)	0.56	7 (8.6)	2.88
Rock sparrow *Petronia petronia* (U)	4 (3.0)	4.86	1 (1.2)	107
Chaffinch *Fringilla coelebs* (F)	55 (41.4)	0.04	45 (55.6)	0.1
Serin *Serinus serinus* (F)	65 (48.9)	0.56	21 (25.9)	0.2
Greenfinch *Carduelis chloris* (F)	13 (9.8)	2.6	1 (1.2)	10.64
Goldfinch *C. carduelis* (U)	25 (18.8)	0.12	22 (27.2)	0.18
Linnet *C. cannabina* (U)	43 (32.3)	0.1	24 (29.6)	0.72
Cirl bunting *Emberiza cirlus* (U)	56 (42.1)	0.04	0 (0.0)	–
Rock bunting *E. cia* (F)	5 (3.8)	150	0 (0.0)	–
Ortolan bunting *E. hortulana* (U)	20 (15.0)	1.2	0 (0.0)	–
Corn bunting *Miliaria calandra* (U)	11 (8.3)	0.09	2 (2.5)	25.24

[a] The number and % of occupied forests and the smallest occupied forest (Sm. Fr., in hectares) are given for each plateau (133 and 81 are the numbers of forests examined on the northern and southern plateaux, respectively). Names of forest species which were finally included in the European comparison (woodlands up to 15.44 ha; see Section 3) are given in bold type. Forest species found in Polish and/or western-northern European pools but not found in the Spanish plateaux (1–15 ha fragments): *Accipiter nisus*, *A. gentilis*, *Jynx torquilla*, *Dryocopus martius*, *Dendrocopus minor*, *Troglodytes troglodytes*, *Luscinia luscinia*, *Turdus philomelos*, *Sylvia borin*, *Phylloscopus trochilus*, *P. sibilatrix*, *Regulus regulus*, *Ficedula hypoleuca*, *Parus palustris*, *P. ater*, *P. montanus*, *Sitta europaea*, *Certhia familiaris*, *Fringilla montifringilla*, *Coccothraustes coccothraustes*, *Pyrrhula pyrrhula*.

Appendix B.

Step-wise logistic regression models for the occupancy probability by 37 individual bird species breeding in the oak fragments studied in central Spain ($n=202$)[a]

	Model	% classif.	χ^2	d.f.	*P*
Wood pigeon (U)	−2.56(0.73) + 0.04(0.01)TREECOVER + 2.10(0.44)PLATEAU + 2.31(0.34)SIZE	78.71	102.87	3	***
Turtle dove (U)	−2.27(0.66) + 1.03(0.52)PLATEAU + 1.95(0.38)SIZE−0.89(0.36)LSHHEIGHT	89.11	43.97	3	***
Great spotted cuckoo (U)	−15.35(6.02) + 2.63(0.53)SIZE + 4.06(2.63)LSHHEIGHT + 1.87(0.94)MEDIUMTREE	91.09	56.54	3	***
Cuckoo (U)	−28.76(7.35) + 0.14(0.04)LSHCOVER + 1.36(0.58)SIZE + 18.92(6.32)TREEHEIGHT + 2.71(1.03)DISTNEIGHB	96.04	44.98	4	***
Red-necked nightjar (U)	−3.35(0.45) + 0.92(0.40)SIZE	94.55	5.97	1	*
Hoopoe (U)	−2.53(0.41)−1.42 (0.53)PLATEAU + 2.22(0.36)SIZE	85.64	68.04	2	***
Green woodpecker (U)	−23.72(5.53) + 0.10(0.04)LSHCOVER + 4.72(0.86)SIZE + 21.53(5.73)TREEHEIGHT	91.58	138.95	3	***

Appendix B (*continued*)

	Model	% classif.	χ^2	d.f.	*P*
Thekla lark (U)	−3.47(0.49) + 1.27(0.40)SIZE	93.56	12.10	1	***
Melodious warbler (U)	−2.87(0.36) + 1.01(0.32)SIZE	91.09	11.02	1	***
Great grey shrike (U)	−3.88(1.29) + 0.06(0.03)SSHCOVER + 1.10(0.48)SIZE-3.61(1.86)SHRUBSP	95.54	12.60	3	**
Woodchat shrike (U)	−3.80(0.57) + 1.29(0.46)SIZE	95.05	9.82	1	**
Magpie (U)	−1.81(0.65) + 0.03(0.01)TREECOVER + 1.04(0.38)PLATEAU + 2.06(0.30)SIZE	78.22	84.25	3	***
Carrion crow (U)	−0.57(0.64)−3.87(1.10)PLATEAU + 2.56(0.47)SIZE-1.28(0.42)LSHHEIGHT	91.58	84.84	3	***
Spotless starling (U)	−1.02(2.02) + 0.05(0.02)HERBCOVER-2.18(0.92)PLATEAU-1.19(0.59)DISTSOURCE + 2.04(0.52)SIZE	93.07	33.33	4	***
Tree sparrow (U)	−7.06(1.38) + 0.09(0.02)HERBCOVER + 1.75(0.55)SIZE	94.06	23.12	2	***
Goldfinch (U)	−1.63(0.31)−0.12(0.03)GRCOVER + 1.45(0.47)PLATEAU + 1.26(0.27)SIZE	80.20	36.13	3	***
Linnet (U)	−1.16(0.60) + 0.06(0.02)GRCOVER + 1.81(0.29)SIZE-0.77(0.30)LSHHEIGHT	80.69	75.19	3	***
Cirl bunting (U)	−1.64(0.22) + 1.13(0.23)SIZE	79.70	29.37	1	***
Ortolan bunting (U)	−5.19(1.75)-0.10(0.04)HERBCOVER + 1.60(0.44)SIZE + 10.56(3.87)TREESP	91.58	33.71	3	***
Corn bunting (U)	−11.39(2.67) + 0.11(0.04)LSHCOVER + 0.12(0.03)HERBCOVER + 2.10(2.67)SIZE	95.05	26.72	3	***
Wood lark (F)	0.49(0.73)−0.06(0.18)TREECOVER−1.01(0.44)PLATEAU + 2.29(0.33)SIZE + 1.53(0.55)LARGETREE	82.67	103.18	4	***
Robin (F)	−13.51(5.34) + 7.78(3.06)SIZE−3.74(1.34)LSHHEIGHT + 3.91(1.89)SMALLTREE	98.02	74.42	3	***
Nightingale (F)	2.05(0.75)−0.08(0.03)LSHCOVER−0.03(0.01)HERBCOVER−6.11(1.22)PLATEAU + 2.74(0.49)SIZE	87.62	140.24	4	***
Blackbird (F)	−4.73(1.02) + 0.08(0.03)LSHCOVER−3.03(0.78) PLATEAU + 2.92(0.51)SIZE	90.59	106.80	3	***
Golden oriole (F)	−14.79(5.22) + 0.12(0.04)TREECOVER + 2.05(0.91)PLATEAU + 4.60(1.01)SIZE + 10.73(5.50)TREEHEIGHT−3.93(1.18)SMALLTREE	94.06	86.10	5	***
Jay (F)	−6.02(1.65)−9.81(41.45)PLATEAU + 3.42(1.11)SIZE	97.03	36.02	2	***
Chaffinch (F)	−5.39(1.56) + 1.36(0.23)SIZE + 7.61(1.90)TREEHEIGHT−2.23(0.89)SHRUBSP	76.24	63.00	3	***
Serin (F)	2.43(1.13)−0.05(0.02)LSHCOVER−1.68(0.48)PLATEAU + 2.85(0.40)SIZE−1.19(0.51)DISTNEIGHB	82.18	116.62	4	***
Greenfinch (F)	−4.13(0.82)−2.32(1.10)PLATEAU + 2.23(0.60)SIZE	93.56	30.37	2	***
Dartford warbler (FF)	1.42(2.10) + 0.07(0.03)LSHCOVER−0.15(0.06)GRCOVER−.00(0.60)DISTSOURCE + 2.47(0.61)SIZE	95.05	54.71	4	***

(*Appendix B continued on next page*)

Appendix B (*continued*)

	Model	% classif.	χ^2	d.f.	*P*
Subalpine warbler (FF)	−10.07(2.84) + 0.05(0.02)LSHCOVER− 3.04(0.65)PLATEAU + 1.34(0.49)DISTSOURCE + 2.97(0.48)SIZE + 7.75(3.80)TREESP + 1.82(0.59)SMALLTREE	87.13	155.98	6	***
Sardinian warbler (FF)	−3.92(0.61) + 1.77(0.46)SIZE	93.07	21.42	1	***
Orphean warbler (FF)	−4.17(0.67) + 2.26(0.50)SIZE	90.59	36.69	1	***
Bonelli's warbler (FF)	−8.56(1.88)−2.63(0.77)PLATEAU + 2.92(0.53)SIZE + 15.07(4.10)TREESP	92.08	88.72	3	***
Long-tailed tit (FF)	−6.79(2.42) + 2.41(0.68)SIZE− 4.86(2.48)SHRUBSP−1.75(0.90)SMALLTREE + 4.40(1.60)MEDIUMTREE	95.54	26.19	4	***
Blue tit (FF)	−3.99(1.14)−0.06(0.03)GRCOVER + 2.13(0.35)SIZE + 1.43(0.63)MEDIUMTREE	81.68	65.24	3	***
Great tit (FF)	−4.35(2.27)−0.08(0.03)GRCOVER + 2.00(0.55)PLATEAU−0.92(0.46)DISTSOURCE + 3.05(0.45)SIZE + 7.29(3.15)TREEHEIGHT	82.18	120.94	5	***

[a] Independent variables were the 12 features used to estimate vegetation structure and composition in the fragments (see Table 3), the four variables used to characterise the landscape of study area (isolation, area and shape variables; see Section 3), and one geographical variable (PLATEAU: 1, northern plateau; 0, southern plateau). The standard errors of the model‘s coefficients are given in parentheses. The percentage of fragments correctly classified as occupied or unoccupied is also shown, as well as the significance level for the whole model (**$P<0.05$*; ** *$P<0.01$*; ****$P<0.001$*).

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