Effects of forest landscape change and management on the range expansion of forest bird species in the Mediterranean region

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ABSTRACT

In the western Mediterranean region of Catalonia (NE Spain), during the last 20 years of the 20th century, the range of many forest bird species has expanded. Our objective was to characterize the roles of (a) spatial population processes (related to dispersal), (b) changes in forest structure (due to forest maturation and management), and (c) landscape composition (resulting from afforestation and fires) in the range expansion of these bird species at the landscape scale (10 × 10 km). After correcting for the differences in sampling effort, colonizations appeared to be more likely near areas in which the species had been present in the 1980s. Patterns of the range expansion were also strongly associated with forest maturation, which seems to affect the spatial arrangement of birds at multiple scales. Changes in forest landscape composition due to afforestation and fires were minor determinants of range changes, and forest management did not seem to prevent range expansion at the spatial scale studied. Colonization events appeared to be driven primarily by landscape changes occurring in nearby localities rather than within the colonized locations themselves, presumably because of source–sink dynamics and connectivity patterns. Our results showed that in Catalonia, at a landscape scale, the impact of forest management on forest bird communities is much smaller than the impact of the widespread maturation of forests following a large-scale decline in traditional uses.

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1. Introduction

Anthropogenic factors such as fire-induced forest fragmentation have shaped the forest landscapes of the Mediterranean over a long period (Blondel and Aronson, 1999). As a result, little virgin forest remains in the Mediterranean and the average age of a stand is usually low. For example, in Catalonia (NE Spain), average age is less than 50 years (Gracia et al., 2000–2004). In contrast, afforestation has augmented in most of the Mediterranean region due to increased abandonment of rural land during the last century (e.g., Debussche et al., 1999; Regato et al., 1999; Poyatos et al., 2003; Roura-Pascual et al., 2005) although in localized areas, fire counteracts the process of vegetation recovery (Mouillot et al., 2005; Vázquez and Rodríguez, 2008). In addition, the unprofitability of traditional forest products and the introduction of new fuel sources have reduced forestry activities and increased forest aging and biomass (Poyatos et al., 2003; Roura-Pascual et al., 2005). The most common forest management practices in the Mediterranean are those of moderate intensity, such as thinning and selective cutting. In some cases, these practices have increased biodiversity in the understory and canopy of forests, as predicted by the intermediate disturbance hypothesis (Torras and Saura, 2008).

Many species of forest birds appear to have benefited from afforestation (Preiss et al., 1997; Moreira et al., 2001; Suárez-Seoane et al., 2002; Laiolo, 2005; Sirami et al., 2007) and from forest aging (Reif et al., 2007). Large-scale forest maturation and afforestation seem to have offset the potentially negative effects of fires on forest bird ranges in the Mediterranean region (Gil-Tena et al., 2009). In addition, the range changes of forest bird species appear to be associated with spatially related population processes such as dispersal (Gil-Tena et al., 2009). In particular, the ranges of some forest bird species of Catalonia have expanded during the last 20 years of the 20th century (Estrada et al., 2004). The processes that mediate the range expansion of forest birds are likely to also influence other taxa (Donald and Fuller, 1998), and the fate of bird species may therefore reflect overall biodiversity (Sekercioglu, 2006). Thus, a more detailed investigation of the range expansion of forest birds in Catalonia could provide additional insight into the determinants of changes in forest biodiversity.

Forest management can also affect forest bird communities at large spatial scales (Mitchell et al., 2008) but these effects are not

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well studied in the Mediterranean region. Furthermore, Mediterranean ecosystems appear to be especially susceptible to the impacts of global change (Lavorel et al., 1998; Metzger et al., 2008). Forest management could mitigate effects of climate change, for example by modifying wildfire behaviour (De Dios et al., 2007). Therefore, a better understanding of the processes that affect the ranges of forest bird species at different spatial scales could be helpful in forest management.

Gil-Tena et al. (2009) evaluated the effects of spatial population processes and forest dynamics on the change in species richness of forest birds in Catalonia in the last 20 years of the 20th century. In the current study, we disentangle the determinants of the range expansion of selected species of forest birds at the landscape scale. For this purpose, we considered the influence on range expansion of (a) spatial processes, (b) large-scale forest maturation (Gil-Tena et al., 2009), (c) changes in forest structure and composition associated with forest maturation, management, afforestation, and fires. We focused on potential effects of forest management on the range expansion of forest birds in order to provide recommendations for sustainable forest management in Mediterranean forest ecosystems.

We evaluated several specific hypotheses: (1) From Gil-Tena et al. (2009), we expected a strong correlation between bird range changes and spatial population processes and a favourable response of species' colonization to the widespread maturation of forest occurring in the region. (2) Because most of the bird species in the Mediterranean forests have a non-Mediterranean origin and are typically associated with advanced forest stages (Blondel and Farré, 1988; Suárez-Seoane et al., 2002), we expected afforestation to increase bird colonization (e.g., Reif et al., 2007; Gil-Tena et al., 2009) but to a lesser extent than maturation. (3) We also anticipated that changes in forest structure resulting from forest management practices would not prevent bird colonization because most of the forest bird species in the Mediterranean appear to be adapted to landscape heterogeneity derived from anthropogenic practices (Tellería and Santos, 1999; Santos et al., 2002; De La Montaña et al., 2006; Robles et al., 2007). (4) Finally, we predicted that forest fires would reduce colonization because

most of the studied species are dependent on unburnt forested habitats (Ukmar et al., 2007; Battisti et al., 2008), even when fire is often associated with an increase in landscape heterogeneity (Herrando and Brotons, 2002; Brotons et al., 2004a).

2. Material and methods

2.1. Study area

Catalonia (NE Spain; Fig. 1) is a climatically and topographically heterogeneous region covering 32,107 km^2. It includes a variety of habitat types from the mountainous areas in the Pyrenees and inland chains to a long coastline along the Mediterranean Sea. As in many other regions of Mediterranean Europe, land abandonment has boosted afforestation in the last decades (e.g., Poyatos et al., 2003). Forests now cover about 38% of the land surface in Catalonia. Counteracting this effect, forest fires burnt approximately 240,000 ha between 1975 and 1998 (Díaz-Delgado et al., 2004). The net increase in the area of Catalan forests was about 1.54% between 1987 and 1997 according to the Land-use Map of Catalonia (Viñas and Baulies, 1995). Catalan forests have also significantly aged during the last years of the 20th century according to the Spanish National Forest Inventory data (Ministerio de Medio Ambiente, 2006). In the study area, the increases in afforested areas and fire impact appeared to occur mainly as patchy processes, whereas the spatial pattern of forest maturation is similar throughout the region (Gil-Tena et al., 2009).

2.2. Changes in the range of forest birds

Data on changes in the ranges of forest birds were gathered from the Catalan Breeding Bird Atlases (CBBA; Estrada et al., 2004). The CBBA data are derived from a series of large-scale surveys covering the whole extent of Catalonia in two different periods: 1975–1983 (Atlas1) and 1999–2002 (Atlas2). A total of 385 10×10 km UTM squares were surveyed in each of the different time periods. The field work was conducted by volunteers from March to July who recorded evidence of breeding either by sound
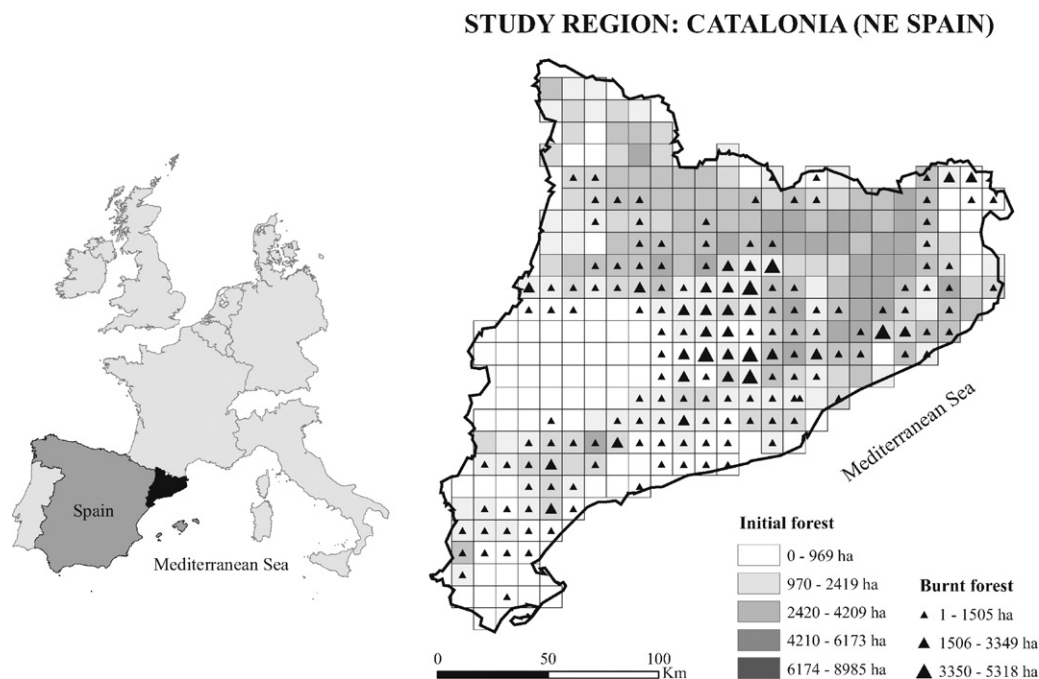

Fig. 1. Location of the study area (marked in black in the left chart), with the initial amount of forest cover and the accumulated amount of burnt forest area during the period between bird atlases (1980–2000) in each 10×10 km UTM.

Table 1
Considered species of expanding specialist forest birds. *N* is the number of 10 × 10 km UTM squares where a species was counted in each bird atlas survey (from a total of 385 10 × 10 km UTM squares). The trend considering sampling effort (% change) is also reported.

	N Atlas1	*N* Atlas2	Trend (%)
Dendrocopos major	182	274	+48
Dendrocopos minor	5	42	+631
Dryocopus martius	42	86	+109
Erithacus rubecula	278	317	+7
Parus ater	220	261	+7
Parus cristatus	284	314	+8
Phylloscopus collybita	136	239	+60
Regulus ignicapilla	248	295	+8
Sitta europaea	132	158	+13
Turdus philomelos	194	260	+22

or sight. We categorised squares according to the recorded changes in occurrence of a particular species as: colonized (present in Atlas2 but not in Atlas1), extinct (present in Atlas1 but not in Atlas2), maintenance (present in both periods) and absence (absent in both periods).

We selected species of specialist forest birds presenting a significant range expansion between Atlas1 and Atlas2 because these species are responsible for the overall increase of forest bird species richness in the forest-dominated areas (Estrada et al., 2004; Gil-Tena et al., 2009). We considered specialist forest species (Gil-Tena et al., 2007, 2008) because generalists may be less susceptible to forest changes at the landscape scale because of their greater tolerance to different environments (Howell et al., 2000; Coreau and Martin, 2007; Jiguet et al., 2007; Devictor et al., 2008 but see Gil-Tena et al., 2009). We identified specialist forest birds by differences in the species' selectivity indices of forest and agricultural habitat derived from the CBBA data (Estrada et al., 2004). Forest specialists were characterized by higher selectivity of forested landscapes and avoidance of agricultural dominated landscapes. The analyzed species did not include (1) the most common species (>90% of total squares in Atlas2) or very scarce (<10% of total squares in Atlas2) because in these cases the Catalan forest habitats were dominated by presence or absence records in the two atlases, respectively, and thus did not allow to discriminate which forest habitat characteristics or their changes (if any) were associated with their expansion. (2) Species with specific problems of detectability were not selected because absence data in the surveys are not reliable and cannot be used as an indication of the lack of use of a particular forest habitat or of their response to changes (Brotons et al., 2004b). (3) We did not consider those species that tend to be irruptive or opportunistic because their presence is not indicative of a causal and stable association with the forest habitat where they are recorded, especially when only two surveys are used to infer changes in a 20-year period (see Estrada et al., 2004). Ten species fulfilled these criteria and were considered in further analyses (see Table 1 and Appendix A).

To control for variation in sampling effort between atlases, we used estimates of effective sampling effort as covariables in our analyses. Analyses of range changes were only carried out on the 309 10 × 10 km UTM squares from which changes in sampling effort could be obtained (for more details see Estrada et al. (2004) and Brotons et al. (2008)).

In the modelling approach, we explicitly included the spatial structure of a species range in Atlas1 to account for spatial population processes related to dispersal in the recorded changes of range. Range changes, and particularly colonization, have been shown to be related to former ranges (Brotons et al., 2005, 2008). Thus, for a given 10 × 10 km UTM square, we summarized the information about neighbouring squares occupied by expanding specialists in Atlas1 by means of neighbourhood variables

(Augustin et al., 1996). Neighbourhood variables were computed by averaging occurrence data on the 10 × 10 km UTM squares that had their centre located within a certain distance from the central 10 × 10 km UTM square, and excluding that central square from the average (see Brotons et al., 2008; Gil-Tena et al., 2009). For each species, two neighbourhood variables were computed at two different extents with a distance of 10 and 20 km from the edge of the central 10 × 10 km UTM square (henceforth Atlas1 10 km and Atlas1 20 km, respectively).

2.3. Forest dynamics

Changes in forest structure and landscape composition (i.e., forest dynamics) were assessed by means of forest inventory and land use map data, respectively. Because there is a paucity of forest inventory data covering the period between the two bird atlases (1975–1983 and 1999–2002), we used data from a narrower time window (1989–2001 for inventory and 1987–1997 for land use maps). Land abandonment and the tendency towards moderate-intensity forest management practices started in the region a few decades ago, so we assumed that the forest dynamics estimated using the narrow time window were representative of the changes in forest composition and structure for the entire period between bird atlases.

To assess forest structure changes we used data from 7712 permanent plots measured in the Second and Third Spanish National Forest Inventory (NFI2 and NFI3, respectively; Ministerio de Medio Ambiente, 2006). In Catalonia, the field work was carried out from 1989 to 1991 for the NFI2 and from 2000 to 2001 for the NFI3. The sampling density was about one NFI plot every 1 km². The size of the NFI plots varied depending on tree diameter at breast height (DBH). The radius of a plot varied from 5 to 25 m. We used only NFI permanent plots that were entirely within the 10 × 10 km UTM squares and were measured in both inventories. Plots affected by fires (612 plots) were excluded from the analysis to avoid confounding effects between silvicultural treatments and fires in those plots. We considered only the silvicultural treatments that can affect stand basal area, differentiating, as in the NFI3, between regeneration (clearcutting, shelterwood and selective cutting) and stand improvement treatments (precommercial thinning and thinning). Plots managed by both regeneration and stand improvement treatments were considered only as regeneration-treated plots because these treatments had been supposed to have a larger influence on stand structure than stand improvement treatments (see Torras and Saura, 2008).

We quantified descriptors of forest structure change separately for unmanaged plots (UNMAN), plots with stand improvement (IMP) and plots with stand regeneration (REG) treatments, using the average of values from the NFI plots in each 10 × 10 km UTM square. We computed eight stand descriptors of change basal area (ΔG), mean diameter at breast height (ΔDBH), mean height (ΔHeight), number of stems per hectare of different diameter classes (ΔStems/ha DC X), and forest canopy cover (ΔFCC). We also considered the removed basal area between forest inventories (Removed G), estimated as the amount of basal area of those tally trees (DBH $\geq$ 7.5 cm) that had been inventoried in the NFI2 but that were not present in the same permanent plots in the NFI3. The removed basal area is an indicator of the intensity of forest management at the plot level. We also computed Removed G in unmanaged localities, which allowed us to consider the impact of other disturbances that may cause natural mortality (other than fire) and loss of stems in stands. In the NFI, the number of inventoried plots depends on the forest cover. Therefore, to characterize the intensity of forest management, we also computed the number of plots in a 10 × 10 km UTM square in which stand improvement or regeneration treatments (Improvement and Regeneration, respectively) had been applied.

Following Gil-Tena et al. (2009), we quantified the effect of natural maturation as a large-scale process, considering its strong relationship with changes in species richness of forest birds shown in that study. We used a neighbourhood variable computed on surrounding 10 × 10 km UTM squares (at the extent of 40 km) by averaging the variation in basal area in unmanaged localities (Regional maturation).

To quantify afforestation, we calculated the absolute variation of forest area (ΔForestA) obtained from the Land-use Map of Catalonia for 1987 and 1997 (see methods in Viñas and Baulies, 1995), subtracting the amount of burnt forest area gathered from government data of fire perimeters. Fires were assessed by means of the accumulated amount of burnt forest area (BurntA) during the first and second edition of the CBBA (i.e., Atlas1 and Atlas2).

2.4. Data analysis

In order to identify uncorrelated gradients explaining the landscape changes in forest structure and composition, we summarized the information on forest dynamics at 10 × 10 km UTM squares by means of a principal component analysis (PCA) with a varimax, normalized rotation, maximizing the correspondence between the factors and the original variables. For this purpose, we included variables related to the initial forest landscape conditions to control for potential correlations between initial forest conditions and bird ranges. We also included the descriptors regarding the landscape changes in forest structure in unmanaged and managed stands and in forest composition (afforestation and fires). In addition, with convenient descriptors of landscape changes in forest structure (ΔHeight, ΔStems/ha of different diameter classes, ΔDBH and ΔFCC) we performed three additional PCAs to describe in more detail what kind of changes had occurred in unmanaged and managed localities (differentiating between stand improvement and regeneration treatments) during the analyzed period.

We used generalized linear models with a multinomial error distribution (McCullagh and Nelder, 1989) to model the historical trajectories of the expanding specialist forest bird species based on the occurrence between the two bird atlases (absence, maintenance and colonization) as a function of different explanatory variables. For the selected bird species, we did not model extinction since there were few related events (see Appendix A), and multinomial regression requires a large sample size for each category because a maximum likelihood method is used. We used a hierarchical modelling approach (three steps) to progressively consider variations in sampling effort between bird atlases, spatial population processes and forest dynamics (Herrando and Brotons, 2002; Brotons et al., 2008; Gil-Tena et al., 2009). We assessed the importance of new variables at each step by means of change in model deviance (McCullagh and Nelder, 1989). Significant variables at each step were included in subsequent steps. For each species, we developed a model according to these steps:

Step 1. Sampling effort. Because changes in bird range in each 10 × 10 km UTM square could be strongly influenced by changes in sampling effort between atlas periods, we included variation of effective sampling effort between the two atlases (log transformed) as the first controlling variable in the models.

Step 2. Neighbourhood influence. Spatial population processes, such as dispersal, may produce changes in bird range between two time periods (Selmi and Boulinier, 2001). Therefore, for each species we included two spatial variables (neighbourhood variables) in the models that incorporated information on species occurrence in the

Atlas1 from multiple squares. We also considered large-scale forest maturation beyond the sampling unit (Regional maturation; Gil-Tena et al., 2009). In this step, we used a forward stepwise selection process.

Step 3. Landscape forest dynamics. We then tested whether forest dynamics occurring within a 10 × 10 km UTM square further explained the range changes of forest birds. This step allowed us explicitly to assess the potential effect of forest management on the bird range changes. In this step, we also performed a forward stepwise selection process with the PCA factors. To assess how the significant variables influenced bird range changes we explored the regression coefficients and the Wald parameters (comparing colonization and maintenance with the reference category (absence)) in the corresponding step in which each variable was considered. For each model, we calculated the area under the curve (AUC) of a receiver operating characteristic plot (ROC) to assess the probability that a model will correctly distinguish a true maintenance and a true colonization event drawn at random.

3. Results

3.1. Landscape forest dynamics

During the time elapsed between forest inventories, 5458 plots remained unmanaged (maturation) while 1642 were managed. From the latter plots, 1369 were managed by regeneration treatments, 273 by stand improvement treatments, and 156 by both regeneration and improvement treatments (i.e., considered in the analysis as regeneration-treated plots).

According to the PCA, we found five different gradients summarizing the information about landscape changes in forest composition and structure in managed and unmanaged localities, which were used in further analyses (Fig. 2). The first factor (Maturation) explained 24% of the variance and mainly corresponded to the natural maturation of trees in unmanaged localities
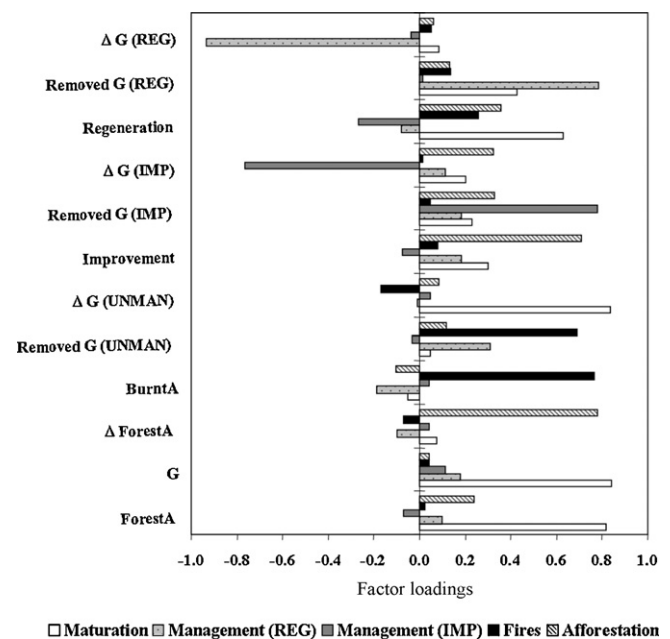

Fig. 2. Factor loadings of the PCA summarizing the information on landscape changes in forest composition and structure in unmanaged (UNMAN) and managed localities (differentiating between stand improvement (IMP) and regeneration (REG) treatments).

Table 2
Factor loadings of the three PCAs describing the changes in forest structure in unmanaged and managed localities. The percentage of the variance that was explained by each factor is shown in brackets.

		ΔHeight	ΔStems/ha DC ≥7.5–12.5 cm	ΔStems/ha DC >12.5–22.5 cm	ΔStems/ha DC >22.5–42.5 cm	ΔStems/ha DC >42.5 cm	ΔDBH	ΔFCC
Unmanaged	Factor 1 (29%)	0.84	−0.34	0.26	0.32	−0.28	0.87	0.46
	Factor 2 (19%)	0.15	0.79	0.66	0.07	0.05	−0.09	0.48
	Factor 3 (18%)	−0.03	−0.02	0.11	0.78	0.82	0.03	0.05
Managed by improvement treatments	Factor 1 (26%)	0.77	−0.10	0.13	0.06	0.70	0.85	−0.06
	Factor 2 (22%)	0.24	0.23	0.77	0.28	−0.01	−0.03	0.89
	Factor 3 (19%)	0.38	−0.73	0.09	0.74	−0.20	0.27	−0.06
Managed by regeneration treatments	Factor 1 (35%)	0.71	0.14	0.62	0.76	0.06	0.52	0.82
	Factor 2 (23%)	−0.43	0.90	0.04	−0.09	0.01	−0.77	0.00
	Factor 3 (15%)	−0.18	−0.06	0.12	0.02	0.98	−0.11	0.01

and to the initial forest conditions (Fig. 2). The second (Management (REG)) and third factors (Management (IMP)) explained 15% and 11% of the variance, respectively, and summarized the changes in forest structure in managed localities. The fourth factor (Fires) explained 10% of the variance and was positively related to the amount of burnt area and to the tree mortality in unmanaged localities (Fig. 2). The fifth factor (Afforestation) explained 13% of the variance and was positively related to afforestation and, to a lesser extent, to the occurrence of stand improvement treatments (Fig. 2).

In unmanaged localities, the size of each diameter class usually increased with maturation, whereas in managed localities, there was also a general development of forest structure but with different trends (Table 2). On the one hand, stand improvement treatments, typically thinning of trees,

decreased the number of stems/ha of the diameter class ≥7.5–12.5 cm and increased those of the diameter class >22.5–42.5 cm (Table 2). On the other hand, most of the regeneration treatments were selective cuttings (94%) and favoured both the thin and thick stems (diameter class ≥7.5–12.5 cm and >42.5 cm, respectively) (Table 2).

3.2. Range changes of forest bird species and forest dynamics

The models assessing the factors driving the range expansion of specialist forest birds had a fair (0.7–0.8) to excellent (0.9–1) model fit as shown by the AUC values (Table 3). Nevertheless, comparing colonization with maintenance patterns, the lowest AUC values always corresponded to colonization (Table 3).

Table 3
Analysis of the factors behind the range expansion of specialist forest birds. Effects of spatial population processes and forest dynamics on range expansion were described using a generalized linear model with a multinomial error distribution (maintenance, colonization and absence categories). χ^2: model deviance. AUC M/C is the area under the curve (AUC values) corresponding to maintenance (M) and colonization (C).

	Null model χ^2	Step 1 Sampling effort	χ^2	Step 2 Neighbourhood influence	χ^2	Step 3 Landscape forest dynamics	χ^2	AUC M/C
Dendrocopos major	634.6	ΔSE[***]	603.5	Atlas1 20 km[***] Regional maturation[**] Atlas1 10 km[*]	444.9 435.2 428.8	Maturation[**]	409.2	0.90/0.76
Dendrocopos minor	244.8	ΔSE	244.5	Regional maturation[***]	163.2	–	–	0.94/0.89
Dryocopus martius	429.7	ΔSE[***]	413.2	Atlas1 20 km[***] Regional maturation[**] Atlas1 10 km[*]	266.9 230.5 223.1	Maturation[***]	189.9	0.97/0.92
Erithacus rubecula	420.8	ΔSE[***]	381.9	Atlas1 10 km[***] Regional maturation[**]	225.5 208.8	Fires[***] Maturation[**] Afforestation[*]	189.3 175.0 167.5	0.97/0.93
Parus ater	561.1	ΔSE[***]	511.1	Atlas1 20 km[***]	318.9	Maturation[***]	303.0	0.94/0.79
Parus cristatus	442.4	ΔSE[***]	414.1	Atlas1 20 km[***]	267.3	Maturation[***] Fires[**] Afforestation[*]	244.2 231.0 221.9	0.91/0.83
Phylloscopus collybita	659.6	ΔSE[***]	609.8	Atlas1 20 km[***] Atlas1 10 km[***] Regional maturation[*]	396.1 376.8 368.4	Maturation[***] Fires[***]	346.6 329.3	0.96/0.83
Regulus ignicapilla	493.5	ΔSE[***]	444.8	Atlas1 20 km[***] Regional maturation[***]	348.1 313.3	Maturation[***] Fires[**]	294.6 284.3	0.87/0.79
Sitta europaea	564.9	ΔSE[***]	521.3	Atlas1 20 km[***]	301.8	Maturation[**]	290.9	0.93/0.84
Turdus philomelos	594.7	ΔSE[***]	561.4	Atlas1 10 km[***] Regional maturation[***]	390.6 359.2	Maturation[***]	327.4	0.92/0.82

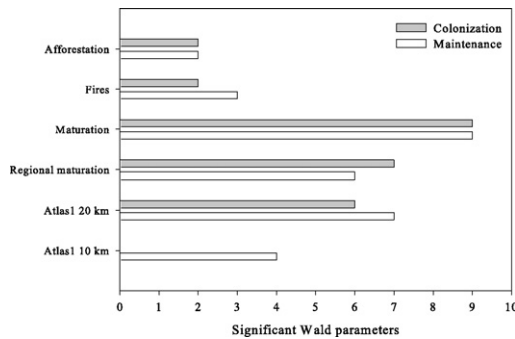[*] $p < 0.05$.
[**] $p < 0.01$.
[***] $p < 0.001$.

Fig. 3. Influence of the significant variables in the models of Table 3 on colonization and maintenance patterns, quantified by the sum of the amount of significant Wald parameters. The variables had a positive regression coefficient when the Wald parameters were significant. The maximum number of significant Wald parameters is 10 (i.e., number of species).

After controlling for the variation in the sampling effort between bird atlases (Step 1, Table 3), the occurrence of the species in neighbouring squares in Atlas1 appeared to be the strongest determinant of the range change of most of the selected species (Step 2, Table 3). A higher probability of colonization and maintenance was associated with neighbouring occupied squares in Atlas1, this being particularly true at the extent of 20 km for colonization (Fig. 3). Large-scale forest maturation (Regional maturation) also favoured the probability of colonization of seven bird species (*Dendrocopos major*, *Dendrocopos minor*, *Dryocopus martius*, *Erithacus rubecula*, *Phylloscopus collybita*, *Regulus ignicapilla* and *Turdus philomelos*) (Step 2, Table 3; Fig. 3). In fact, in the case of *D. minor* large-scale forest maturation was the only significant variable in the model (Step 2, Table 3). In addition, 10 × 10 km UTM squares with a higher degree of maturation had a much higher probability of being colonized or remaining occupied (Step 3, Table 3; Fig. 3). Conversely, afforestation was not a good predictor of colonization and maintenance and was only significant in the case of two species (*E. rubecula* and *Parus cristatus*) (Step 3, Table 3). Despite the significance of fires in the models of four species (*E. rubecula*, *P. cristatus*, *P. collybita* and *R. ignicapilla*) (Step 3, Table 3), only for *P. cristatus* and *P. collybita* did the squares more affected by fires have a significantly higher probability of being colonized (Fig. 3). At the scale of analysis, changes in forest structure due to management did not appear to influence the range changes of any species.

4. Discussion

4.1. Influence of spatial population processes and large-scale forest maturation on the range expansion of forest birds

Based on our results, the range expansion of specialist forest birds was related primarily to spatial population processes occurring at scales greater than 10 × 10 km. These results are consistent with those of Gil-Tena et al. (2009) and with the view that dispersal is a key constraint on the range of forest bird species (Selmi and Boulinier, 2001; Gimona and Brewer, 2006; Bahn et al., 2008). Moreover, large-scale forest maturation explained much of the range change of seven species evaluated in this study. Large-scale forest maturation was the sole determinant of the range expansion of *D. minor* but this species was extremely scarce in the first atlas (Atlas1). The range of *D. minor* expanded rapidly (see Appendix A) mainly because of the development and maturation of riverside poplar plantations (Estrada et al., 2004).

Large-scale forest maturation could have two interacting effects. On the one hand, maturation could favour forest landscape connectivity and facilitate dispersal of bird species. On the other hand, forest maturation could increase the amount and quality of available habitat, which could increase the size of populations that inhabit maturing core of forested regions. Some of these individuals then would disperse to other areas (Pulliam, 1988; Donald and Fuller, 1998).

4.2. Influence of landscape forest dynamics on the range expansion of forest birds

The strong influence of forest maturation on the range expansion of forest birds at the landscape scale (10 × 10 km) strengthens the role played by this process at larger scales (see above), indicating its effect as a multi-scale process. In contrast, changes in forest landscape composition due to afforestation did not have a large effect on the range of bird species. However, afforestation due to land abandonment in the Mediterranean has been expected to favour forest birds (e.g., Preiss et al., 1997; Suárez-Seoane et al., 2002; Sirami et al., 2007) and to prevent the decline of forest bird population in some parts of Europe (Gregory et al., 2007). Therefore, our results support the hypothesis that the range expansion of specialist forest bird species is associated with forest maturation but not with afforestation.

Changes in the structure of managed forests did not significantly influence the range of forest birds at the landscape scale in our study. This result could be explained by the fact that the forest management in the region is of moderate intensity and may not prevent the development of forest structure (Table 2). Alternatively, our results could in part be due to a lack of power to detect effects of management at smaller spatial scales. Other studies in the Mediterranean region performed at smaller scales have shown the influence of different intensities and types of forest management at the bird species or community level (Camprodon and Brotons, 2006; De La Montaña et al., 2006). This influence depends on the ecological requirements of the bird species. Therefore, varying the intensity of forest management could reduce the risk to some sensitive species (Camprodon and Brotons, 2006; De La Montaña et al., 2006). In addition, Taboada et al. (2006) in Spain and Spitzer et al. (2008) in Central Europe agree with the need to restore moderate-intensity forest practices in order to favour the diversity of epigeic invertebrates or a variety of herbaceous-layer, woodland species (Van Calster et al., 2008). Torras and Saura (2008) showed that moderate-intensity silvicultural treatments may result in an increase in species diversity in the vegetation of Mediterranean forest landscapes. In this region, bird species richness increases with the diversity of plant species (Gil-Tena et al., 2007, 2008). In this respect, the lack of forest management in most of the reforestations carried out in Spain within the second part of the 20th century has resulted in an excessive forest canopy cover and very high tree densities. Because adequate forest development has been hampered, diversity of forest bird species and the fire-resistance of forest landscapes could have been constrained (see Gil-Tena et al., 2007).

Contrary to our expectations, the range of three specialist forest birds (*E. rubecula*, *P. cristatus* and *P. collybita*) increased with the frequency of forest fires. Nevertheless, the range expansion of these species was linked more to spatial population processes and forest maturation (Table 3). This suggests that the net increase in forested area and the parallel forest maturation at the landscape scale have overridden the negative effects of fires on the range of forest birds (Gil-Tena et al., 2009). Nevertheless, we cannot discount different levels of impact of forest fires on forest birds at smaller scales (e.g., Herrando and Brotons, 2002; Brotons et al., 2004a; Ukmar et al., 2007; Battisti et al., 2008). This would be particularly true if we consider the increasing number and extent of forest fires in the entire Mediterranean region during the last years of the 20th century

(Mouillot and Field, 2005), as well as the large impacts that climate change and fire increase are expected to have on Mediterranean forest landscapes (Colombaroli et al., 2007).

4.3. Study limitations and concluding remarks

The robustness of our study is somewhat limited because environmental heterogeneity and population dynamics can affect spatial and temporal variation in the abundance of a bird species within its range (Brown et al., 1996). Nevertheless, changes in the range of a bird species are often strongly related to overall species population trends (see Donald and Fuller, 1998). Our data set is one of the best currently available for assessing the range changes of an entire taxonomic group at 10×10 km scale in the Mediterranean region. Furthermore, multi-scale analyses have been advocated to analyze effects of changes in vegetation on the spatial pattern of bird species (Coreau and Martin, 2007; Mitchell et al., 2008; Gil-Tena et al., 2009).
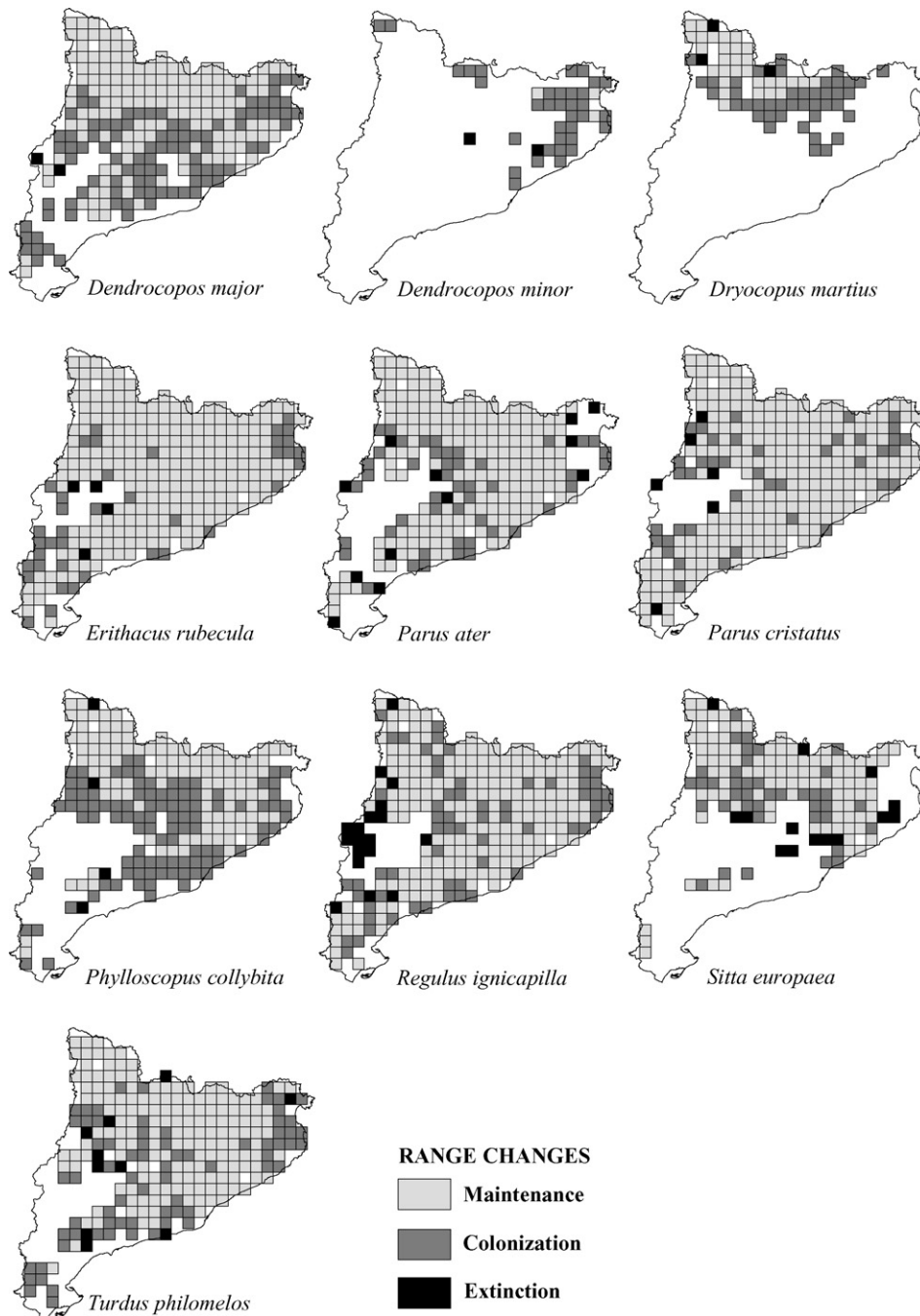
Overall, it appears that forest landscape connectivity and forest landscape dynamics in areas with source populations have a greater effect on range expansions of specialist forest birds than the landscape dynamics occurring within newly formed habitats. This is consistent with the source–sink theory in which good habitats produce a surplus of individuals who colonize new or depleted habitats (Pulliam, 1988). Current rates of forest maturation and afforestation may favour species (re)colonization through source–sink dynamics in regions in which the landscape structure enhances dispersal through increased landscape connectivity. In this sense, an adequate management of the landscape connectivity pattern may allow species to better face range changes associated with climate change and landscape dynamics resulting from rural land abandonment. New improved methods and tools that may be particularly suitable for these purposes are available, such as the Conefor Sensinode software (Pascual-Hortal and Saura, 2006; Saura and Torné, 2009). These methods have been used previously to analyze some forest bird species in Catalonia (Saura and Pascual-Hortal, 2007; Pascual-Hortal and Saura, 2008).

To conclude, our results indicated that forest management in the Mediterranean has a secondary, minor impact on forest bird communities at the landscape scale. The effect of management is largely overridden by the general tendency towards rapid maturation of forests after large-scale decrease in traditional uses.

Appendix A. Range expansion of specialist forest bird species during the period between bird atlases (1980–2000).

Dendrocopos major   *Dendrocopos minor*   *Dryocopus martius*

Erithacus rubecula   *Parus ater*   *Parus cristatus*

Phylloscopus collybita   *Regulus ignicapilla*   *Sitta europaea*

Turdus philomelos

RANGE CHANGES

☐ Maintenance

▨ Colonization

■ Extinction

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