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Effects of forest composition and structure on bird species richness in a Mediterranean context: Implications for forest ecosystem management

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Abstract

There is a growing need to manage forest ecosystems for biodiversity conservation. However, there is still a lack of knowledge on which forest characteristics have a greater influence on biological diversity, particularly in Mediterranean forests. To provide further insights in this respect, we analyzed how different characteristics related to forest composition and structure (forest area, canopy cover, canopy cover diversity, development stage, development stage diversity, coniferous species percentage, tree species diversity, and mono-specific forest percentage) influence the richness of forest breeding bird species (considering 22 specialist and 31 generalist species) in a large dataset comprising 2923 UTM 1 km × 1 km cells in Catalonia (NE Spain). Bird species richness was estimated through presence/absence data obtained from surveys conducted within the framework of the Catalan Breeding Bird Atlas (1999–2002). Forest characteristics were obtained from the Spanish Forest Map (scale 1:50,000), which was developed within the Third Spanish National Forest Inventory. Best regression models for forest specialists accounted for up to 53% of the variability in species richness, while models for generalist and total species richness accounted for 34% and 49% of total variability, respectively. Species richness was favoured by more developed forest stages and by tree species diversity, but very dense, closed forest canopies (>70%) decreased species richness for both groups. For specialist species richness the percentage of coniferous forest cover had a slightly negative influence, while generalists were favoured by more diverse canopy closure. We discuss the implications of these results for Mediterranean forest management considering the current situation of Catalan forests.

Keywords: Bird species richness; Mediterranean region; Forest canopy cover; Catalonia; Forest landscape

1. Introduction

Mediterranean forests have been managed for centuries but there is still a large gap of knowledge on how forest management and biodiversity are related at the stand level and also at coarser scales. Understanding the degree to which forest habitat factors influence species' distribution is an essential step for successful conservation of forest biodiversity and for the development of appropriate and well-founded forest land management (Scarascia-Mugnozza et al., 2000). Previous research on the effects of forest management on wildlife has basically focused on the stand scale and small study areas, but the effects at coarser scales on biotic communities remain poorly understood (Wigley and Roberts, 1997), particularly in the Mediterranean.

As in other regions of the world, in the Mediterranean region forest birds play an essential functional role in forest ecosystems and are often considered as good biodiversity indicators (Sekercioglu, 2006). Forest birds usually regulate forest trophic chains at the predation level (predation of insects, small mammals, etc.) and, for instance, frugivorous birds play a critical role as seed-dispersers of many plants in Mediterranean forested habitats (Herrera, 1984, 1985). Several studies have shown that bird distribution is related to forest habitat characteristics at different spatial scales (Mitchell et al., 2001, 2006; Loehle et al., 2005; Warren et al., 2005; Yamaura et al., 2005); that is, not only at the stand level where the forest practices are implemented, but also at the landscape scale. However, the effects of landscape composition on avian communities in forest dominated landscapes are not well studied (Rodewald and Yahner, 2001), especially in the

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Mediterranean region. In this context, the extensive character of ornithological atlas data allows assessing how environmental features (e.g., forest characteristics) are associated to bird distribution at the landscape scale over large regions (Donald and Fuller, 1998).

In this study, we investigated the relationships between specialist and generalist forest bird species richness and forest characteristics at 1 km × 1 km scale in Catalonia (about 32,000 km^2, NE Spain). We used bird atlas data from the recent Catalan Breeding Bird Atlas 1999–2002 at 1 km^2 resolution and the Spanish Forest Map (developed in coordination with the Third Spanish National Forest Inventory). The purposes of this paper were (1) to determine how relevant are forest characteristics at the 1 km × 1 km level for explaining forest bird species richness in a Mediterranean context. (2) To evaluate which forest characteristics are more related with specialist and generalist species richness. (3) To provide general guidelines and forest management recommendations to promote forest bird species richness in the Mediterranean, considering also the current situation of Catalan forests.

2. Methods

2.1. Study area

The region of Catalonia is located in the Northeast of Spain (Fig. 1) and has a total extension of 32,107 km^2. Catalonia is a heterogeneous region comprising both mountainous areas like the Pyrenees (with an altitude up to 3143 m) and a long coastline along the Mediterranean Sea. In this region, there are three types of climates according to the Papadakis classification (Elías, 1973): Mediterranean temperate, comprising the largest proportion of Catalonia; Maritime temperate climate occurring in the coast; temperate cold climate, in the Pyrenean zones.

Forests represent about 38% of the total area of Catalonia, and about 80% are privately owned (Terradas et al., 2004). Catalonia is characterised by a wide diversity of forest types and tree species; a hundred of different tree species were recorded in the Catalan Forest and Ecological Inventory (Gracia et al., 2004). However, 90% of the total number of trees is from the 14 most common tree species, which are *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), *Pinus nigra* (about 11% of the total forest area), *Quercus humilis*, *Quercus suber*, *Pinus uncinata*, *Pinus pinea*, *Fagus sylvatica, Pinus pinaster*, *Abies alba*, *Castanea sativa*, *Quercus petraea* and *Betula pendula* (Gracia et al., 2004).

Fig. 1. Geographic location of the study area. Black dots in the enlarged map of Catalonia represent the 2923 UTM 1 km × 1 km cells considered in the study.

2.2. Forest bird data

The recent Catalan Breeding Bird Atlas (Estrada et al., 2004) includes information about the distribution of breeding birds in Catalonia during the period 1999–2002. In this study, we estimated the richness of forest diurnal bird species at a landscape scale from the census bird data collected by volunteers within that atlas in a sample of 3077 UTM 1 km × 1 km cells throughout Catalonia (Estrada et al., 2004). Two 1-h surveys (between sunrise and 11 a.m., and between 6 p.m. and sunset) in the period March-July were conducted in each UTM 1 km × 1 km cell within that atlas. We discarded 154 UTM 1 km × 1 km cells that were not completely inside Catalonia or for which the Spanish Forest Map data were not entirely available, resulting in a total of 2923 UTM 1 km × 1 km cells for subsequent analyses.

We included in the study 53 forest breeding bird species recorded in the UTM 1 km × 1 km cells (see Appendix A). We classified 22 species as specialist forest birds and the remaining 31 as generalists according to the habitat selection matrix for each species as reported in the Catalan Breeding Bird Atlas (Estrada et al., 2004). We classified as specialists those species that are strongly associated with only forest habitats and as forest generalists those birds that mainly use forest but also other non-forested habitats. Grouping of species in such a coarse classification (generalist and specialist species) was appropriate and particularly suited to this study since we were dealing with a large extension of territory and number of species (53) and it would not be possible to manage all species individually. We were conscious of our limitations and, although richness does not represent abundance of species, interrelationships among them, nor the specific identity of each of the species counted, it is one of the key variables to consider in forest biodiversity assessment, and is regarded as a good indicator of biodiversity (Gaston, 1996).

2.3. Forest composition and structure variables

We obtained forest characteristics for the 1 km × 1 km cells from the Spanish Forest Map at a scale of 1:50,000, created within the recent Third Spanish National Forest Inventory (Ministerio de Medio Ambiente, 2006). The Spanish Forest Map for Catalonia was developed from the interpretation of aerial photographs, combined with pre-existing maps and field inventory data. The minimum mapping unit is in general 0.0625 km^2, decreasing to 0.022 km^2 in the case of forest patches embedded in a non-forest land use matrix. The Spanish Forest Map provides information about the land use type, the tree species present in each forest patch (up to three different species), their abundance (in terms of cover), the total forest canopy cover (FCC) and the development stage in each forest patch (recently regenerated (up to canopy closure), thicket (up to natural pruning), trees with diameter at breast height (DBH) $\leq$ 20 cm, and trees with DBH $>$ 20 cm). We did not consider information on shrub strata because the Spanish Forest Map does not include this type of data, despite shrubs are essential, among others, for several passerine species (Camprodon, 2001).

We obtained the following forest composition and structure variables:

- AreaFCC, defined as the area of land (m^2) with a forest tree canopy cover above a certain FCC threshold. Ten variables were derived from this definition for 10 different FCC thresholds: Area5 (comprising land area with forest tree canopy cover ranging from 5% to 100%), Area10 (land area with FCC from 10% to 100%), Area20, Area30, Area40, Area50, Area60, Area70, Area80, and Area90 (land area with FCC between 90% and 100%). No additional variable regarding average FCC in the UTM cell was considered in the analysis since it was highly correlated with AreaFCC.
- FCC diversity, quantified through the Shannon-Wiener index for 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, computed as the area-weighted average for each forest patch, where we assigned a numerical value ranging from 1 (recently regenerated) up to 4 (trees with DBH $>$ 20 cm) to the four different development stages discriminated in the Spanish Forest Map (see above).
- Forest development stage diversity, quantified through the Shannon-Wiener index for the proportion of forest land area corresponding to the four development stages described above.
- Coniferous species percentage, measured as the percentage of forest lands covered by coniferous species. As it is opposed to the cover of broadleaved species, only the former was considered in the analyses.
- Mono-specific forest percentage, 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 management plans in Spain (Madrigal, 1994).
- Forest tree species diversity, quantified through the Shannon-Wiener index for the proportion of forest land area covered by each tree species. This variable summarises a different information from that conveyed by the mono-specific forest percentage; for example, a 1 km × 1 km cell where all forest stands are a mix of two different species will have no mono-specific forests, but if these two species are the same in all the patches that cell will have a low tree species diversity.

All the forest landscape variables were standardised to zero means and unit variances to eliminate the effect of differences in the measurement scale.

2.4. Data analysis

Analyses were performed separately for specialist, generalist and total species richness. We first calculated correlations with the AreaFCC variables in order to evaluate the relationships between forest area and canopy cover and the dependent variables, and specifically to determine which definition of forest area presented a higher association with the species richness for the different groups. Due to the large number of AreaFCC variables considered (30 in total) we performed Bonferroni corrections to avoid the occurrence of spurious positives when testing for significant correlations (Rice, 1989). The influence of forest characteristics on forest bird richness was analyzed through a forward–backward stepwise regression (p-to-enter = 0.05, p-to-remove = 0.10). As the AreaFCC variables were highly correlated, we included in the regression only the variable with the highest correlation with species richness (one for each of the dependent variables) to perform the regression analysis and avoid multicollinearity problems.

3. Results

Area FCC was positively correlated with forest bird species richness for all the FCC thresholds and the three groups of species (Fig. 2), but showed significantly stronger correlations ($p < 0.01$) with specialist than with generalist species richness. For specialist and total species richness, the highest correlation was obtained for Area40 ($r = 0.678$ and 0.632, respectively), while for generalists ($r = 0.499$) this occurred for Area5; thus, these were the AreaFCC variables considered in the regression analysis. Most of the correlations between AreaFCC and

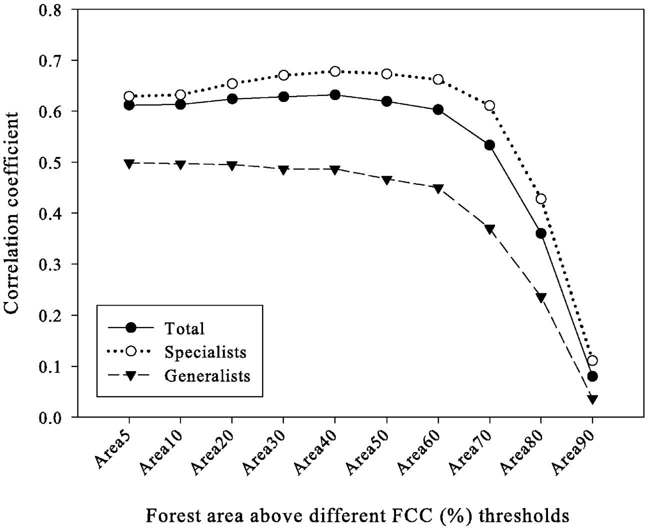

Fig. 2. Correlations between forest bird species richness and AreaFCC (m^2) for different forest canopy cover thresholds for the 2923 UTM 1 km × 1 km cells. All the correlations but the one between generalist species richness and Area90 were significant ($p < 0.01$) after Bonferroni corrections.

Table 1
Regression model for specialist forest bird species richness

	Regression coefficient ± standard error	Accumulated R^2	Standardized coefficient (β)	Significance
Constant	4.709 ± 0.045			<0.0005
Area40	1.866 ± 0.055	0.459	0.527	<0.0005
Forest tree species diversity	0.617 ± 0.069	0.506	0.174	<0.0005
Mean forest development stage	0.787 ± 0.072	0.517	0.222	<0.0005
Coniferous species percentage	−0.377 ± 0.058	0.526	−0.106	<0.0005
Forest development stage diversity	−0.184 ± 0.060	0.527	−0.052	0.002

Area40 is the area of land with a forest tree canopy cover from 40% to 100%.

Table 2
Regression model for generalist forest bird species richness

	Regression coefficient ± standard error	Accumulated R^2	Standardized coefficient (β)	Significance
Constant	8.019 ± 0.053			<0.0005
Area5	1.016 ± 0.065	0.249	0.289	<0.0005
Mean forest development stage	0.956 ± 0.067	0.328	0.272	<0.0005
Forest tree species diversity	0.373 ± 0.071	0.338	0.106	<0.0005
FCC diversity	0.202 ± 0.061	0.341	0.057	0.001

Area5 is the area of the land with a forest tree canopy cover ranging from 5% to 100%.

Table 3
Regression model for total (specialist + generalist) forest bird species richness

	Regression coefficient ± standard error	Accumulated R^2	Standardized coefficient (β)	Significance
Constant	12.728 ± 0.086			<0.0005
Area40	2.832 ± 0.104	0.399	0.435	<0.0005
Mean forest development stage	1.563 ± 0.137	0.463	0.240	<0.0005
Forest tree species diversity	1.018 ± 0.124	0.487	0.156	<0.0005
FCC diversity	0.283 ± 0.101	0.488	0.043	0.005
Coniferous species percentage	−0.276 ± 0.111	0.489	−0.042	0.013

Area40 is the area of land with a forest tree canopy cover from 40% to 100%.

species richness were not significantly different (within the same group of species) for FCC ranging from 5% to 60%, but they were significantly lower ($p < 0.01$) for AreaFCC above a canopy cover of 70% (Fig. 2), indicating that forest with too high FCC had lower bird species richness.

The best regression model resulted for specialist species richness, closely followed by the one for total species richness ($R^2 = 0.527$ and 0.489, respectively), with $R^2 = 0.341$ for generalist species richness (Tables 1–3). The first and most relevant variable in the specialist species richness model was Area40 ($R^2 = 0.459$), see Table 1. After that, the positive effect of forest tree species diversity indicated that a heterogeneous forest mosaic with different forest tree species was important for specialist species richness. Mean development stage did not increase so much as forest tree species diversity the determination coefficient, but it also had a positive significant effect on species richness. Coniferous species percentage had a negative influence on specialist species richness, although with a much lower influence than the former variables.

For the generalist species richness regression model Area5 was the variable that most contributed to explain richness variation ($R^2 = 0.249$), see Table 2. A more developed forest stage had a positive influence on generalist species richness and it represented a considerable increase in the determination coefficient ($R^2 = 0.079$). Forest tree species and canopy closure diversity also favoured generalist species richness but with a much lower influence.

Finally, regression analysis of total species richness (Table 3) somehow summarized the results from the previous models. Area40 also had the strongest effect on total species richness ($R^2 = 0.399$). As for generalists, development stage was the most noteworthy variable for total species richness apart from AreaFCC. Similarly to the specialist species richness model, although in a smaller degree, total richness was also considerably favoured by forest tree species diversity.

4. Discussion

4.1. Forest composition and structure and bird species richness

Forest bird species primarily required a significant amount of forest habitat (AreaFCC), apart from other needs regarding forest structure and composition. Indeed, forest area also showed a strong relationship with bird species distributions in other studies (McGarigal and McComb, 1995; Trzcinski et al., 1999; Villard et al., 1999; Westphal et al., 2003; Radford et al., 2005). AreaFCC was more associated with specialist than with generalist species richness, which is quite consistent with the fact that generalist species do not select forest habitats exclusively, but use or appear in other non-forest habitats more frequently than specialist species. This result is in accordance with Mitchell et al. (2001), who found that generalists were less sensitive to forest characteristics in two managed coniferous forests in South Carolina (USA), whereas specialists appeared to respond to them strongly.

We found that an excessive FCC (above 70%) might be detrimental to forest bird species richness at the landscape scale considered, which agrees with other authors studying forest density or canopy closure effects on species richness along the Iberian peninsula (Tellería and Santos, 1994) and at finer scales (James and Wamer, 1982; Swift et al., 1984; Carrascal, 1987). This may be due to the limited development of shrub and herbaceous species in the understory of high density forests, probably as a result of reduced sunlight penetration. Shrubs provide food and foraging and nest sites, and the associated forest structural heterogeneity may also reduce predation risk for many bird species through a greater visual obstruction (Martin, 1993).

Although we did not study forest age directly, an advanced forest development stage had a positive effect on species richness. More developed forest stages may benefit forest bird species richness by providing more cavities and a higher amount of dead wood as breeding and feeding substrates (e.g., invertebrates) for many bird species (Camprodon, 2001). The literature consulted confirmed higher species richness in older forests (e.g., Hobson and Bayne, 2000b; Jansson and Andrén, 2003; Díaz, 2006). Moreover, studies about ecological successions in Europe showed that bird species with non-Mediterranean origin, which is the case of many of the species we studied, were more associated with advanced development stages (Blondel and Farré, 1988). Advanced development stages could provide more complex structures with more vegetation strata that can support more species, as shown in Jack pine (*Pinus banksiana*) forest succession in boreal Ontario (Venier and Pearce, 2005). Nevertheless, the available information in the Spanish Forest Map did not allow to specifically discriminate the presence of old-growth or late seral development stages, which may be those more closely related to the presence of different specialist forest species like *Tetrao urogallus*, *Dryocopus martius*, *Dendrocopos major*, *Certhia familiaris*, among others (Estrada et al., 2004). Development stage was more important for generalist and total species richness than for specialist species richness, although previous studies showed that specialization in bird communities generally increases in the course of forest succession (Helle and Mönkkönen, 1990) and, for instance, generalist species were more frequently associated with young stands in Jack pine boreal forest (Kirk and Hobson, 2001).

Our results suggest that in the Mediterranean forest tree species diversity is an important variable explaining bird species richness distribution, by providing higher availability of specific habitats for a great number of forest bird species as shown by some authors (Carrascal and Tellería, 1990; Berg, 1997; López and Moro, 1997; Díaz et al., 1998; Hobson and Bayne, 2000a; Santos et al., 2002; Díaz, 2006). Thus, very few species have habitat requirements met only by one tree species (Avery and Leslie, 1990) and this is more obvious in specialist species since they select more forest habitats.

The abundance of broadleaved forest, in contraposition to the presence of conifers, affected positively specialist species richness. However, the influence was quite small compared to other forest characteristics, which agrees with the hypothesis that avian richness is less strongly linked to any particular forest type *per se* than to forest structure and successional stages (Mitchell et al., 2006). The positive role played by broadleaved species compared to coniferous trees could be due to the greater facility for the establishment of breeding sites, especially in softwood trees (Camprodon, 2001), and the greater availability of arthropods (Illera and Atienza, 1995), among others. Our results are in agreement with previous works (James and Wamer, 1982; Berg, 1997) but see Loehle et al. (2005) and Hobson and Bayne (2000a).

4.2. *Implications for forest ecosystem management*

Our results suggest that forest policies and management for favouring forest avian biodiversity in a Mediterranean region like Catalonia should focus on preserving or extending forest area but avoiding the dominance of too closed canopies. Forest management should also promote forest tree diversity (with a significant presence of broadleaved species) and more mature forest stands.

Management oriented only to intensive timber production may clearly not meet these recommendations, since intensive production forests are typically managed as mono-specific stands, with canopy cover of about 100%, and with short rotations that lead to young forest stands. However, management typically applied for obtaining other non-timber forest products that are increasingly important in the Mediterranean region may not be so conflictive with our recommendations. For instance, pine nut (*P. pinea*) production benefits from longer rotations and more open stands than those optimal for timber production, and also cork production requires *Q. suber* trees from 40 years to more than 170 years (Saura and Piqué, 2006).

The reforestations carried out in Spain within the second part of the 20th century would have been beneficial for increasing forest area and for providing potentially suitable habitat for many avian species (see Carrascal, 1987; Carrascal and Tellería, 1990; Díaz et al., 1998). However, these reforested lands are commonly characterized by the presence of a unique forest tree species (usually conifers), and the lack of subsequent management has resulted in excessive FCC and very high tree densities that hamper an adequate forest development. This may not favour either forest bird species or fire-resistant forest structures, since too dense forests and homogeneous landscapes have been shown to be more prone to burn due to wildfires (Lloret et al., 2002; Vega-García and Chuvieco, 2006). For this reason, we believe of particular importance an adequate management in these recently forested lands, noting that both fire-control and biodiversity improvement may benefit from measures like more intense and frequent thinnings. Quite the same considerations would be applied for the new forest area produced by natural colonization (mainly *Pinus halepensis*, *Quercus ilex*, and other Oak species in Catalonia) after the abandonment of rural activities in the last decades in Spain and most of the Mediterranean.

On the other hand, most forest owners in Catalonia have commonly implemented negative selection cuttings, especially in uneven aged private stands. They chose the best and bigger trees in the forest, not allowing the forest to reach more advanced development stages (Camprodon, 2001). Thus, sustainable and multifunctional forest practices that avoid the application of short rotations systematically all throughout the landscape would be desirable, as well as creating an old-growth forest conservation network in Catalonia, such as the local initiative of ‘‘Pirineu viu’’ (Garriga and Hidalgo, 2001).

It is remarkable that the two different bird species categories considered in our study showed remarkably similar responses to forest characteristics (forest area, forest tree species diversity and forest development stage favoured all of them). Nonetheless, there were also significant differences between them and the lower explanatory power of forest variables in the generalist species richness model would indicate the need to consider other non-forest characteristics for the management of this group of species.

We believe that our results and scale of analysis (100 ha) match those needed for an adequate forest management, especially for the case of Catalonia, where most of the forest ownership is small and private, with an average size of about 20 ha (Terradas et al., 2004). However, we recognise that other scales may also be considered and additional research is needed in this respect since ecological processes do not occur only at a single scale.

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Appendix A. Breeding forest bird species studied

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

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