RELATIONSHIPS BETWEEN FOREST LANDSCAPE STRUCTURE AND AVIAN SPECIES RICHNESS IN NE SPAIN

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SUMMARY.—*Relationships between forest landscape structure and avian species richness in NE Spain.*
Aims: To examine how forest landscape structure (including composition and configuration features) affects forest bird species richness at the scale of 10 x 10 km in Catalonia (NE Spain), considering different degrees of specialization of forest birds.

Location: NE Spain.

Methods: Bird presence data were obtained from the Atlas of Spanish Breeding Birds and forest landscape variables were extracted from the Spanish Forest Map developed within the Third Spanish National Forest Inventory. The analyses were carried out through multiple linear regressions and considering multicollinearity and spatial autocorrelation problems.

Results: Forest landscape characteristics influenced more on specialist than on generalist bird species richness, explaining 62 % and 52 % of total variation, respectively. Forest area was the most important landscape factor, although bird species richness was also considerably favoured by tree species diversity and by the abundance of coniferous forest. Forests with too closed canopy cover (equal or bigger than 80 %) supported less bird species. The effects of forest landscape configuration were weak compared to composition; the only significant configuration index was the mean circumscribing circle index, as a potential indicator of the naturalness of forest landscapes.

Conclusions: Forest landscape management should focus on forest habitat availability and forest structure features rather than on a particular forest landscape configuration, promoting an amalgam of forest tree species and avoiding an excessively closed canopy. However, and especially for generalists, it is necessary to consider the characteristics of other non-forest land cover types for an adequate management and conservation of forest bird communities.

Key words: forest birds, forest configuration and composition, forest landscape management, Mediterranean basin, shape irregularity.

RESUMEN.—*Relaciones entre la estructura del paisaje forestal y la riqueza de especies de aves en el NE de España.*
Objetivos: Estudiar cómo la estructura del paisaje forestal (incluyendo características de composición y configuración) afecta a la riqueza de especies de aves forestales a escala 10 x 10 km en Cataluña (NE de España), considerando diferentes grados de especialización de las aves forestales.

Localidad: NE de España.

Métodos: Los datos de presencia de aves se obtuvieron del Atlas de las Aves Reproductoras de España y las variables referentes al bosque se extrajeron del Mapa Forestal de España, realizado en el marco

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del Tercer Inventario Forestal Nacional. Se llevaron a cabo regresiones lineales múltiples, considerando los problemas de multicolinealidad y de autocorrelación espacial.

Resultados: Las características del bosque a escala de paisaje influyeron más en la riqueza de aves forestales especialistas que en la de generalistas, explicando el 62 % y el 52 % de la variación total, respectivamente. El área de bosque fue el factor más determinante, aunque también influyeron considerablemente en la riqueza de especies la diversidad de especies arbóreas y la abundancia de bosques de coníferas. Los bosques con una fracción de cabida cubierta demasiado elevada (igual o superior al 80 %) presentaron menos especies de aves. Los efectos de la configuración fueron débiles comparados con los de composición; el único índice de configuración significativo fue el índice del círculo circunscrito medio, como potencial indicador de la naturalidad de los paisajes forestales.

Conclusiones: La gestión del paisaje forestal debe centrarse en la disponibilidad de hábitat y en las características estructurales del bosque más que en una determinada configuración del paisaje, evitando una fracción de cabida excesiva y favoreciendo la mezcla de especies arbóreas. Sin embargo, y especialmente para las generalistas, es necesario considerar otras características de las cubiertas no boscosas para una adecuada gestión y conservación de las comunidades de aves forestales.

Palabras clave: aves forestales, configuración y composición del bosque, gestión forestal a escala de paisaje, irregularidad de formas, región mediterránea.

INTRODUCTION

Forest management and other natural and anthropogenic disturbances influence on forest ecosystems not only at the stand level but also at coarser landscape scales (Loehle *et al.*, 2005; Warren *et al.*, 2005) by affecting the availability of suitable habitat and their features (landscape composition) and the spatial arrangement of forest patches (landscape configuration). The relationship between landscape structure (landscape composition and configuration) and ecological processes is one of the main focuses of landscape ecology (Turner, 1989). When considering forest landscape structure effects on birds, several studies have shown the importance of landscape configuration and the need to consider it for forest management (Villard *et al.*, 1999; Westphal *et al.*, 2003; Brennan and Schnell, 2005; Betts *et al.*, 2006), while others have found a weak or secondary influence compared to forest landscape composition (McGarigal and McComb, 1995; Trzcinski *et al.*, 1999; Radford *et al.*, 2005). Thus, the elucidation of the relative importance of forest composition and configuration on forest biodiversity still requires further

research, particularly in Mediterranean forest ecosystems, which have been subjected to a long-lasting management and at the same time are within a biodiversity hotspot (Myers, 2000). Regarding forest Mediterranean ecosystems, a previous study by Gil-Tena *et al.* (2007) evaluated the effects of forest characteristics on bird species richness at the scale of 1 x 1 km in the Mediterranean but only considering composition features. Moreover, forest landscape influences forest bird species at different scales (Mitchell *et al.*, 2001; Loehle *et al.*, 2005; Warren *et al.*, 2005; Mitchell *et al.*, 2006). Thus, there is a need to study the relevance of forest composition and configuration for forest bird species richness at other landscape scales in a Mediterranean context.

On the other hand, in recent years valuable biodiversity databases have been created which can be of great interest for the assessment, management and conservation of forest ecosystems (Fearer *et al.*, 2007). There are numerous available atlases on bird distribution that can be related with forest maps and forest inventory data to extract the relationships between forest characteristics and biodiversity (Donald and Fuller, 1998).

In this context, this study aimed to study the relationships between forest landscape structure and bird species richness at the scale of 10 x 10 km in the Mediterranean region of Catalonia (NE Spain). Specific objectives were to explore how forest landscape characteristics explain forest bird species richness, to evaluate which forest landscape characteristics (either composition or configuration) are more relevant for forest bird species richness at 10 x 10 km, and to provide recommendations for forest landscape management focused on Mediterranean forest biodiversity conservation. Significant correlations between forest landscape features and forest bird species richness are expected, especially for specialists (Gil-Tena *et al.*, 2007), with stronger effects of composition compared to configuration (McGarigal and McComb, 1995; Trzcinski *et al.*, 1999; Radford *et al.*, 2005). Large extensions of forests, with advanced development stages but not an excessive forest canopy cover and a diversity of tree species would be main determinants for forest birds in Catalonia (see Gil-Tena *et al.*, 2007 and the literature therein cited). Regarding forest configuration, a greater association of forest shape to biodiversity is expected since forest fragmentation metrics may not necessarily provide additional information apart from that already conveyed by other composition features (Saura *et al.*, 2008).

MATERIAL AND METHODS

Study area

Catalonia (NE of Spain) comprises a total extension of 32,107 km^2 and is characterized by a heterogeneous geomorphology including mountainous areas like the Pyrenees (with an altitude up to 3,143 m) and a long coastline along the Mediterranean Sea. This region is dominated by the Mediterranean temperate climate, with presence also of maritime temperate climate in the coast and temperate cold climate in the Pyrenees. Forests represent about 38 % of the total area of Catalonia (Terradas *et al.*, 2004), and although about a hundred of different tree species have been recorded in recent forest inventories (Gracia *et al.*, 2004), 90 % of the total number of trees is from the 14 most common tree species, mainly *Pinus halepensis* (about 20 % of the total forest area), *Pinus sylvestris* (about 18 % of the total forest area), *Quercus ilex* (about 15 % of the total forest area), and *Pinus nigra* (about 11 % of the total forest area).

Forest bird data

Data were gathered from the Atlas of Spanish Breeding Birds, which includes information on the distribution of bird species during the period 1999-2002 in UTM 10 x 10 km cells (Martí and Moral, 2003), as derived for Catalonia from the Catalan Breeding Bird Atlas 1999 - 2002 (Estrada *et al.*, 2004). Bird species richness was here estimated from the atlas censuses conducted by volunteers (for a detailed description of the sampling methodology see Martí and Moral, 2003 and Estrada *et al.*, 2004) in a total of 283 UTM 10 x 10 km cells for which at least 90 % of its area was covered by the information from the Spanish Forest Map for Catalonia (discarding cells falling only partially within the territory of Catalonia).

The habitat selection matrix reported in the Catalan Breeding Bird Atlas (Estrada *et al.*, 2004) was used to determine the 53 diurnal breeding bird species that selected forests as their main habitat (see Appendix 1), classifying 31 as generalists and 22 as specialists like in Gil-Tena *et al.* (2007). Forest specialists were characterised by higher selectivity of forest landscapes and avoidance of agricultural dominated landscapes, whereas generalists, despite showing positive selection of forest landscapes, did not clearly avoid agricultural landscapes.

Forest landscape variables

Forest landscape characteristics for the 10 x 10 km cells were obtained from the Spanish Forest Map (scale 1:50,000), recently developed within the recent Third Spanish National Forest Inventory (Ministerio de Medio Ambiente, 2006). This map was obtained for Catalonia from the interpretation of aerial photographs, combined with pre-existing maps and field inventory data. The minimum mapping unit is in general 6.25 ha, decreasing to 2.2 ha in the case of forest patches embedded in a non-forest land use matrix. From the Spanish Forest Map the following forest composition variables were obtained:

- Area of land (ha) with a forest tree canopy cover (FCC) above a certain FCC threshold (AreaFCCX). Ten variables were derived from this definition for ten different FCC thresholds: AreaFCC5 (comprising land area with forest tree canopy cover ranging from 5 to 100, AreaFCC10 (land area with FCC from 10 to 100 %), and so on in intervals of 10% up to AreaFCC90 (land area with FCC between 90 and 100 %).
- FCC diversity (FCC div), obtained from the proportion of forest land area covered by five different FCC classes (5 - 20 %, 20 - 40 %, 40 - 60 %, 60 - 80 %, and 80 - 100 %).
- Mean forest development stage (Development), computed as the area-weighted average of the development stage for each forest patch, where a numerical value ranging from 1 up to 4 (increasing with the degree of forest development) was assigned to the four different development stages discriminated in the Spanish Forest Map: recently regenerated (up to canopy closure), thicket (up to natural pruning), trees with diameter at breast height (DBH) ≤ 20 cm, and trees with DBH > 20 cm.
- Forest development stage diversity (Development div), obtained from the proportion of forest land area corresponding to the four development stages described above.
- Coniferous species percentage (Coniferous), measured as the percentage of forest lands covered by coniferous species.
- Mono-specific forest percentage (Mono-specific), measured as the percentage of forest lands covered by stands in which at least 90 % of the trees correspond to the same (dominant) tree species, as defined for forest management plans in Spain (Madrigal, 1999).
- Forest tree species diversity (Tree div), obtained from the proportion of forest land area covered by each tree species.

All the forest diversity variables (FCC diversity, forest development stage diversity and forest tree species diversity) were quantified through the Shannon-Wiener index.

The following landscape configuration metrics (in the original vector format of the Spanish Forest Map) were calculated for all the forest patches within each UTM cell, the five first related to forest fragmentation and the rest quantifying the shape irregularity of the forest boundaries:

- Number of forest patches (NP).
- Mean forest patch size (ha).
- Largest forest patch (ha).
- Edge density (m/ha), defined as the length of edges between forest and non-forest patches divided by the total forest area within the cell.
- Total core area (ha) for distances of 100 and 300 m from the forest edge.
- Number of shape characteristic points (NSCP; Moser *et al.*, 2002), obtained as the minimum number of points necessary to describe a patch boundary. More complex shapes present a larger number of shape characteristic points.
- Density of shape characteristic points (DSCP), calculated by dividing the former variable by the total perimeter of forest patches (km).
- Mean perimeter-area ratio and area-weighted mean perimeter-area ratio.

- Mean shape index and area-weighted mean shape index (MSI and AWMSI, respectively), attaining their minimum value (1) for circles and increasing for more complex or elongated shapes.
- Mean largest axis index, where the largest axis is the straight line connecting the two furthest-apart points in a forest patch.
- Mean circumscribing circle index (MCIR), attaining its minimum value (0) for circular patches and increasing for more elongated or complex patches (up to a maximum value of 1).

See Saura and Carballal (2004) and Saura *et al.* (2008) for a detailed description of the four last shape indices. All the forest landscape variables were standardised to zero means and unit variances to eliminate the effects of differences in the measurement scale for the different independent variables.

Data analysis

Analyses were performed separately for specialist, generalist and total forest bird species richness. Two different statistical models were developed for explaining bird species richness: (1) a model including all the variables described in the previous section (both landscape composition and configuration), some of which are not usually available in continuous datasets on forest characteristics that cover large areas (*e.g.* forest canopy cover, development stage) and (2) a model only including those variables that are available in any forest or land cover map (provided that forests are discriminated as one of the land cover classes), which are forest area and the variables regarding forest landscape configuration that can be extracted from the spatial arrangement of forest patches as depicted in that map. These two models were considered separately in order to evaluate how much is gained (in terms of explaining bird species richness distribution at the landscape

scale) from using more detailed forest databases (including structural and compositional characteristics) compared to standard land cover maps that just convey information on the amount of forest area and its spatial configuration.

The influence of forest characteristics on forest bird species richness was analyzed through a forward-backward stepwise regression (*P*-to-enter = 0.05, *P*-to-remove = 0.10). R^2 values were used to determine the explanatory power of the regression model; the proportion of variance explained by each additional variable selected by the regression procedure was calculated as the difference between the R^2 value after and before that variable entered in the model.

Correlation analyses between all landscape variables were previously performed in order to avoid multicollinearity problems and select the final independent variables to be included in the regression procedure (see Table 1). Forest landscape characteristics were discarded when Pearson's correlation coefficients between pairs of variables were *r* > 0.6, removing the variable which was considered to be the least biologically meaningful to the bird community. Because nine of the ten variables regarding forest area (computed for different FCC thresholds) were highly correlated among them (*r* ranging from 0.583 to 0.998), for the regression analysis only the forest area variable for the FCC threshold that most correlated with the richness of each group of forest birds was selected, apart from the AreaFCC90, which was weakly correlated with all the other forest area variables. Most of the fragmentation indices were also highly correlated with forest area, and several of the configuration variables were correlated between them, resulting in that only one fragmentation index and five shape indices were finally selected for the analysis (Table 1). It is necessary to be aware of the problem of testing the independent effects of landscape configuration due to the confounding effects with

TABLE 1

Summary statistics of forest bird species richness and the forest landscape variables in the 283 UTM 10 x 10 km cells analysed in the region of Catalonia.
[Estadísticos descriptivos de la riqueza de especies de aves forestales y las variables de bosque a escala de paisaje en las 283 UTM 10 x 10 km celdas analizadas en la región de Cataluña.]

	Mean	SD	Minimum	Maximum
DEPENDENT VARIABLES				
Total bird species richness	30.90	8.55	5	47
Specialist bird species richness	12.02	4.59	0	20
Generalist bird species richness	18.87	4.30	4	28
INDEPENDENT VARIABLES*				
AreaFCC10 (ha)	5,120	2,747	0	9,610
AreaFCC40 (ha)	4,357	2,683	0	9,242
AreaFCC90 (ha)	73	210	0	2,062
FCC div	1.02	0.33	0	1.48
Development	3.22	0.56	0	3.95
Development div	0.84	0.24	0	1.35
Coniferous (%)	55.80	28.70	0	99.50
Mono-specific (%)	14.30	15.10	0	80.00
Tree div	1.37	0.46	0	2.50
NP	39.15	39.56	0	214.00
MSI	2.42	1.15	0	15.70
AWMSI	3.54	1.23	0	10.65
NSCP	10,325	6,231	0	35,839
DSCP	17.24	5.10	0	32.66
MCIR	0.71	0.10	0	0.94

* See material and methods section for a full description of the variables. *[* Véase la sección material y métodos para una descripción completa de las variables.]*

landscape composition, particularly with forest area as shown above. Instead of applying regression of residuals like in previous studies (McGarigal and McComb, 1995; Trzcinski *et al.*, 1999; Villard *et al.*, 1999; Westphal *et al.*, 2003), ordinary least square regression (OLSR) was used because OLSR estimates the slope of the relationship between the dependent variable and a determined independent variable controlling for all the other independent variables (see Freckleton, 2001). Moreover Koper *et al.* (2007) found that regression of residuals cannot distinguish ad-equately between the ecological effects of habitat amount and fragmentation.

Finally spatial autocorrelation was also considered since it is an intrinsic propriety of biological and environmental (*e.g.* forest) variables (Legendre, 1993), and lattice datasets are almost always spatially autocorrelated. It is necessary to control for spatial autocorrelation (Legendre, 1993) because it can cause non-independent errors than can invalidate regression assumptions. For this reason, after all the significant landscape variables were selected by the regression procedure, a final re-

gression step including the nine terms of a trend surface analysis (Borcard *et al.*, 1992) was performed:

$$f(x, y) = b_0 + b_1 x + b_2 y + b_3 x^2 + b_4 xy + b_5 y^2 + b_6 x^3 + b_7 x^2 y + b_8 xy^2 + b_9 y^3$$

where x and y are the central longitude and latitude coordinates of each UTM 10 x 10 km cell, respectively, and b_i are the corresponding regression coefficients. After centring the spatial variables, the spatial variables were standardized and rescaled between -1 and 1 with regard to the geographic dimension with greater variation (longitude), recomputing the latitude variation according to the maximum standardised longitude for avoiding problems with the polynomial terms of the trend surface analysis equation (Ramírez and Tellería, 2003). The non-significant spatial terms of the third degree polynomial were removed and the significant ones were included in that regression step. Afterwards some of the landscape variables initially included in the models may be no longer significant, case in which were dropped from the final explanatory model (see Hortal and Lobo, 2002). The absence of spatial autocorrelation in the residuals of the resultant final models was checked and confirmed through the Durbin-Watson statistics (that ranged from 1.528 to 1.739) and Moran's I correlograms. The results hereafter refer only to the final models with the significant forest landscape variables once accounted for spatial autocorrelation, but without including the significant terms of the trend surface analysis.

RESULTS

Specialist and total species richness were more correlated with AreaFCC40 ($r = 0.681$ and $r = 0.668$, respectively), while for generalists ($r = 0.608$) was AreaFCC10; therefore these were the forest area variables considered

in the regression models. In addition, forest area (considering the different FCC thresholds above described) was in all the cases positively correlated with forest bird species richness. Nevertheless, there was a decreasing trend in species richness as the FCC threshold increased above 40 %, although the decrement was only significant ($P < 0.01$) for a FCC threshold equal or bigger than 80 %.

The regression models explained up to 62 % for specialists and 52 % for generalists, and none of the configuration indices were significant when considered together with the full set of forest landscape composition variables (Table 2). In all the models (Tables 2 and 3) forest area was the variable with the greatest contribution to explain bird species richness, about 70 % for the forest landscape composition and configuration models and more than 90 % for the forest area and landscape configuration models (in terms of R^2), although forest area increased less the determination coefficient for generalists than for specialists. After accounting for forest area, forest bird species richness was also favoured by forests with high tree species diversity (Tree div) and in a lesser extent by the abundance of coniferous trees, contributing similarly and independently of the degree of bird species specialization (Table 2).

When considering forest area and landscape configuration, only one shape irregularity metric (MCIR) was significant (Table 3), although the influence was quite small (about 4.9 % for generalists and 1.5 % for specialists, in terms of R^2). The rest of the configuration indices were not significant after accounting for spatial autocorrelation (Table 3). Thus landscape configuration explained a considerably lower proportion of species richness variation than the model including other forest composition variables different from forest area (less than 5 % and about 30 %, respectively). For both types of statistical models, the total species richness model resulted as a summary of those for the specialist and generalist bird

Stepwise multiple regression analysis of specialist, generalist and total forest bird species richness against forest composition and configuration variables. AreaFCC40 and AreaFCC10 are the area of land covered by forests with a canopy cover above 40% and 10%, respectively. Only significant variables after accounting for spatial autocorrelation are included in the models.
[Análisis de regresión múltiple stepwise entre la riqueza de especies de aves forestales especialistas, generalistas y total y las variables de composición y configuración del bosque. AreaFCC40 y AreaFCC10 son el área cubierta por bosque con una fracción de cabida cubierta por encima del 40% y del 10%, respectivamente. Sólo se incluyen en los modelos las variables significativas después de considerar la autocorrelación espacial.]

Model		Partial R^2			Total R^2	P
		Area	Tree div	Coniferous		
Specialists	12.025 + 2.400 AreaFCC40 + 2.070 Tree div + 1.259 Coniferous	0.462	0.097	0.063	0.622	< 0.0005
Generalists	18.873 + 1.903 Area FCC10 + 1.938 Tree div + 1.134 Coniferous	0.368	0.098	0.057	0.523	< 0.0005
Total	30.898 + 4.297 AreaFCC40 + 4.015 Tree div + 2.505 Coniferous	0.444	0.103	0.072	0.619	< 0.0005

* See material and methods section for a full description of the variables. *[* Véase la sección material y métodos para una descripción completa de las variables.]*

species richness, with the same significant variables and similar proportions of relevance (Tables 2 and 3).

DISCUSSION

As expected, forest landscape structure explained more specialist than generalist forest bird species richness, which agrees with previous studies about forest birds (Mitchell *et al.*, 2001; Gil-Tena *et al.*, 2007), reflecting the higher preference of specialists for forests rather than for other non-forested habitats. The models here reported at 10 x 10 km explained considerably more variability than those by Gil-Tena *et al.* (2007) at the finer scale of 1 x 1 km for the same study area and dealing only with composition features (62 % and 53 % for specialists and 52 % and 34 % for generalists, respectively). This could

be due to the greater data variability at 1x1 km (with a dataset of 2,923 UTM cells studied) and it may also reflect a better match with some species' home range at the scale of 10 x 10 km than at 1 x 1 km.

The large contribution of forest area to explain bird species richness agrees with previous results on bird distribution at different landscape scales (*e.g.*, Westphal *et al.*, 2003; Radford *et al.*, 2005; Gil-Tena *et al.*, 2007), indicating that forest bird species primarily require a significant amount of forest habitat, apart from other needs regarding forest landscape characteristics.

The decreasing trend in species richness as forest closure increases has also been reported at finer scales, although with a slightly different significant FCC threshold of above 70 % (Gil-Tena *et al.*, 2007). Forests with too closed canopies are usually very dense and therefore may present lower forest bird species richness

TABLE 3

Stepwise multiple regression analysis of specialist, generalist and total forest bird species richness against forest area and configuration indices (fragmentation and shape). AreaFCC40 and AreaFCC10 are the area of land covered by forests with a canopy cover above 40 % and 10 %, respectively. Only significant variables after accounting for spatial autocorrelation are included in the models.

[Análisis de regresión múltiple stepwise entre la riqueza de especies de aves forestales especialistas, generalistas y total y el área de bosque y los índices de configuración (fragmentación y forma). AreaFCC40 y AreaFCC10 son el área cubierta por bosque con una fracción de cabida cubierta por encima del 40 % y del 10 %, respectivamente. Sólo se incluyen en los modelos las variables significativas después de considerar la autocorrelación espacial.]

Model		Partial R^2		Total R^2	P
		Area	MCIR		
Specialists	11.898 + 2.111 AreaFCC40 + 0.604 MCIR	0.462	0.007	0.469	< 0.0005
Generalists	19.717 + 1.587 AreaFCC10 + 0.662 MCIR	0.368	0.019	0. 387	< 0.0005
Total	31.535 + 3.796 AreaFCC40 + 1.330 MCIR	0.444	0.014	0.458	< 0.0005

* See material and methods section for a full description of the variables. *[* Véase la sección material y métodos para una descripción completa de las variables.]*

(James and Wamer, 1982; Carrascal, 1987; Tellería and Santos, 1994). The lack of development of inferior vegetation strata (shrubs) associated to these dense forests affects negatively to the availability of feeding and foraging substrates or nest sites that can supply more habitat niches for a great number of forest bird species, and also may increase nest vulnerability (see Díaz and Carrascal, 2006).

It is widely recognised that more diverse forest landscapes, with a high number of tree species, supply greater variety of potentially suitable niches for bird species than landscapes with homogeneous characteristics (Carrascal and Tellería, 1990; Díaz *et al.*, 1998; Hobson and Bayne, 2000; Gil-Tena *et al.*, 2007). On the other hand, the positive effect of coniferous species abundance on forest bird species has also been found in other studies (Loehle *et al.*, 2005), although results from previous studies are often contradictory and dependent on the scales and study areas. For instance, several authors found less species richness in coniferous compared to broadleaved forests (James and Wamer, 1982; Barbaro *et al.*, 2005; Gil-Tena *et al.*, 2007) or a greater association of bird communities with the latter (Berg, 1997). Hobson and Bayne (2000) could not associate more species richness to coniferous or deciduous forests, and studies conducted in the Iberian Peninsula regarding the environmental patterns associated with the distribution of forest avian communities also have pointed out this uncertainty (Tellería and Santos, 1994; Carrascal and Díaz, 2003). It is noteworthy that at the scale of 10 x 10 km forest development did not affect forest bird species richness, in contrast to what found for forest birds at finer scales in this study area (Gil-Tena *et al.*, 2007). Although older forests are often considered to be richer in bird species (Barbaro *et al.*, 2005; Díaz, 2006), Sallabanks *et al.* (2002) also found that stand age *per se* was not correlated with forest avian distribution.

As expected, forest landscape composition characteristics seem to be more important than

configuration for determining forest bird species distribution, which supports the results of some previous studies (McGarigal and Mc-Comb, 1995; Trzcinski *et al.*, 1999; Radford *et al.*, 2005, Betts *et al.*, 2006). Nevertheless, and according to the initial prediction, more irregular shapes in the forest landscape may be an indicator of forest bird species diversity, as already found for plant species richness in agricultural lands (Moser *et al.*, 2002) and for different taxa in forest areas (Saura *et al.*, 2008), as a consequence of the association between forest shape irregularity and more natural and less intensively managed forests (Saura and Carballal, 2004), which may contain a greater number of bird species (Hill, 1998; Rodewald and Yahner, 2001). The results obtained for the mean circumscribing circle index also agree with those obtained by Radford *et al*. (2005), for the area-weighted version of this index. It is also remarkable that MCIR was the only shape metric that perfectly discriminated native forests (with more complex and elongated boundaries) from exotics in Northern Spain (Saura and Carballal, 2004). Other indices related to shape complexity (fractal dimension) were also positively associated with the abundance of most of the bird species studied in Brennan and Schnell (2005), and irregular landscape shapes also favoured forest birds in maritime pine plantations in Southwestern France (Barbaro *et al.*, 2005). Despite the former studies just cited regarding forest shape, there has been comparatively much more focus on forest fragmentation than on shape irregularity for assessing the relationships of landscape configuration with forest biodiversity (*e.g.*, Trzcinski *et al.*, 1999; Villard *et al.*, 1999; Mitchell *et al.*, 2006; Betts *et al.*, 2006). However, shape irregularity was a more relevant forest landscape feature than fragmentation in the present study and others (Saura *et al*., 2008), and shape metrics were also less correlated and redundant with forest area than fragmentation ones (compare the variables initially considered in the Material and methods section and those finally included in the analysis. See Table 1).

Landscape management implications

According to the results obtained and to the scale of the analysis, forest landscape management should focus on forest habitat availability and forest structure features rather than on a particular forest landscape configuration, with perhaps the minor exception of shape irregularity features. Some previous studies concur with this general guideline (*e.g.*, Trzcinski *et al.,* 1999) although others concluded that is also important to consider the spatial arrangement of forest habitats (*e.g.*, Villard *et al.*, 1999; Westphal *et al.*, 2003; Betts *et al*., 2006). Nonetheless, and agreeing with Trzcinski *et al.* (1999), at smaller scales forest landscape configuration (e.g. fragmentation) may have a larger effect on forest bird communities, particularly when forest area is low (Andrén, 1994; Radford *et al*., 2005; Betts *et al*., 2006).

As shown, in Catalonia it is important to manage forest landscapes for promoting availability of forest habitat without an excessively closed canopy, and with an amalgam of forest tree species including a sufficient amount of coniferous trees. Tellería (1992) also highlighted the need of forests with physiognomic and floristic diversity which would not be met when forest landscapes are managed only for intensive timber production, since they are typically managed as mono-specific stands, with dense canopy covers and homogeneous structures.

Because it is unfeasible to monitor forest biodiversity exhaustively, the information available in biodiversity databases (*e.g.*, Atlas of Spanish Breeding Birds) and forest maps (*e.g.*, Spanish Forest Map) has been shown to be of great utility for evaluating the relative importance of the factors influencing on forest birds. Moreover, great part of these databases are carried out or funded by public institutions and are easily accessible for managers and scien-

tists. This can provide valuable recommendations in a cost-effective way for forest managers and conservation policies seeking to address biodiversity criteria at different scales.

To conclude, in Catalonia biodiversity-oriented forest management should focus on forest habitat availability and forest structure features rather than on a particular forest landscape configuration. Especially for the conservation of generalists, other non-forest landscape characteristics have to be considered. Besides a multiscale approach for both managing forest landscape and explaining the distribution of biodiversity is needed, focusing on a few endangered or threatened species at particular locations when required.

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APPENDIX 1 *[APÉNDICE 1]*

Forest breeding bird species studied.
[Aves forestales nidificantes estudiadas.]

Specialist forest birds	Generalist forest birds
Accipiter gentilis	*Anthus trivialis*
Accipiter nisus	*Buteo buteo*
Aegithalos caudatus	*Carduelis spinus*
Certhia familiaris	*Certhia brachydactyla*
Coccothraustes coccothraustes	*Circaetus gallicus*
Dendrocopos major	*Columba palumbus*
Dendrocopos minor	*Corvus corax*
Dryocopus martius	*Corvus corone*
Erithacus rubecula	*Cuculus canorus*
Fringilla coelebs	*Emberiza cia*
Garrulus glandarius	*Emberiza citrinella*
Loxia curvirostra	*Falco subbuteo*
Parus ater	*Ficedula hypoleuca*
Parus caeruleus	*Hieraaetus pennatus*
Parus palustris	*Lullula arborea*
Phylloscopus collybita	*Milvus milvus*
Regulus ignicapilla	*Oriolus oriolus*
Regulus regulus	*Parus cristatus*
Sitta europaea	*Parus major*
Sylvia atricapilla	*Pernis apivorus*
Tetrao urogallus	*Phylloscopus bonelli*
Turdus philomelos	*Picus viridis*
	Prunella modularis
	Pyrrhula pyrrhula
	Serinus citrinella
	Sylvia borin
	Sylvia cantillans
	Troglodytes troglodytes
	Turdus merula
	Turdus torquatus
	Turdus viscivorus