

# Mediterranean forest dynamics and forest bird distribution changes in the late 20th century

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## Abstract

Processes derived from global change such as land-use changes, climate warming or modifications in the perturbation regime may have opposite effects on forest extent and structure with still unknown consequences on forest biodiversity at large spatial scales. In the present study, we aimed at determining forest dynamics associated with global change processes (forest spread, maturation and fire) that have driven the variation in forest bird distributions in Mediterranean forest ecosystems in recent years. The study was located in Catalonia (NE Spain) and used changes in richness of specialist and generalist forest bird species in the last 20 years of the 20th century as indicators of forest biodiversity change. Forest bird distribution changes showed strong spatial patterns and appeared to be related to population processes occurring beyond sampling units (10 km × 10 km squares). Forest maturation appeared as the most important driver of such changes because most of the studied species have a non-Mediterranean origin and are associated with more mature forests. To a lower degree, forest spread also contributed to forest bird distribution changes whereas the impact of forest fires was not associated to a decrease in the richness of either group of forest species. Given the relatively coarse scale at which our study was conducted, caution should be taken when extrapolating our results to the possible future impacts of climate change on fire regime and forest bird distribution. Our results indicate that large-scale forest maturation and spread due mainly to land abandonment in Catalonia has overridden the potentially negative effects of fires on forest bird distributions and are currently driving changes in forest biodiversity patterns across the region.

**Keywords:** dispersal, forest maturation, forest spread, generalist and specialist forest bird species, hierarchical modelling, land abandonment, mixed models, regional processes, spatial autocorrelation, wildfires

Received 9 May 2008 and accepted 28 July 2008

## Introduction

Humans are increasingly having profound effects on the environment at a global scale. Current global environmental change is commonly viewed as a combination of processes acting at different spatial and temporal scales on the current state of ecological communities (IGBP, 2001). Interactions between climate change and other components of global change such as land-use changes are expected to have strong impacts in the

structure of communities (Sala *et al.*, 2000; Thomas *et al.*, 2004). Because of their high exposure to human activities (Blondel, 2006) and sensitivity to climatic conditions (Peñuelas *et al.*, 2002), Mediterranean ecosystems appear to be especially susceptible to the impacts of global change (Lavorel *et al.*, 1998). This is because many large-scale factors such as climate and land-use changes or modifications in the perturbation regime are expected to be simultaneously impacting these regions with largely unknown overall effects on current biodiversity patterns (Sala *et al.*, 2000).

In most of the Mediterranean region, rural land abandonment has occurred during the last century leading to the naturalization and vegetation closure of many areas and favouring the spread of forest (e.g.

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Debussche *et al.*, 1999; Poyatos *et al.*, 2003; Roura-Pascual *et al.*, 2005). The reduction in forestry activities due to the low profitability of traditional forest products, the introduction of new fuel sources and the subsequent abandonment of firewood and charcoal production have boosted the trend from open woodlands to dense forests with increasing forest age (maturation) and biomass (Poyatos *et al.*, 2003; Roura-Pascual *et al.*, 2005). Climatic and atmospheric changes occurred during the second half of the past century such as increasing temperatures and CO<sub>2</sub> concentrations may also have contributed to the growth and maturation of forest ecosystems especially in areas where water is not a limiting factor (Boisvenue & Running, 2006).

On the other hand, fire is a common disturbance in Mediterranean forest landscapes counteracting in many areas the effects of forest spread associated to land abandonment (Mouillot *et al.*, 2005). Fire regime is the result of a complex combination of factors including fuel accumulation and climatic conditions, and there is evidence that forest fire occurrence and extent have increased during the last years of the 20th century in large regions of the Mediterranean (Mouillot & Field, 2005), particularly in the form of large wildfires. Fuel accumulation and landscape homogeneity derived from rural land abandonment (Lloret *et al.*, 2002; Vega-García & Chuvieco, 2006) together with a higher number of ignitions derived from land-use changes and an increased number of extreme dry and hot summer events associated to climatic change (Piñol *et al.*, 1998) have been argued to be the main factors behind recent changes in fire regime in the region.

Processes related to global change such as land-use changes and fire may lead to opposite trends on forest structure and extent, and their relative effects on biodiversity patterns are likely to depend on the importance of each process at the landscape scale and the interactions established between them (Moreira & Russo, 2007). A large number of forest bird species appears to benefit from forest spread at local (Preiss *et al.*, 1997; Moreira *et al.*, 2001; Suárez-Seoane *et al.*, 2002; Laiolo, 2005; Sirami *et al.*, 2007b) and regional scales (Reif *et al.*, 2007). Forest maturation related to land abandonment has also been suggested as beneficial to forest birds (Reif *et al.*, 2007) but has not been directly tested.

Although, in general, the population of many common forest birds appears to be declining in some parts of Europe (Fuller *et al.*, 2005), there is a degree of variation across the continent with increasing populations of some others which may be linked with land abandonment and the subsequent natural afforestation (Gregory *et al.*, 2007). As suggested by Preiss *et al.* (1997) at the landscape scale, an increased and less fragmented

forest cover could allow a regional colonization by some mid-European forest birds that the absence of large forest tracts has kept away from the Mediterranean lowlands.

To our knowledge, the weight of different ecological processes in driving the changes in the distribution area of forest bird species in the Mediterranean region is still unknown, and particularly, which of these processes are related with forest dynamics. In this context, the Catalan Breeding Bird Atlases (CBBA) offer a new regional perspective of temporal changes in the species distribution in Catalonia (NE of Spain) in a period 20 years apart, being changes in bird distribution often strongly related with species' population trends (see Donald & Fuller, 1998). In addition, the development of forest databases such as the Spanish National Forest Inventory and other land cover maps can gather information about the dynamics of forest ecosystems in this region. Thus, our study is, to our knowledge, the first to quantify the relative effect of contradicting processes of different components of global change on the distribution of forest bird diversity in a Mediterranean context.

In this study, we aimed at determining the type of forest dynamics associated mainly with land abandonment that may have potentially driven the variation in forest bird distributions in Mediterranean forest ecosystems in recent years. We analysed two indicators of forest bird distribution changes in the study area: the variation in species richness during the period between atlases for specialist and generalist birds. We considered three different types of forest descriptors associated to changes in forest characteristics related with land abandonment as possible drivers of forest bird distribution changes: increases in forest area (estimated from land-use maps), forest maturation (estimated from large-scale forest inventory data) and the area affected by forest fires (estimated from official forest fire perimeters). We specifically wanted to determine the following: (i) At which scale have changes in forest bird distributions occurred? We expect here that in the case that local processes are the main drivers of change, changes in bird distributions will have a weak spatial structure and show low spatial autocorrelation patterns. If, on the contrary, bird distribution changes are caused by landscape or regional processes, they will have a strong geographical response showing strong spatial autocorrelation patterns (Diniz-Filho *et al.*, 2003; Gimona & Brewer, 2006). (ii) Which forest descriptors are the best predictors of forest bird distribution change and at which spatial scale? We anticipate that if forest dynamics, mostly derived from land abandonment, are the main drivers of forest bird distribution change, both forest spread and increases in forest growth stocks (maturation) will be the main predictors (see Estrada

*et al.*, 2004). On the other hand, if wildfires have a predominant role, we expect a local effect of fire impact on forest bird distribution change (Brotons *et al.*, 2004).

## Material and methods

### Study area

Catalonia ( $32\,107\text{ km}^2$ ) is a region located in northeast Spain (Fig. 1) comprising a range of habitat types from mountainous areas in the Pyrenees and inland chains (with an altitude up to 3143 m) to a long coastline along the Mediterranean Sea. The climate is mainly Mediterranean temperate, with maritime influence in the coast and a cold influence in the Pyrenees. Prominent land abandonment in the last decades has favoured shrub encroachment and the natural colonization of forest, mostly in less productive and less accessible areas (e.g. Poyatos *et al.*, 2003).

According to the Land Cover Map of Catalonia, about 61% of Catalonia is covered by forests and other shrubby lands (Terradas *et al.*, 2004). Forests are characterized by a wide diversity and about a hundred different tree species exist in this region, although 90% of the total number of trees is from the 14 most common species (Gracia *et al.*, 2004). Despite the fact that forest fires had burned approximately 240 000 ha between



Fig. 1 Geographic location of the study area (Catalonia), shown in black colour.

1975 and 1998 (about 12% of the total area covered by forest and other shrubby lands; Díaz-Delgado *et al.*, 2004), Catalan forests have still increased their absolute cover by about 1.54% between 1987 and 1997 according to the Land-use Map of Catalonia (Viñas & Baillies, 1995). In line with these data, Catalan forests have significantly aged and accumulated biomass during the last years of the 20th century. Comparing data from the Second and Third National Forest Inventory between 1989 and 2001 in Catalonia, there was a significant increment of both forest basal area ( $\text{m}^2\text{ ha}^{-1}$ ) and top height (m) of 27% and 8%, respectively.

### Forest bird changes

To assess the factors behind variations in forest bird distribution, we used species occurrence data derived from the CBBA (Estrada *et al.*, 2004). The CBBA consisted on large-scale surveys covering the whole extent of Catalonia in two different periods: 1975–1983 (Atlas 1) and 1999–2002 (Atlas 2). A total of 385  $10\text{ km} \times 10\text{ km}$  UTM squares were surveyed during the atlas field work in each of the different time periods. The aim of the survey was to detect the highest number of breeding species in each sample square. To do this, the observers were asked to gather, from March to July inclusive, breeding evidences of bird species occurring in all habitats within their square, including the scarce ones. For a particular species, variations in distribution at a regional scale can be estimated by means of an analysis of the variations occurred in every  $10\text{ km} \times 10\text{ km}$  UTM squares between atlases (Donald & Fuller, 1998).

To analyse potential differences between ecological groups, we considered the variation in species richness between atlases separately for specialist and generalist forest bird species. We identified forest specialists and generalists by differences in the species forest and agricultural habitat selectivity indices derived from the bird atlas data (Estrada *et al.*, 2004). Forest specialists were characterized by higher selectivity of forested landscapes and avoidance of agricultural dominated landscapes, whereas generalist species, despite showing positive selection of forested landscapes, did not clearly avoid agricultural landscapes (Appendix Table A1). The analysed species did not include: (i) the most common species (>90% of total squares in Atlas 2) or very scarce (<10% of total squares in Atlas 2), (ii) with specific problems of detectability (e.g. *Tetrao urogallus*) or (iii) those species which tend to be irruptive or opportunistic (e.g. *Carduelis spinus*) (see Estrada *et al.*, 2004). The total number of forest species complying with these criteria was 30 (16 specialists and 14 generalists). According to the CBBA (Estrada *et al.*, 2004), most of the forest species considered here are expanding (12

specialists and six generalists), while the rest remained stable but showing some local changes in distribution (two specialists and four generalists) or significantly contracted their range (two specialists and four generalists). From the species occurrence data for each Atlas period, we obtained the species richness for specialists and generalists for each 10 km × 10 km UTM square.

Observed distribution changes may be related to temporal variation in sampling effort, which may mask real distribution changes (Donald & Fuller, 1998). To differentiate between real changes in distribution and simple variations in the sampling effort between atlases, we applied regressions between the richness variables for each atlas and the variability in sampling effort available for each UTM square (log transformed; Estrada *et al.*, 2004). We used the residuals of the former regressions to compute the variation in richness of forest bird species between atlases, which were the final dependent variables. Analyses of distributional variations were only conducted on the 80% of squares ( $N = 309$ ) from which changes in sampling effort could be obtained [see also Estrada *et al.* (2004) and Carnicer *et al.* (2008) for more details on the procedure and its applications].

Species distributions and their dynamics often show a strong spatial component originated through a variety of ecological processes occurring at different spatial scales (Selmi & Boulinier, 2001; Diniz-Filho *et al.*, 2003). In our study, we explicitly included the spatial structure of specialist and generalist species pools in the modelling approach in order to account for spatial population processes related to dispersal in the recorded changes in the distribution of the species. In particular, population processes occurring in a given location may be related to changes occurring in the neighbourhood (Brotons *et al.*, 2005, 2008; Gimona & Brewer, 2006). We summarized, for a given 10 km × 10 km UTM square, the information about specialist and generalist species richness variation on surrounding squares by means of contagion variables (Augustin *et al.*, 1996). Avian contagion variables were computed by averaging specialist and generalist species richness variation on the UTM squares that had their centre located within a certain distance from the central UTM square, and excluding the values of that central UTM square from the average. For both types of dependent variables, four avian contagion variables were computed at different extents with a distance of 10, 20, 30 and 40 km from the edge of the central UTM square.

#### *Forest dynamics*

We considered forest spread and maturation, related to land abandonment and forest growth, and the area

burnt by fires as the main components of the forest dynamics affecting the study area during the last 20 years. The absence of forest inventory and land-use map data matching the two atlases, forced us to quantify forest dynamics based on data from a somewhat narrower time window (1989–2001 for inventory data and 1987–1997 for land-use maps) than the time elapsed between the two bird atlases (from 1975–1983 to 1999–2002). We assumed that the estimation of the forest dynamics using the time window above is representative of the changes in forest extent and structure corresponding to the whole period between bird atlases since global change processes as land abandonment started a few decades ago in the study area (Terradas *et al.*, 2004).

To evaluate forest spread, we considered the absolute variation of forest area obtained from the Land-use Map in Catalonia for 1987 and 1997 (Viñas & Baulies, 1995). Forest fire data considered the amount of forest burnt area between Atlas 1 and Atlas 2 from fire perimeter government statistics data for 1980–2000 at the municipal level (Catalan Department of Housing and Environment, 2007).

To assess forest maturation we considered the absolute variation of basal area obtained from the permanent plots measured in the Second and Third Spanish National Forest Inventory (NFI 2 and 3, respectively; Ministerio de Medio Ambiente, 2006). In Catalonia, the field work for the NFI 2 was carried out from 1989 to 1991 whereas for the NFI 3 was from 2000 to 2001. The sampling density is about one NFI plot every 1 km<sup>2</sup>. The size of the NFI plots varies depending on the tree diameter at breast height, with a minimum plot radius of 5 m and a maximum of 25 m. We used a subset of 7712 permanent plots measured in both inventories that were entirely within the UTM squares, considering for this study 5346 plots that had not been harvested or burnt by fires, thus estimating the variation of basal area due to maturation of the forest already existing in the NFI 2.

To determine whether the initial conditions of forest influence bird distribution change, we also computed the initial state of both basal and forest area. All the variables described above were computed at the 10 km × 10 km UTM extent; besides, we also calculated four contagion variables for each descriptor in the same way as for the avian contagion variables.

#### *Analytical approach*

To determine at which scale forest bird distribution changes and forest dynamics operate, spatial patterns of bird distribution changes and forest dynamics were analysed by means of general linear modelling (Gimona & Brewer, 2006). In this modelling approach, we considered that different processes may act at different

spatial scales: local at the 10 km × 10 km UTM square extent, landscape for the contagion variables at the extent of 10 and 20 km and regional for the contagion variables at extents equal or greater than 30 km.

Forest bird species richness variation was tested by means of mixed models where specialization group (specialist vs. generalist), avian contagion variables and forest dynamics descriptors were introduced as fixed effects, and each value was corrected for the UTM square effect, being introduced in the model as a random factor to take into account the relationship between measurements within each UTM square. The MIXED procedure of SAS software (version 9.1, SAS Institute Inc., Cary, NC, USA) was used, and the effects of main fixed and random factors were studied (*F*-test,  $P < 0.05$ ). Least-square means were computed for the specialization group effect, and statistically separated using pairwise *t*-tests when a significant ( $P < 0.05$ ) *F*-test was observed.

To assess differences between specialization groups, we computed the interaction between the variable of specialization group and the significant forest dynamics' predictors. Interactions between the significant forest descriptors were also included to consider potential synergies between forest dynamics on forest bird distribution changes. In the case of significance of the linear component of variables describing forest dynamics, we also checked the effect of the quadratic term of each predictor to account for nonlinear relationships.

We developed three different models using a hierarchical modelling approach to progressively assess the role of these variables in different steps according to specific hypotheses (Herrando & Brotons, 2002). Significant variables at each step were introduced in later steps and their contribution to the model evaluated by means of the increment of the determination coefficient ( $R^2$ ). To obtain the best set of explanatory variables, we employed the following selection process: first, the significant variable that accounted for the highest reduction in the Akaike's Information Criterion (AIC) respective to the null model was selected; then all the remaining variables were added one-by-one to the model and tested again for their significance and reduction in the change of AIC. The selection process was stopped when the variables to include were not significant or did not reduce AIC. We developed different statistical models according to different hypotheses:

MODEL 1. Forest bird distribution changes are associated not only to forest dynamics but also to bird spatial population processes both acting at different scales. In this model, we assessed the role of forest dynamics after accounting for the spatial structure of forest bird distribution changes. The steps followed in the hierarchical model were:

- Step 1. Because spatial processes are likely to underline changes in distribution between two time periods via ecological processes (Selmi & Boulinier, 2001), we included four spatial variables (contagion variables) summarizing information on the species richness variation in the vicinity of a given square. With the contagion variables' approach, we are also explicitly accounting for spatial autocorrelation in the bird data.
- Step 2. Availability of habitat was assumed to be the first determining factor on bird species population in previous studies (see Moreira *et al.*, 2001). Moreover, it was shown that forest area was the first determinant of forest bird species richness in the study area apart from other forest composition and structural features (Gil-Tena *et al.*, 2007). Thus, in this step we considered those forest dynamics related with habitat availability such as forest spread and fire. We included the variation and the initial amount of forest area and their respective contagion variables as predictors in this model; regarding forest fires we considered the amount of forest burnt area during the 20-year period between atlases and its contagion variables.
- Step 3. After accounting for the availability of forest, forest maturation was considered, as a change of forest structure, by including in the model the forest maturation descriptors (initial basal area, its variation and their respective contagion variables).

MODEL 2. If forest bird contagion variables are not considered, forest dynamics may still explain forest bird distribution changes if these are mediated by changes in forest structure or extent at large spatial scales. This hierarchical model was similar to MODEL 1, but did not include step 1 (assessment of contagion variables).

MODEL 3. Forest maturation acting at regional scales may be the main forest dynamic influencing forest bird distribution changes as most of the considered forest bird species (see Appendix Table A1) are associated with more mature forests (Blondel & Farré, 1988). We developed three different regression models considering separately each of the variables describing different forest dynamics, that is, change in forest area for forest spread, change in basal area for forest maturation and burnt area for fires together with their respective contagion variables.

## Results

### *Spatial patterns of bird distribution change and forest dynamics*

The observed changes in the distribution of both specialist and generalist forest birds showed a strong and

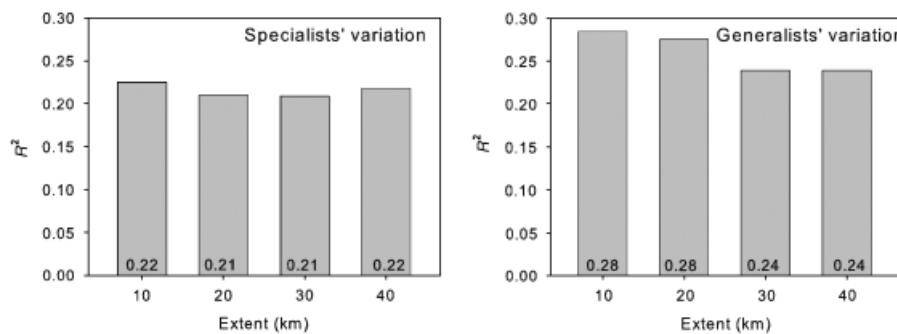
quite uniform spatial structure indicated by the high correlation between changes occurring at a single  $10\text{ km} \times 10\text{ km}$  UTM square and variations recorded in neighbouring squares at the landscape and regional extents (Fig. 2).

The processes affecting forest extent and structure during the study period showed a variety of patterns in their spatial structure (Fig. 3). Increases in forest cover and fire impact appeared to occur mainly as local or landscape processes (decreasing autocorrelation trends at greater spatial extents), especially for forest spread ( $R^2$  from 0.46 to 0.13). Regarding forest maturation, the

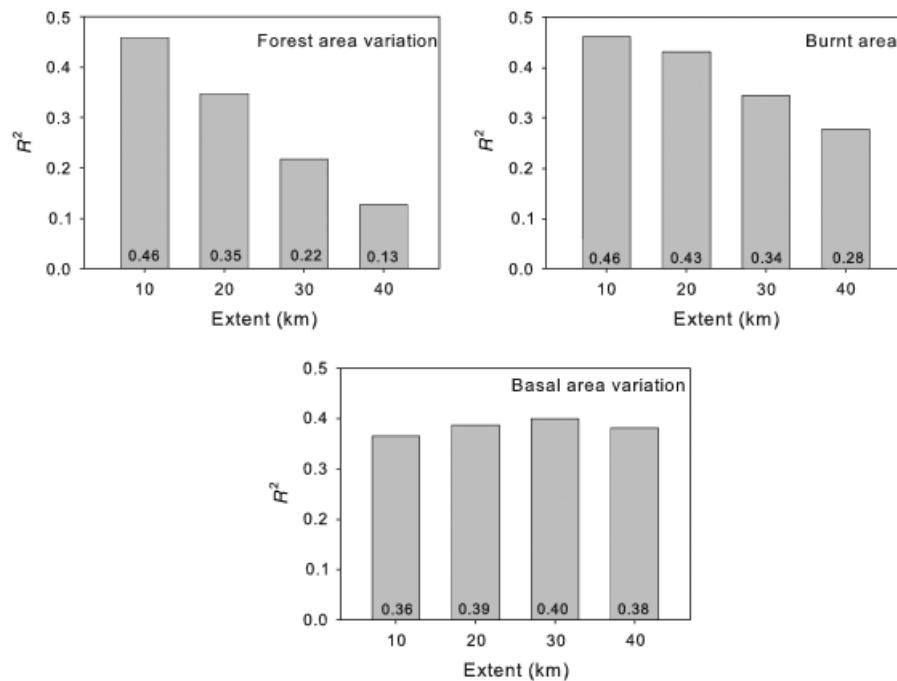
spatial pattern of forest structure change seemed to be uniform with still a strong correlation at regional scales (Fig. 3).

#### *Relationships between forest and bird change*

Changes in forest bird distribution in a given square were significantly associated to both those occurring in the neighbouring squares and also to forest dynamics at the local scale ( $R^2 = 0.29$ ; MODEL 1; Table 1). Avian contagion variables explained 96% of the variability, being the contagion at the landscape scale the most



**Fig. 2** Spatial patterns of bird distribution changes (species richness variation) according to the specialization group. The scales of analysis were: local at the  $10\text{ km} \times 10\text{ km}$  UTM square extent, landscape for the contagion variables at the extent of 10 and 20 km and regional for the contagion variables at extents equal or greater than 30 km. The models developed were significant at  $P < 0.0005$ .



**Fig. 3** Spatial patterns of forest dynamics: forest spread, maturation and fires described by forest and basal area variation and burnt area, respectively. The scales of analysis were: local at the  $10\text{ km} \times 10\text{ km}$  UTM square extent, landscape for the contagion variables at the extent of 10 and 20 km and regional for the contagion variables at extents equal or greater than 30 km. The models developed were significant at  $P < 0.0005$ .

**Table 1** Analysis of the factors behind changes in species richness between the two atlas periods considering avian contagion variables and forest dynamics (corresponding to MODEL 1). The mixed models were conducted in three steps according a hierarchical process. Step 1: with avian contagions as independent variables; Step 2: with the significant variables of the former step (1) and forest spread and fire descriptors as independent variables; Step 3: with the significant variables of the former steps (1 and 2) and forest maturation descriptors as independent variables. The best model had an AIC value of 2552.8. The information in the table concerns to that of each variable in their corresponding step of assessment

	Influence	Type III, F	P	R <sup>2</sup>
Step 1: Avian contagion variables				
Variation 10	+	156.43	<0.0001	0.261
Variation 40	+	20.20	<0.0001	0.017
Step 2: Forest spread and fires				
None				
Step 3: Forest maturation				
Basal area variation	+	10.33	0.0014	0.012
Model				0.290

Variations 10 and 40 are the avian contagion variables at the extent of 10 and 40 km.

influencing (Variation 10), although the regional scale (Variation 40) was also associated to forest bird distribution changes occurring at the local scale. After accounting for avian contagion variables, changes in forest bird distribution were only weakly related to forest maturation at the local scale ( $\Delta$ Basal area).

When we excluded avian contagion variables (MODEL 2; Table 2), the amount of explained variation decreased compared with the former model (a decrease in the explained variation of 28%; Tables 1 and 2). In MODEL 2, variables describing forests at broader scales became important. In particular, these changes were strongly associated with the increase of forest area at the regional extent ( $\Delta$ Forest area 40;  $R^2 = 0.18$ ). In addition, there was a significant relation of forest maturation with species richness variation, not only at the regional extent ( $\Delta$ Basal area 40;  $R^2 = 0.02$ ) but also at the local scale ( $\Delta$ Basal area;  $R^2 = 0.01$ ).

Finally, when considering separately the effects of forest dynamics on forest bird distribution changes (MODEL 3; Table 3), forest maturation, mainly as a regional process occurring all over the study area ( $\Delta$ Basal area 40), was confirmed as the best predictor of forest bird distribution changes explaining 20% of the total variability in forest birds. Nevertheless, forest spread considered as a regional process also seemed to be a major predictor of forest bird distribution changes ( $R^2 = 0.18$ ). As in the former models, forest

**Table 2** Analysis of the factors behind changes in species richness between the two atlas periods considering only forest dynamics (corresponding to MODEL 2). The mixed models were conducted in two steps according a hierarchical process. Step 1: with forest spread and fire descriptors as independent variables; Step 2: with the significant variables in the former step (1) and forest maturation descriptors as independent variables. The best model had an AIC value of 2628.3. The information in the table concerns to that of each variable in their corresponding step of assessment

	Influence	Type III, F	P	R <sup>2</sup>
Step 1: Forest spread and fires				
Forest area variation 40	+	69.28	<0.0001	0.177
Step 2: Forest maturation				
Basal area variation 40	+	59.64	<0.0001	0.021
Basal area variation	+	9.03	0.0028	0.012
Model				0.210

Forest area variation 40 and basal area variation 40 are the contagion variables for forest and basal area variation, respectively, at the extent of 40 km.

**Table 3** Analysis of the factors behind changes in species richness between the two atlas periods considering each forest dynamic individually and including the absolute variation and their respective contagion variables (corresponding to MODEL 3). The best model had an AIC value of 2652.2 for forest spread and 2628.1 for forest maturation

	Influence	Type III, F	P	R <sup>2</sup>
Forest spread				
$\Delta$ Forest area 40	+	69.28	<0.0001	0.177
Model				0.177
Forest maturation				
$\Delta$ Basal area 40	+	139.38	<0.0001	0.184
$\Delta$ Basal area	+	9.50	0.0021	0.013
Model				0.197

Forest area variation 40 and basal area variation 40 are the contagion variables for forest and basal area variation, respectively, at the extent of 40 km.

fires did not appear to affect forest bird changes. For all the models carried out, there was a lack of significance of the specialization group and an absence of significant interactions (Tables 1–3).

## Discussion

As shown by our results, forest dynamics mainly associated with land abandonment as forest maturation and forest spread have played a fundamental role in shaping forest bird changes in Catalonia during the last 20

years. Both forest dynamics influenced changes in forest birds mainly at the regional scale, although forest spread was identified as being more a local or landscape process (Fig. 3). There were no significant differences in distribution changes between specialists and generalists and, thus, forest dynamics appeared to equally affect both ecological groups.

Forest maturation was revealed as the most influencing dynamic in line with the view that most of the forest bird species in the Mediterranean, such as elsewhere in Europe, are more related with advanced forest development stages than with initial successional stages as those typical of young (recently colonized) forests (Blondel & Farré, 1988; Suárez-Seoane *et al.*, 2002). Usually, more forest bird species are associated with older age classes, which may be linked with a more developed and complex forest vertical structure (Herrando & Brotons, 2002; Venier & Pearce, 2005), where forest species may find more and varied resources. Besides, maturation is especially important in the Mediterranean where old-growth forests are scarce due to long-lasting human interference. The average stand age of Catalan forests is under 50 years for most of the forest types (Gracia *et al.*, 2004). Despite the prevalent role of forest maturation in forest bird distribution changes shown in the present study, previous studies have not explicitly considered the effect of forest maturation and focused on forest spread (e.g. Reif *et al.*, 2007).

Although new forests may not apparently fulfil the habitat requirements for those forest bird species more linked to advanced development stages, the general forest spread occurring in Catalonia, acting mainly as a local or landscape process, seemed to have favoured the expansion of this group of birds. New forests in former agricultural lands may be indicating their new role as sink or supplementary habitats for forest birds (Bowen *et al.*, 2007). Besides, new available forest habitats may be beneficial for some pioneer species, but the landscape homogenization produced by the spread of forest may also be a threat for those forest bird species which need mosaics or more open habitats (see Sirami *et al.*, 2007b). Therefore, and on a species idiosyncratic manner, it may be necessary to manage new forested habitats to maintain heterogeneous landscapes.

Thus, forest bird species in the Mediterranean appear to be favoured by both forest maturation and spread. This contrasts with the situation in other parts of Europe as Britain, where most forest birds may be declining due to several factors such as the lack of management and subsequent loss of young forests and other specific problems at local scales as the effect of deer grazing (Fuller *et al.*, 2005).

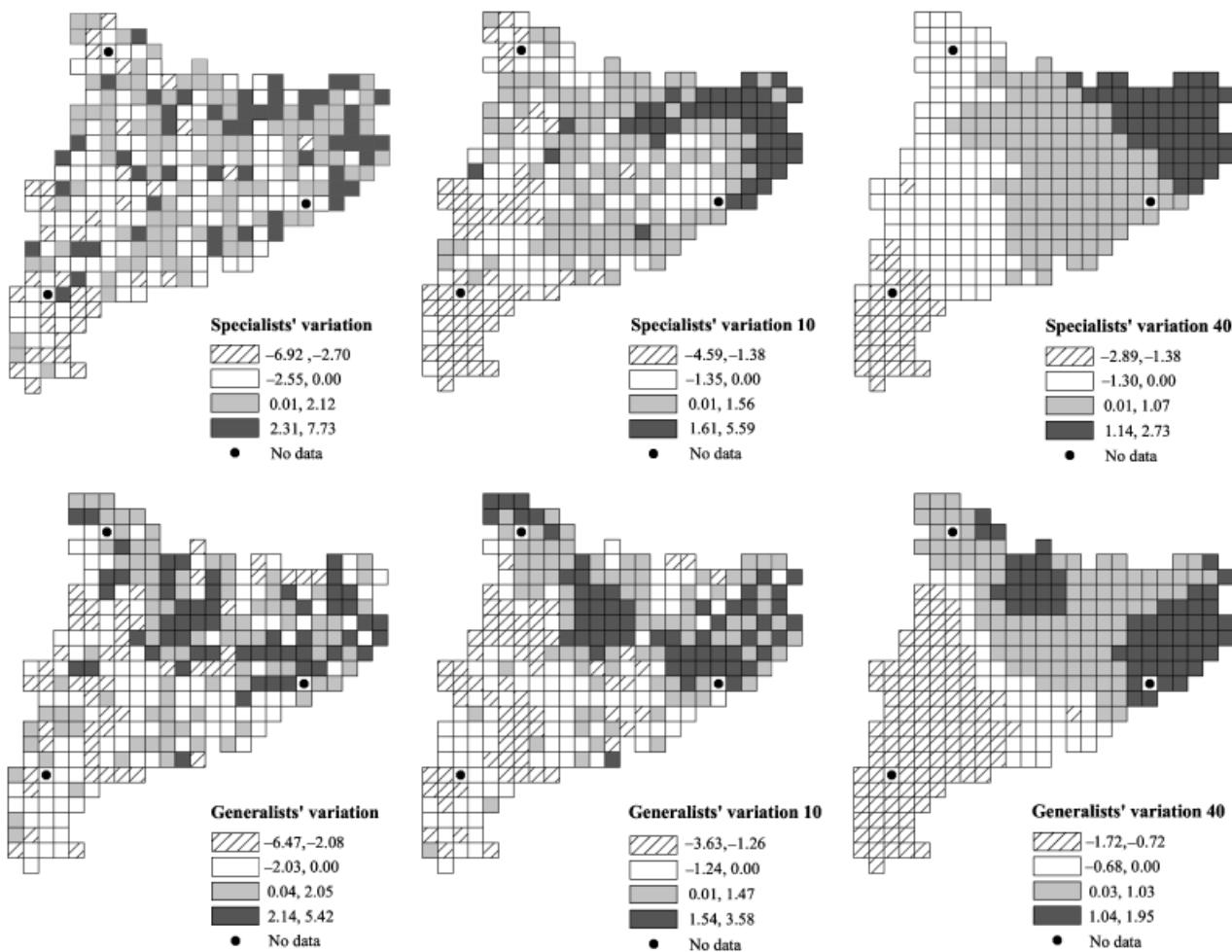
Another possible pointed factor causing forest bird declines may be climate change (Archaux, 2003; Fuller

*et al.*, 2005; Leech & Crick, 2007); nevertheless, in the French Alps, Archaux (2004) showed that most of the forest bird species here considered did not seem to manifest a negative response to climate change, despite the significant warming produced in the zone during the last decades. In the Mediterranean region, land-use change may be the main cause of recent changes in bird populations (Sirami *et al.*, 2007a; Seoane & Carrascal, 2008), which agrees with the positive influence of forest maturation and spread on forest bird changes. Besides, recently Bowen *et al.* (2007) pointed out that regrowth forests may play an important role in buffering against the adverse effects of climate change by improving population or metapopulation persistence through increasing habitat area and enhanced landscape connectivity.

Despite the fact that fires are a prominent factor impacting landscapes across the entire Mediterranean basin, we did not find a negative influence on forest bird distribution changes at the scales analysed here. Nevertheless, we cannot claim that at finer scales ( $<10\text{ km} \times 10\text{ km}$ ), forest fires did not have a negative effect on this group. It is worth noting, however, that fire-related landscapes seem to have a low impact on forest bird species in the Mediterranean basin. Herrando & Brotons (2002) showed that the mosaic-like landscapes shaped by fires in the Mediterranean basin are not strongly associated with negative fragmentation effects on forest birds other than those related with habitat loss. In addition, forest fragments within Mediterranean mosaics created by wildfires allow some forest bird species to respond positively to the disruption because habitat heterogeneity at a local scale appears a key factor in maintaining bird diversity in fire-driven Mediterranean landscapes (Brotons *et al.*, 2004). As suggested by Moreira & Russo (2007), in the Mediterranean, wildfire impacts will not necessarily be always negative for vertebrates at certain scales depending on the fire regime.

The absence of differences between specialization groups on forest bird changes agrees with the weak relation showed between habitat breadth and bird population trends in Spain (Seoane & Carrascal, 2008), although Julliard *et al.* (2004) found that habitat specialization is related to bird-declining rates in France. This lack of differences between specialists and generalists may be related to the fact that the Mediterranean region lacks true forest specialists and most species of both groups may be considered relatively generalists from a European perspective (Covas & Blondel, 1998), thus leading to minor differences in overall responses to changes in forest structure.

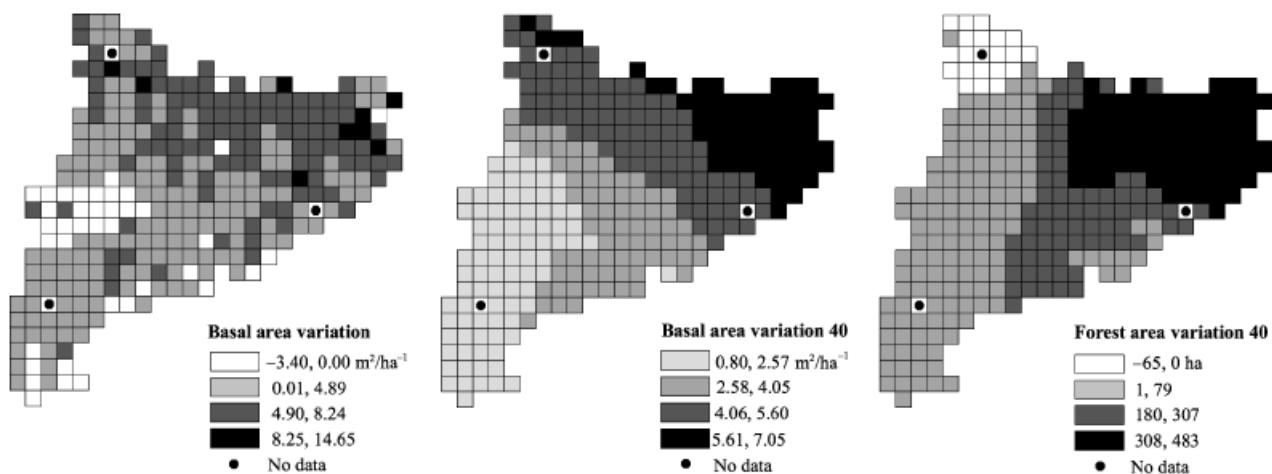
According to our results, forest bird distribution changes were strongly related to spatial population



**Fig. 4** Patterns of distribution in Catalonia of the species richness variation after considering sampling effort and of their significant contagion variables in the mixed models according to their specialization degree. Specialists' variations 10 and 40, and Generalists' variations 10 and 40 are the avian contagion variables after considering sampling effort at the extent of 10 and 40 km for each specialization group.

processes occurring not only at the local level but also at neighbouring locations as shown previously (Brotóns *et al.*, 2005, 2008; Gimona & Brewer, 2006). Besides, there was also an influence of forest dynamics occurring at multiple scales on forest birds (Fig. 2). Processes occurring at regional scales were the main drivers of forest bird distribution changes, although once accounted for regional processes the local scale took relevance. Thus, a multiscale analysis is needed to evaluate the influence of land changes due to global change on bird distribution variations as done previously (Sirami *et al.*, 2007b). Moreover, spatial population processes followed similar distributional patterns at regional scales with forest dynamics by means of a south-to-north gradient of increasing values across the study region (Figs 4 and 5). This gradient may explain why forest dynamics at greater extents gained importance when avian contagion variables were not considered, reflecting common

underlying biogeographical patterns associated to them as climate. In general, the unexplained variation of the models may evidence that other large-scale factors not considered here affected forest bird distribution changes or maybe other processes acting at finer scales than 10 km × 10 km. For instance, at local scales the role of forest management in forest bird distribution changes should be considered. Mediterranean forest ecosystems have been managed for centuries and forest management might affect the availability and quality of forest habitats, which would influence on bird distribution and also on the severity of forest fires by modifying horizontal and vertical fuel continuity. In addition, further research is needed to evaluate the herein considered forest dynamics in future scenarios where climate warming and fire increase are expected to have a large impact in the Mediterranean forests in next decades (see Colombaroli *et al.*, 2007).



**Fig. 5** Patterns of distribution in Catalonia of the significant variables in the mixed models concerning forest dynamics. Basal area variation 40 and forest area variation 40 are the contagion variables at the extent of 40 km for basal and forest area variation, respectively.

### Acknowledgements

We want to thank and recognize the careful and collaborative task of all the contributors of the CBBA and all the ICO volunteers. We thank Xavier Averós Florensa and M. Àngels Colomer Cugat from the University of Lleida for their advice in data analysis. This work has received financial support from the MEC (Spain) and FEDER funds through the IBEPFOR (CGL2006-00312/BOS) and DINDIS (CGL2005-00031/BOS) projects and is a contribution to the European Research Group GDRE 'Mediterranean and mountain systems in a changing world'. The NFI data was supplied by the DGB (MIMAM, Spain). We also like to thank Asier Larrañaga and Edgar Nebot from the GRAF brigade and Josep Llaquet (Catalan government) for the fire data. A. Gil-Tena benefited from a predoctoral grant (2008FIC-00195) with the support of the CUR of the DIUE and the European Social Fund, and L. Brotons from a Ramon y Cajal contract (Spanish government).

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## Appendix A

**Table A1** Forest bird species considered, classified depending on their degree of specialization (class) in specialists (S) or generalists (G)

Forest bird species	N	Trend*	Class
<i>Accipiter gentilis</i>	195	-18	S
<i>Aegithalos caudatus</i>	333	ns	S
<i>Anthus trivialis</i>	87	ns	G
<i>Caprimulgus europaeus</i>	278	+ 32	G
<i>Circaetus gallicus</i>	298	+ 56	G
<i>Corvus corax</i>	295	ns	G
<i>Corvus corone</i>	256	ns	G
<i>Dendrocopos major</i>	274	+ 48	S
<i>Dendrocopos minor</i>	42	+ 631	S
<i>Dryocopus martius</i>	86	+ 109	S
<i>Erythacus rubecula</i>	317	+ 7	S
<i>Falco subbuteo</i>	177	+ 35	G
<i>Fringilla coelebs</i>	304	ns	S
<i>Hieraaetus pennatus</i>	97	+ 1638	G
<i>Lullula arborea</i>	299	+ 20	G
<i>Otus scops</i>	293	-13	G
<i>Parus ater</i>	261	+ 7	S
<i>Parus caeruleus</i>	331	-3	S
<i>Parus cristatus</i>	314	+ 8	S
<i>Parus palustris</i>	54	ns	S
<i>Phylloscopus collybita</i>	239	+ 60	S
<i>Picus viridis</i>	346	-2	G
<i>Regulus ignicapilla</i>	295	+ 8	S
<i>Sitta europaea</i>	158	+ 13	S
<i>Strix aluco</i>	279	ns	G
<i>Sylvia atricapilla</i>	335	+ 6	S
<i>Sylvia cantillans</i>	256	+ 31	G
<i>Troglodytes troglodytes</i>	325	-3	G
<i>Turdus philomelos</i>	260	+ 22	S
<i>Turdus viscivorus</i>	327	-4	G

\*Trend considering sampling effort (% change).

N is the number of 10 km × 10 km UTM squares where a species was counted in the Atlas 2 (from a total of 385 10 km × 10 km UTM squares surveyed).