

Dangers of predicting bird species distributions in response to land-cover changes

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Abstract. Land-cover changes from the last decades are leading to important declines in habitat quality, giving rise to changes in bird species distribution all over the world. However, land-cover changes result from a variety of different processes, and it is not clear how effective species distribution models are in capturing species responses to these changes. In this study, we evaluated our ability to predict the effects of land-cover changes on shifts in species distributions at large spatial and temporal scales using Mediterranean landscapes and early-successional, open-habitat birds as study models. Based on presence–absence data from the second Catalan Breeding Bird Atlas (1999–2002), we applied six different species distribution modeling techniques for 10 bird species using climate, topographic, and land-cover data as predictor variables. Then we back-projected the models on land-cover conditions from 1980 to evaluate the projections with field observation data from the first Catalan Breeding Bird Atlas (1975–1983). Finally, we assessed if, in addition to changes in habitat suitability resulting from land-cover shifts, descriptors of fire impact contributed to further explain species distribution dynamics: colonization and local extinction.

We developed accurate model projections of current and past global patterns of species distribution, but our ability to predict species distribution dynamics was reduced. Colonization dynamics were generally more strongly related to fire descriptors than to changes in overall habitat suitability derived from land-cover changes. Our results warn of the dangers of projecting species distribution models onto future conditions if processes behind species distribution dynamics are not explicitly included. Consideration of ecologically meaningful processes for species (i.e., fire disturbance) when modeling species' distribution might contribute to a better explanation of species' colonization dynamics.

Key words: *Catalan Breeding Bird Atlas, Spain; colonization; dynamic landscape; early-successional birds; ensemble forecasts; extinction; fire disturbance; habitat suitability; land-cover changes; model evaluation; model uncertainty; species distribution models.*

INTRODUCTION

In a global change context, land-cover changes are expected to have one of the greatest effects on biodiversity (Sala et al. 2000, Thuiller 2007). The last decades have seen natural and anthropogenic land-cover changes, resulting in a decrease in suitable habitat for many animal and plant species and leading to radical shifts in species composition (Thuiller 2007). A major challenge in current ecology is predicting where and under which scenarios changes in species composition are likely to occur. Attempts to predict the impact of global changes on species distribution are usually performed by developing species distribution models that rely on the estimation of statistical species–environment relationships (Guisan and Zimmermann 2000, Guisan and Thuiller 2005). These models are

currently developed under given conditions and then projected under future scenarios to predict potential changes of species distribution (Broennimann et al. 2006, Thuiller et al. 2006, Beaumont et al. 2007; see Heikkinen et al. 2006 for a review). However, when predicting changes in species distribution arising from land-cover changes, it may be important to consider the processes behind such changes. Land covers are under continuous change and constitute the outcome of different simultaneous processes shaping the landscape. One of the most important processes leading to radical modification in landscape composition and structure are disturbances (Pickett and White 1985). The importance of disturbance to the ecology and conservation of the species has gained widespread recognition due to the critical role in maintaining heterogeneity of environmental conditions in space and/or time (Brawn et al. 2001, Herrando et al. 2003, Bradstock et al. 2005). Hence, to predict the impact of land-cover changes on species distribution, we need a comprehensive approach where ecological processes such as disturbances are considered.

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However, most predictions on species distribution rely on models that still show important uncertainties related to both algorithms and biotic factors (i.e., species interactions) (Araújo and Guisan 2006, Heikkinen et al. 2006, Pearson et al. 2006, Thuiller et al. 2008). Since one of the applications of species distribution models is to be applied to new data to predict future changes, the test of the robustness of model projections using independent data is strongly required (Chatfield 1995, Vaughan and Ormerod 2005, Araújo and Guisan 2006). Nevertheless, assessments of the predictive performance of different modeling techniques with independent and empirical data are still scarce (Araújo et al. 2005, Elith et al. 2006).

In this study we evaluated the effects of land-cover changes on shifts in species distributions at large spatial and temporal scales using Mediterranean landscapes and early-successional, open-habitat birds as study models. Historically, land uses have heavily impacted and structured Mediterranean landscapes, giving rise to significant land-cover changes. Main processes yielding land-cover changes during the last decades have been urbanization, agricultural intensification, and land abandonment (Preiss et al. 1997, Suárez-Seoane et al. 2002, Brotons et al. 2004, Sirami et al. 2007). In a general context of land abandonment, fire takes the lead in determining changes in landscape structure and composition (Moreira et al. 2001). Fire is considered one of the main disturbances of Mediterranean ecosystems, and it is expected to have one of the largest impacts on species distributions (Moreno and Oechel 1994, Almeida et al. 1997). Hence, we also included disturbance processes (i.e., fire) as potential predictors of changes in species distributions. First, we hypothesized that land-cover changes occurring within a 20-year period determined changes in habitat suitability of open-habitat bird species and led to changes in species distributions. For this purpose, we developed a broad set of modeling techniques of species distributions using available bird atlas data, and projected models to land-cover data prevailing 20 years ago. In this way, we empirically evaluated the capability of species distribution models to predict changes by using bird data derived from field observations from two bird atlases. Second, we hypothesized that, in addition to changes in the overall habitat suitability index derived from land-cover changes, fire dynamics may contribute to a better explanation of our focal species distribution dynamics: colonization and local extinction. Although land-cover changes implicitly include fire-induced changes in habitat availability (i.e., shrubland increases in detriment to forest), complementary information about fire occurrence is expected to provide more adequate insights on the impact of such disturbance on the dynamics of species distributions.

METHODS

Bird species distribution data

This work focused on 10 early-successional, open-habitat species with variable preferences for shrublike

habitats and dry, extensive farmlands in Mediterranean landscapes (Estrada et al. 2004): Red-legged Partridge (*Alectoris rufa*), Thekla Lark (*Galerida theklae*), Wood Lark (*Lullula arborea*), Tawny Pipit (*Anthus campestris*), Black-eared Wheatear (*Oenanthe hispanica*), Western Orphean Warbler (*Sylvia hortensis*), Southern Grey Shrike (*Lanius meridionalis*), Linnet (*Carduelis cannabina*), Ortolan Bunting (*Emberiza hortulana*), and Corn Bunting (*Emberiza calandra*). We selected these species because they have been associated with colonization processes in recently burned areas (Pons and Prodon 1996, Herrando et al. 2002). In addition, most of them appear to show significant species expansion at the regional level favored by fire (Estrada et al. 2004, Brotons et al. 2008).

Data on bird species were obtained from the two breeding bird atlas surveys carried out in Catalonia, Spain. The fieldwork from the first atlas (Atlas 1) was conducted between 1975 and 1983, with most of the data collected after 1980 (Muntaner et al. 1984), while the second atlas survey (Atlas 2) was carried out between 1999 and 2002 (Estrada et al. 2004). The two atlases are large-scale surveys of breeding birds covering the whole extent of Catalonia (~32 000 km²). Atlas 1 was surveyed using a coarse-grained scale of 10 × 10 km squares, whereas Atlas 2 comprised two approaches with two different grid resolutions: a coarse-grained resolution (10 × 10 km squares) matching the same grid system of Atlas 1 and a fine-grained resolution of 1 × 1 km squares. At this fine-grained scale, 3076 squares of 1 × 1 km were sampled by means of two-hour long censuses of species presence. These sampled squares were distributed in a stratified fashion to cover the main habitat types present within each of the main 10 × 10 km squares (Hirzel and Guisan 2002). In summary, we could obtain fine-grained bird data at 1-km resolution for the period 1999–2002 and coarse-grained bird distribution data at a 10-km resolution for both the 1999–2002 (Atlas 2) and 1975–1983 (Atlas 1) study periods.

Land-cover changes

Land-cover changes in Catalonia were described through the comparison of two land-cover maps roughly matching the time periods of the two bird atlases. The map matching Atlas 2 was derived from Landsat-TM remote sensing imagery from 1997 (Viñas and Baulies 1995) and also included burned areas from 1998 (Table 1). The map matching Atlas 1 was a modified version of the older land-cover map (available from the web site of Departament de Medi Ambient i Habitatge [DMAH]) from 1987 (Viñas and Baulies 1995).⁵ This map was backdated to 1980, assuming that between 1986 and 1980 the main landscape changes could be attributed to fire occurrence. In this way, we incorporated land-cover

⁵ (<http://mediambient.gencat.net/cat/inici.jsp>)

TABLE 1. Variables used in the models at the fine-grained scale (1 km) arranged into four main groups.

Group	Variable
Climatic	minimum temperature from January total precipitation
Topographic	slope proportion of sunny surface radiation
Land cover	nonvegetated bare: bare land, rocky outcrops, sparse vegetation, badlands, mineral extraction, and stream beds nonirrigated herbaceous crops nonirrigated fruit trees irrigated herbaceous crops irrigated fruit trees nonirrigated vineyards shrublands: maquis brushwood, mountain grassland, pastures, abandoned crops, burned areas from 1998, and areas of transition between forest and secondary vegetation coniferous forest: <i>Pinus halepensis</i> , <i>P. pinea</i> , <i>P. pinaster</i> , <i>P. nigra</i> , <i>P. sylvestris</i> , <i>P. uncinata</i> , and <i>Abies alba</i> deciduous forest: <i>Quercus faginea</i> , <i>Q. pubescens</i> , <i>Q. petraea</i> , <i>Q. robur</i> , <i>Fagus sylvatica</i> , <i>Populus</i> sp., <i>Salix</i> sp., <i>Castanea sativa</i> sclerophyllous forest: <i>Quercus ilex</i> , <i>Q. suber</i> alpine grasslands built-up areas: urban areas, industrial areas, and infrastructures sandy areas and beaches wetlands water
Miscellaneous	distance to rivers (log-transformed) distance to forest (log-transformed) distance to roads (log-transformed) linear distance to urban areas land number: number of land-cover classes within each 1 × 1 km square

information from 1980 only within the perimeters of fires that occurred between 1980 and 1986 (from *Mapa de cultivos y aprovechamientos [MCA] del Ministerio de Agricultura, Pesca y Alimentación*; MAPA 1980). Direct comparative analysis between MCA and the land-cover map from 1998 for the whole area would have produced larger errors due to the differences between the two sources in the procedures used to categorize vegetation cover. In addition, MCA lacks information from large areas, which renders this source of information unsuitable for the analyses. Land-cover type variables were finally derived from these maps by calculating the proportion of each land-cover type (minimum mapping unit of 0.36 ha) within each 1 × 1 km square (Table 1).

The comparison between both land-cover maps using the grid size of 1 × 1 km was interpreted as an approximation of the general trend in landscape changes in the study area. In the last two decades of the 20th century, the largest proportional change in land-cover types in Catalonia can be attributed to urbanization (increase of built-up areas by more than 60%), mainly along the coast. Forest and shrubland areas do not appear to have changed their overall extent in a striking way over the whole study area (decrease of ~3% and increase of 5%, respectively). However, this overall stability hides a remarkable proportion of cells (~80%) in which either forest changed to shrub or shrub to forest, indicating that both land covers in the study area are currently under a dynamic equilibrium (Picket and White 1985). Spatial

patterns of change in forest and shrubland are largely influenced by land abandonment (shrub to forest transitions) and especially by fire (forest to shrub transitions; Díaz-Delgado et al. 2004).

Data on wildfire occurrence

We derived information on fire occurrence during the time period between the two atlases from the fire perimeters provided by Departament Medi Ambient i Habitatge (DMAH; see footnote 5) for the period 1986–1999 and by Centre de Recerca Ecològica i Aplicacions Forestals (CREAF) for fires that occurred between 1980 and 1985 (Fig. 1), with a minimum mapping unit of 0.09 ha. Fire perimeters identify areas that were affected by fire a given year, which allows for describing the spatial and temporal pattern of fire occurrence (Díaz-Delgado et al. 2004). Fire perimeters were used to record fire-related variables at the coarse-grained scale (10 km). These variables include: (1) the proportion of forest and shrubland affected by fire from 1980 onward, (2) the total burned area, and (3) the area burned more than once (i.e., fire recurrence). The proportions of forest and shrubland affected by fire between 1980 and 1999 were calculated considering fires from different time periods: period 1 (p1) from 1980 to 1987 (110 000 ha affected by fire), period 2 (p2) from 1988 to 1993 (15 000 ha burned), and period 3 (p3) from 1994 to 1999 (85 000 ha burned). This temporal partitioning of fire disturbance may allow us to identify likely time lags in species response to fire. In total, fire affected >130 000 ha of forests and nearly

80 000 ha of shrublands in the last 20 years of the 20th century.

Species distribution modeling and projection to past land-cover conditions

We developed species distribution models using a modified version of BIOMOD (Thuiller 2003) implemented within the R statistical software (R Development Core Team 2007). BIOMOD allows the development of six species distribution models with different statistical methods: General Linear Model (GLM), Generalized Additive Model (GAM), Generalized Boosting Model (GBM), Breiman and Cutler's random forest (Random Forest), Mixture Discriminant Analysis (MDA), and Multivariate Adaptive Regression Splines (MARS). Predictor variables included in the models were climate, topography, land-cover classes, and other miscellaneous variables calculated separately for the two time periods of the bird atlases (Table 1). Only land-cover changes were considered when projecting the models back to past conditions. As climatic data are originated from 15–20 years of average data (Ninyerola et al. 2000), we assumed that climate has not significantly changed between Atlas 1 and Atlas 2. The probability of occurrence derived from model projections was considered in terms of the habitat suitability index (HSI) for the species.

The modeling process to predict changes in bird distributions comprises four steps (Fig. 2):

Step 1.—We performed model calibration using bird species data available from Atlas 2 at the fine-grained scale ($n = 3076$). Model calibration consists in the estimation of the parameters determining the relationships between bird species and environmental variables. We randomly partitioned the data set, using 70% of the data for model calibration and the remaining 30% for model evaluation of the predictive performance under current conditions. We evaluated the model's accuracy using the area under the curve (AUC) of receiver operating characteristics (ROC). This measures ranges from 0.5 to 1 with larger values as model performance increase (Fielding and Bell 1997). Step 1 allowed identifying models with higher predictive accuracy under current conditions.

Step 2.—Using all the modeling techniques for each of the species, we projected the estimated relationship from calibration on the environmental variables used, which were available on the total extent of Catalonia for the conditions in Atlas 2. In the same way, we projected the models back to the landscape conditions prevailing 20 years ago (Atlas 1). Model projection consists in the transferability in space (for conditions in Atlas 2) and in time (for conditions prevailing in Atlas 1) of the estimated species–environment relationship to generate predictions of species distributions. Step 2 allows for the development of habitat suitability maps of the whole study area for 1980 and 1999.

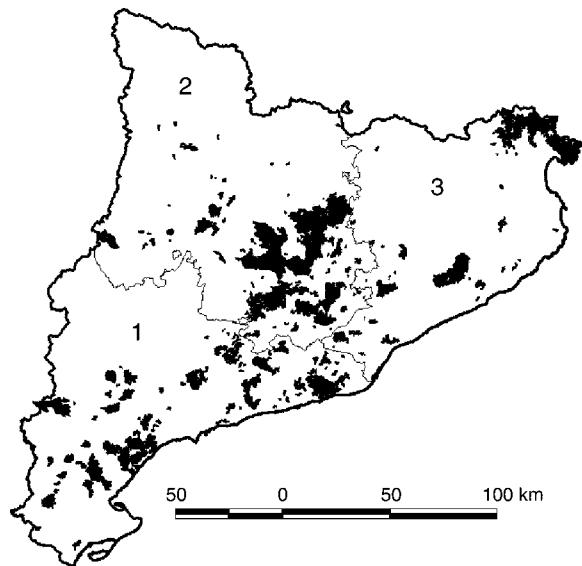


FIG. 1. Fire perimeters that occurred between 1980 and 1998 (black polygons) and a representation of three defined regions in Catalonia, Spain (black thin line, delimiting regions 1, 2, and 3). These regions differ broadly in climatic patterns and dominant forest species, as shown in Table 2 (DGMN 1994, Burriel et al. 2000).

Since projections of species distributions under different time scenarios can be widely variable between different model techniques (Thuiller 2003, Thuiller 2004, Pearson et al. 2006), we accounted for the variability among back-projections derived from the modeling techniques used. To obtain more robust projections on the past scenario, we calculated for each species separately two ensemble forecasts (*sensu* Araújo and New 2007). The first ensemble forecast was calculated by averaging all model projections, assigning the same importance to all model techniques (average projection from here onward). The second ensemble forecast was based on a multivariate analysis approach (principal components analyses [PCA]) to reduce the amount of variation among back-projections for each species (Westerhuis et al. 1998, Thuiller 2004). The first axis of PCA (PC1) captured the largest part of variation among projections that were ranked according to higher correlation with PC1. The four models most positively correlated with PC1 were averaged to deal with the dominant trend in model projections, capturing the shared information among them (PCA consensus from here onward).

Step 3.—We aggregated single and ensemble forecast back-projections by means of averaging the HSI for all fine-grained squares (1×1 km) within each coarse-grained square (10×10 km). This is a required step to obtain HSI resolution from model back-projections (fine-grained scale) matching field observation data from Atlas 1, only available at the coarse-grained scale (10 km).

Step 4.—We evaluated the aggregated back-projections (single and ensemble forecasts) with observed bird

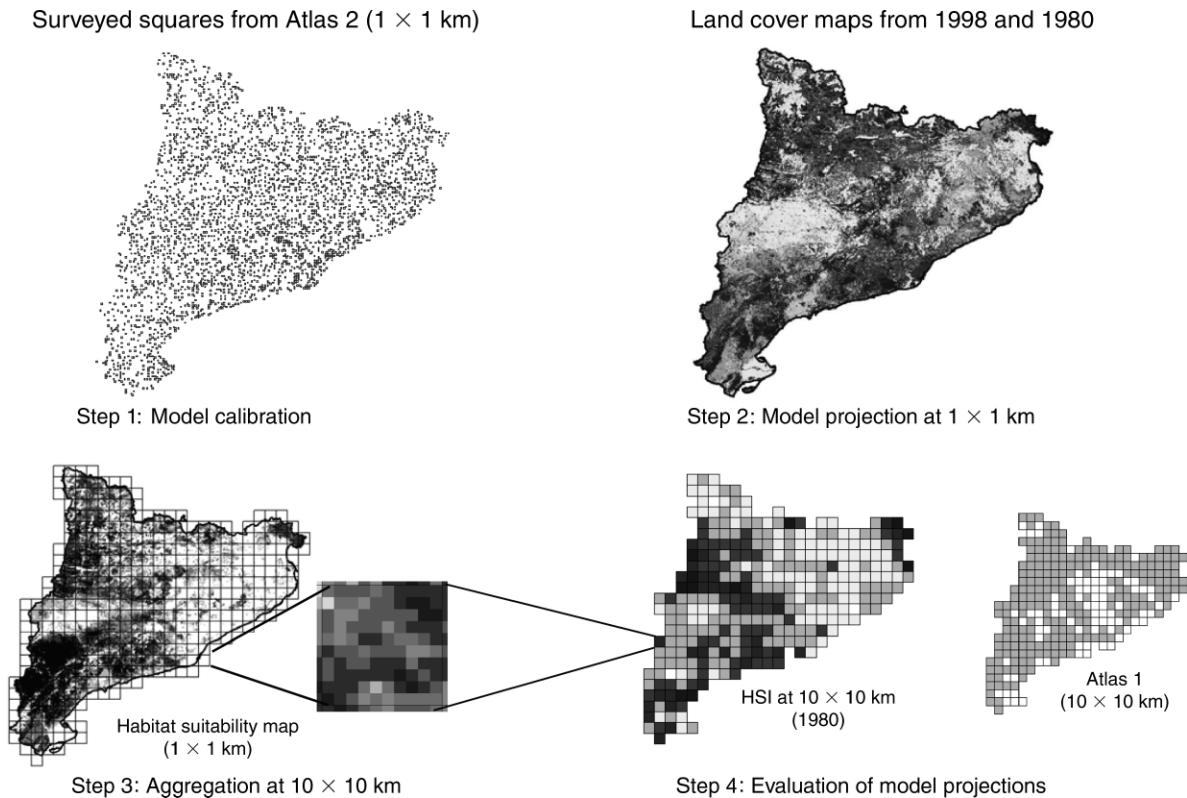


FIG. 2. A schematic representation of the steps followed to develop species distribution models for 10 open-habitat bird species. In Step 1, model calibration was performed with data from the second Catalan Breeding Bird Atlas (Estrada et al. 2004). In Step 2, the models were projected on land-cover maps from 1980 and 1998, yielding habitat suitability maps at 1×1 km (levels of shading represent specific habitat types). In Step 3, the map from 1980 was aggregated at 10×10 km. In Step 4, evaluations of model projections were performed with empirical data from the first Catalan Breeding Bird Atlas, available at 10×10 km (Muntaner et al. 1984). As an example, we show the habitat suitability maps of *Carduelis cannabina* (Steps 3 and 4), showing dark gray for suitable habitats. See *Methods: Species distribution modeling and projection to past land-cover conditions* for further details.

distribution data from Atlas 1. Given the differences in sampling effort among the grid squares from Atlas 1, we evaluated the model projections against field-observed data, weighting by the sampling effort available for each 10×10 km square (see Estrada et al. [2004] for further details). Evaluations were performed by means of the AUC statistic (function *somers2*; package *Hmisc*, R-software).

Land-cover patterns in Catalonia have been to a large extent shaped by fire; thus it might be advisable to include information from the disturbance process explicitly as a predictor in the modeling (Guisan and Zimmermann 2000). Unfortunately, there was no detailed information available on fire occurrence patterns for the 20 years prior to 1980. Since we could not include fire occurrence explicitly in the models as predictive variables, we considered fire only when analyzing the species distribution dynamics between both atlases and not explicitly within species distribution models.

Analyses of bird distribution dynamics

We performed hierarchical General Linear Models (HGLM) to assess progressively the potential role of

different factors explaining the colonization and extinction dynamics of observed species distributions between Atlas 1 and Atlas 2 at the coarse-grained scale. HGLM consisted in the development of three different hierarchical models. In this way, we evaluated the residual deviance explained by the successive addition of explanatory factors for which a hierarchy has been previously defined (McCullagh and Nelder 1989).

Model 1.—We included differences in sampling effort between both atlases in the model; likely differences in sampling effort when comparing data from the two atlases at the coarse-grained scale could mask real distribution changes if it was not considered in the analysis (Link and Sauer 1994, Donald and Fuller 1998):

$$\text{SDD} \sim \Delta \text{ Sampling Effort} \quad (1)$$

where SDD indicates species distribution dynamics. We analyzed separately colonization (absence in Atlas 1 and presence in Atlas 2) and extinction events (absence in Atlas 2 and presence in Atlas 1). Both processes were considered only if $>5\%$ of the 10×10 km squares showed either colonization or local extinction events. The change in sampling effort between Atlas 1 and Atlas

TABLE 2. Characterization of the three regions considered in the study in Catalonia, Spain, according to dominant forest species, mean annual temperature (T), and mean annual precipitation (P).

Region	Mean annual T (°C)	Mean annual P (mm)	Dominant forest species
1	14.41	533.91	<i>Pinus halepensis</i> , <i>Quercus ilex</i> , <i>Pinus nigra</i>
2	10.00	810.42	<i>Pinus sylvestris</i> , <i>Pinus nigra</i> , <i>Quercus ilex</i> , <i>Quercus humilis</i>
3	13.02	841.99	<i>Quercus ilex</i> , <i>Quercus humilis</i> , <i>Pinus sylvestris</i> , <i>Quercus suber</i>

Note: Data are from DGMN (1994) and Burriel et al. (2000).

2 (Δ Sampling Effort) was forced into the model, even if it was not significant.

Model 2.—We evaluated if changes in the habitat suitability index (Δ HSI) accounted for the residual deviance left unexplained by model 1. For this analysis, we used the HSI derived from the species distribution modeling, choosing the most accurate projection after performing the evaluation of single and ensemble forecasts:

$$\text{SDD} \sim \Delta \text{ Sampling Effort} + \Delta \text{HSI} \quad (2)$$

where the change in the habitat suitability index (Δ HSI) was calculated from species distribution models.

Model 3.—We evaluated here whether, in addition to changes in habitat suitability derived from land-cover shifts, fire impact descriptors contributed to explain the residual deviance. Here we also included a regional factor to account for potential effects of spatial variation in the dynamics of species distributions within the study area. With this aim, we defined three different regions in Catalonia differing broadly in climatic patterns and dominant forest species (derived from Direcció General del Medi Natural, DGMN 1994, Burriel et al. 2000) (Fig. 1, Table 2). As shown in other works, burned areas show spatial variability in species composition according to the regional context (Brotons et al. 2005). For this reason, we also evaluated at this stage whether species exhibit contrasting responses to fire depending where fire occurred (region and total burned area interaction). We selected the fire descriptors and region variables according to their statistical significance using forward regression:

$$\begin{aligned} \text{SDD} \sim & \Delta \text{ Sampling Effort} + \Delta \text{HSI} + \text{Fire} + \text{Region} \\ & + \text{Region} \times \text{Fire} \end{aligned} \quad (3)$$

where Fire represents fire variables describing fire impact between the study periods and Region corresponds to the three different bioclimatic regions into which Catalonia has been divided.

RESULTS

Species distribution models and projection to past land-cover conditions

Evaluation of model calibrations conducted on fine-grained bird atlas data, using 30% of the data set randomly selected, showed differences among different

species distribution modeling techniques and species in their potential to predict current bird species distributions (area under the curve [AUC] values between 0.66 and 0.93 for the different species and the six modeling approaches). Overall, the Random Forest method appeared as the best predictive model for current conditions (average values for all species: AUC = 0.84) while Mixture Discriminant Analysis (MDA), although having a relatively good predictive accuracy, was the least accurate (average AUC = 0.78; see Appendix).

Once models had been obtained (step 1), they were back-projected to the land-cover conditions prevailing in the early 1980s. Principal components analyses (PCA) performed on model projections to derive PCA consensus (ensemble forecast) showed rather good agreement among the back-projections obtained from the different modeling techniques. The first axis from the PCA explained between 91% (Corn Bunting) and 53% (Ortolan Bunting) of the variability between model back-projections. The four models showing the highest correlation with PC1 were in all cases the Generalized Additive Model (GAM), the Generalized Boosting Model (GBM), the General Linear Model (GLM), and Random Forest (RF), except for Southern Grey Shrike, for which Multivariate Adaptive Regression Splines (MARS) replaced GAM.

After aggregating back-projections to the coarse scale (10 km), we evaluated single and ensemble forecast projections with field data from Atlas 1 (see evaluation in Appendix). This evaluation process showed relatively high accuracy in the back-projections for all species (average AUC = 0.75). We found that all models predicted overall species distributions fairly similar (AUC values between 0.72 and 0.77), however the back-projection derived from PCA consensus tended to be slightly better (average AUC = 0.77) than single model techniques (average AUC = 0.75; see evaluation results in the Appendix).

Species distribution dynamics

Analyses of changes in species distributions at the coarse scale were performed using changes in habitat suitability maps derived from PCA consensus projections. Comparison of habitat suitability index (HSI) maps generated for the two time periods over the whole extent of Catalonia revealed a general decrease in

TABLE 3. Trends of species distribution and colonization and extinction dynamics between the Catalan Breeding Bird Atlas 1 and Atlas 2 at the coarse-grained scale (10 km), and global change of the habitat suitability index (HSI) between both atlases derived from species distribution modeling at the fine-grained scale (1 km).

Bird species	Abbreviated name	Distribution trends†	Colonization‡ (% of 10 × 10 km squares)	Extinction‡ (% of 10 × 10 km squares)	Global change of HSI (%)
<i>Alectoris rufa</i>	<i>A. rufa</i>	0	7	2	-19.72
<i>Galerida theklae</i>	<i>G. thek</i>	44	19	6	-22.01
<i>Lullula arborea</i>	<i>L. arbo</i>	20	25	8	-1.39
<i>Anthus campestris</i>	<i>A. camp</i>	88	28	9	-17.24
<i>Oenanthe hispanica</i>	<i>O. hisp</i>	-20	9	3	-20.4
<i>Sylvia hortensis</i>	<i>S. hort</i>	34	25	8	-20.77
<i>Lanius meridionalis</i>	<i>L. meri</i>	-26	17	6	-5.18
<i>Carduelis cannabina</i>	<i>C. cann</i>	0	21	7	-22.53
<i>Emberiza hortulana</i>	<i>E. hort</i>	82	24	8	-11.97
<i>Emberiza calandra</i>	<i>E. cala</i>	-5	7	2	-13.22

Notes: Information on the percentage of squares showing an increase and decrease in the HSI, mean, and standard deviation (mean \pm SD) is also given.

† Distribution trends are given for the whole of Catalonia, even for the squares where sampling effort could not be calculated.

‡ Colonization and extinction rates are only given for the squares where sampling effort was calculated, which were considered in the analyses of this study.

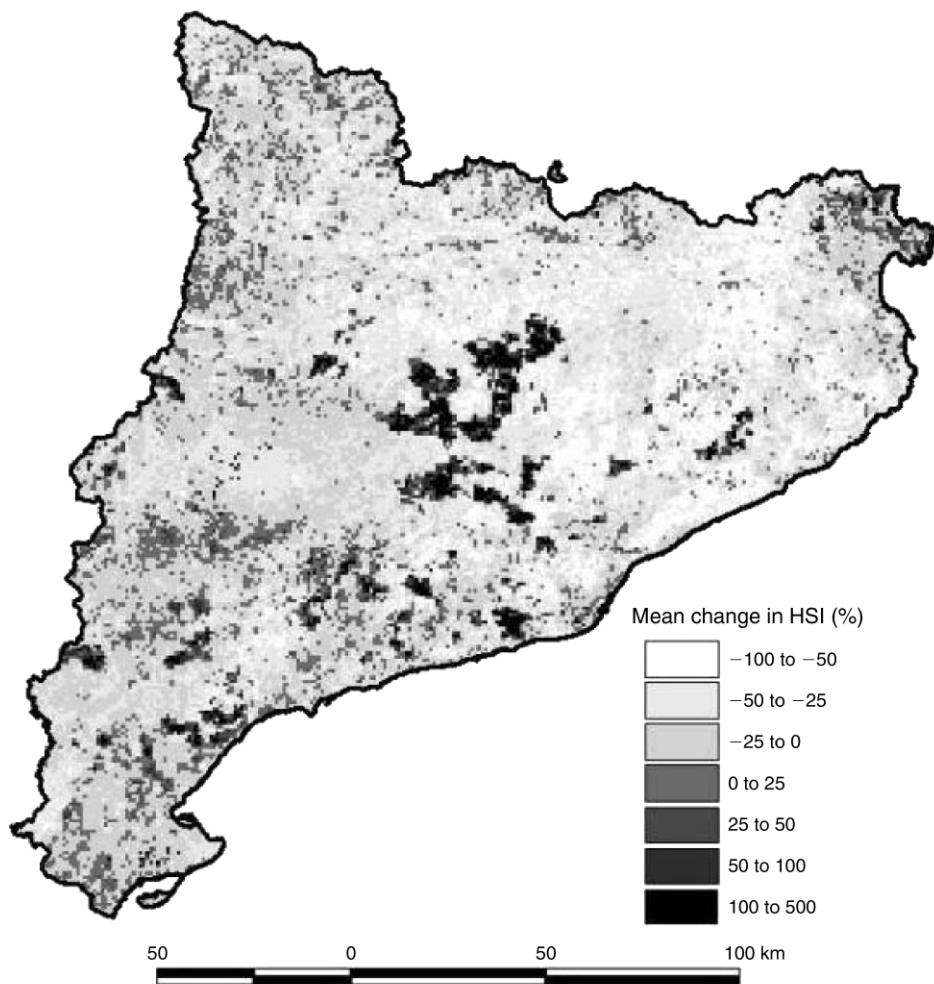


FIG. 3. Mean changes (%) in the habitat suitability index (HSI) between ca. 1980 and ca. 2000, averaged for all studied species. It was calculated in relative percentage for each species to consider comparable changes in the HSI for abundant and rare species.

TABLE 3. Extended.

HSI decrease (at 1 × 1 km)		HSI increase (at 1 × 1 km)	
Grid cells (%)	Mean ± SD	Grid cells (%)	Mean ± SD
78	-0.08 ± 0.06	21	0.05 ± 0.05
82	-0.04 ± 0.05	15	0.05 ± 0.07
56	-0.06 ± 0.06	43	0.07 ± 0.07
78	-0.02 ± 0.02	19	0.03 ± 0.05
80	-0.05 ± 0.07	16	0.07 ± 0.1
77	-0.02 ± 0.03	20	0.03 ± 0.03
68	-0.02 ± 0.02	29	0.02 ± 0.03
83	-0.12 ± 0.1	16	0.05 ± 0.06
74	-0.02 ± 0.02	22	0.05 ± 0.06
73	-0.08 ± 0.07	25	0.05 ± 0.06

habitat suitability values for our focal species (Table 3, Fig. 3).

After controlling for the difference in sampling effort between Atlas 1 and Atlas 2, the role of changes in HSI derived from land-cover changes and fire descriptors to determine species distribution dynamics was found to be highly variable among species. The HGLM procedure indicated that for some species, such as Red-legged Partridge, Corn Bunting, and Western Orphean Warbler, the colonization process was not related to either ΔHSI or fire (Table 4). Changes in HSI were only weak predictors of colonization dynamics for four species, whereas for six of the 10 species analyzed, fire descriptors explained a larger proportion of the colonization dynamics deviance than changes in HSI (Fig. 4a). For all these species except for the Linnet, burned area (forest or shrubland) from the first time period (from 1980 to 1987) was significant, suggesting long-term

species responses to fire impact. However, more recent fires (period 3) appeared also to be important for species like the Black-eared Wheatear and Linnet (Table 4). In addition, the interaction between total burned area and regions was found to be significant for two of our focal species, the Wood Lark and the Ortolan Bunting, indicating that these species also exhibited a significant response to fire impact; however it varied depending on the region where fire occurred (Table 4). Eventually, the contribution of regional variability for four of the species analyzed (Fig. 4a) when explaining colonization processes suggests an important role of spatial components.

Extinction dynamics were poorly related to the factors included in our hierarchical analytical approach. Changes in the HSI and the impact of fires were weak significant predictors of extinction changes for only two species each (Fig. 4b), suggesting that factors other than changes in land cover or fire impact are likely to be more related to range contractions in our set of early successional bird species.

DISCUSSION

At large spatial scales, species distribution models relying on climatic, topographic, and land-cover data are useful tools to predict general patterns of species distributions (Guisan and Zimmermann 2000). However, projecting species distribution models in time has been challenged due to the limitations associated with these modeling approaches (Guisan and Thuiller 2005, Dormann 2007) and to the many challenges ahead in our quest to understand how the species respond to environmental changes. Regardless of obtaining accurate and robust predictions using ensemble forecasts of different modeling techniques, model projections on new scenarios based in land-cover data were not reliable enough to explain the dynamics of species distributions

TABLE 4. Hierarchical General Linear Models for colonization dynamics.

Species	Model 1		Model 2		Model 3						
	Sampling effort		ΔHSI		Fire		Region		Region × Fire		
	P	Coef.	P	Coef.	Variables†	P	Coef.	P	Coef.	P	Coef.
<i>A. rufa</i>	0.122	0.007									
<i>G. thek</i>	0.012	0.008	0.002	-13.04	forest p1	0.016	0.007	<0.001	-1.300		
					forest p2	0.023	0.047				
					total burned	0.015	0.002				
<i>L. arbo</i>	0.204	0.004	<0.001	-10.25	total burned	0.057	0.006	<0.001	0.853	0.027	-0.003
<i>A. camp</i>	0.002	0.010			forest p1	0.023	0.005	0.015	-0.430		
					shrub p3	0.035	0.009				
<i>O. hisp</i>	0.036	0.009	0.049	-6.08	forest p1	0.003	0.007				
					forest p3	<0.001	0.009				
<i>S. hort</i>	0.003	0.009									
<i>L. meri</i>	0.113	0.005			shrub p1	0.043	0.004				
<i>C. cann</i>	0.010	0.008	0.002	-6.54	shrub p3	<0.001	0.021				
<i>E. hort</i>	0.008	0.008	0.026	13.49	total burned	0.001	0.004	0.028	-0.437	0.007	-0.004
<i>E. cala</i>	0.538	0.003									

Notes: Only significant terms were included, except sampling effort that was forced into the model. HSI is the habitat suitability index. Significance (P) and coefficients (Coef.) from each model in the analyses are shown. Complete names of the species are given in Table 3.

† Fire variables included in the analyses were forest and shrub area burned in different time periods, total burned area, and area burned more than once (i.e., recurrence). Period 1 (p1) is 1980–1987; period 2 (p2) is 1988–1993; period 3 (p3) is 1994–1999.

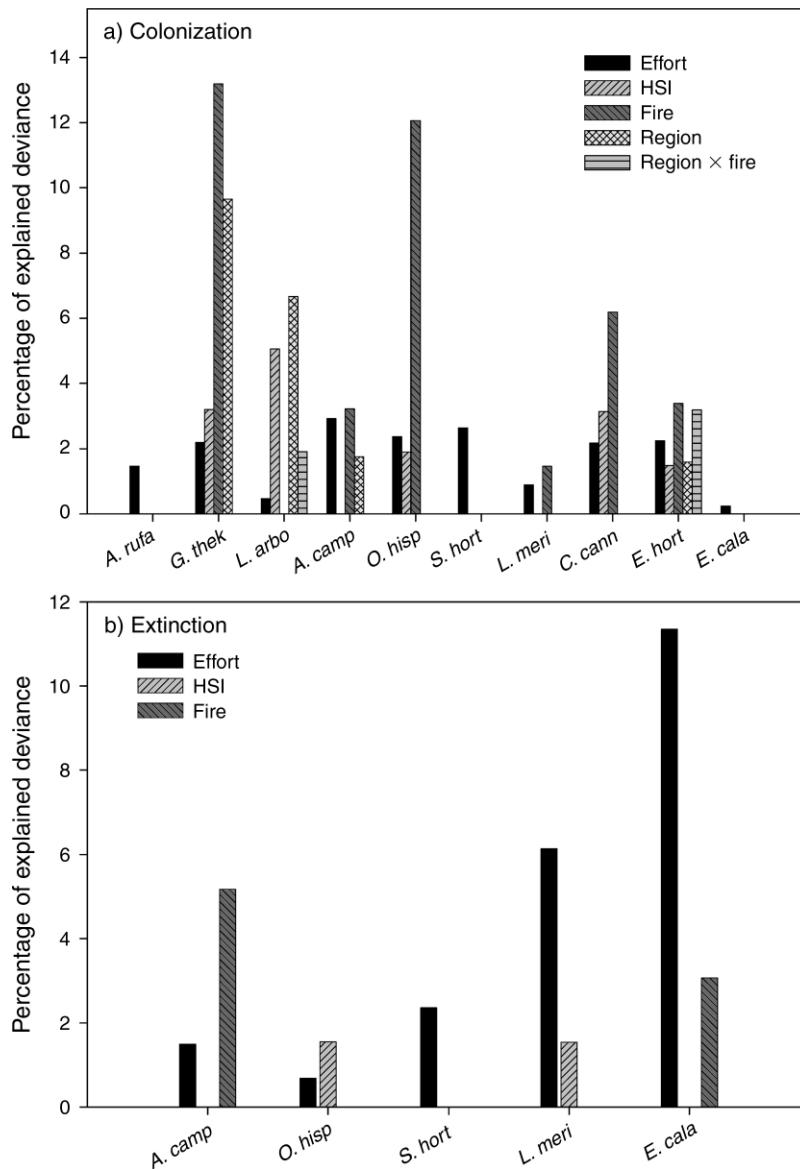


FIG. 4. Percentage of explained deviance from (a) colonization dynamics and (b) extinction dynamics based on performing the hierarchical General Linear Model procedure. Analyses were only performed when colonization and extinction dynamics occurred in $>5\%$ of the coarse-grained scale (10 km). Predictor variables were Effort (changes in sampling effort between both atlases), HSI (changes in the habitat suitability index derived from the principal components analysis consensus of species distribution models; see *Methods: Species distribution modeling and projection to past land-cover conditions*), Fire (a set of variables gathered from fire occurrence), Region (differing broadly in climatic patterns and dominant forest species), and the interaction between Region and Fire. Complete names of the bird species are given in Table 3.

in this changing landscape. Colonization and extinction dynamics of the species studied appeared to be a more complex process, not really well captured by changes in land-cover patterns.

Since the convenience of using the area under the curve (AUC) to evaluate the accuracy of distribution models is doubtful (McPherson et al. 2004, Lobo et al. 2007), the assessment of the predictive ability of changes in the habitat suitability index (HSI) when explaining colonization and extinction dynamics constitutes an

alternative approach for the evaluation of model projections. In this context, we demonstrate that large AUC values do not guarantee reliability in our capability of predicting where changes in species distributions took place (i.e., local colonization and extinction).

As we have shown, prediction of species distribution dynamics requires additional information not considered in land-cover-based habitat models. Our general poor ability to predict distributional changes suggests that capturing the processes driving distribution dynam-

ics is a complex task. Indeed, causal processes underpinning species distribution dynamics, such as disturbance, appear to contribute to a better understanding of the colonization dynamics for some species than changes in the estimated HSI. Fire disturbance, in addition to inducing land-cover changes favoring local increases in the HSI (Fig. 3 and Fig. 1 for comparison), exerted a positive role on colonization dynamics for seven of the 10 studied species when considering fire occurrence from a long time period (Table 4). For all these species, information provided by a more comprehensive inclusion of fire impact descriptors increased our capability of understanding changes in species distribution, colonization in our case. For species like the Thekla Lark, Wood Lark, and Black-eared Wheatear, fire impact may counteract the general decrease in the HSI estimated from land-cover changes and eventually lead to species expansion (Table 4). According to our results indicating a positive effect of old fires (15–20 years old) on colonization patterns for some of these species, fire effects on distribution dynamics may be extended over long periods of time at large spatial scales.

When explicitly considering fire descriptors in our model, we are including important information lacking in simpler land-cover data. These descriptors allowed differentiating burned areas from other open-shrub unburned habitats, which may be less suited for early successional species, thus leading to an increase in their explanatory power. For instance, burned areas favor open-habitat heterogeneity (Lloret et al. 2002), contributing to the maintenance of different open and shrub-like habitats through time and thus favoring colonization and species persistence at the landscape scale (Brotons et al. 2005). However, the positive effect of fire on colonization could have been enhanced to some extent by the general decline in habitat suitability in Catalonia during the study period, magnifying immigration of individuals from habitats of decreasing suitability into new open-habitat patches. Although population data on the dynamics of species such as the Ortolan Bunting are line with this hypothesis (Dale et al. 2005; L. Brotons, *unpublished data*), further information at the population level would be needed to obtain confirmation of the magnitude of this effect in Mediterranean landscapes affected by fire.

In addition to the need for considering processes behind changes in species distributions, drawbacks of habitat modeling approaches increase the lack of confidence in model predictions (Austin 2002, Araújo and Guisan 2006, Dormann 2007, Thuiller et al. 2008). One of the main drawbacks of these kinds of models appears to be that model projections represent just the area in which a species could potentially inhabit. However, the potential distribution of a species may not necessarily match the realized distribution of that species under a new scenario (Araújo and Guisan 2006). One of the main reasons behind the mismatches between potential and realized distributions is likely to be the

influence of spatially related processes of the species' biology, such as dispersal limitations or historical factors (Guisan and Thuiller 2005). Indeed, dispersal constraints have been found to be a major factor behind bird colonization in recently burned areas by favoring colonization of areas nearby population sources (Brotons et al. 2005). Dispersal constraints are further exacerbated by the likely lack of permeability in the landscape (Wiens 2001). Hence, species movements over an area in response to land-cover changes will be also largely influenced by the habitat context (Brotons et al. 2005, Vallecillo et al. 2008). The large contribution of regional effects explaining variability in colonization dynamics for some species (i.e., Thekla Lark and Wood Lark), suggest that important spatially dependent factors were not explicitly included in this study. In addition, the Wood Lark and Ortolan Bunting showed variable colonization dynamics of burned areas depending on the region where fire occurred. This spatial variation in the influence of the species response to fire impact is likely to be also related to dispersal constraints (Brotons et al. 2005).

Other factors favoring a possible mismatch between potential and realized distribution are the likely time lags of the species response to environmental changes (Austin 2002). Bird extinctions following habitat loss typically take place after prolonged time periods (Diamond 1972, Brooks et al. 1999, Ambrosini et al. 2002) or at smaller spatial scales than colonization events (Sirami et al. 2008), showing that nonequilibrium conditions between species distributions and the environment may be common in nature. Therefore, we are violating one of the main assumptions of species distribution models: the equilibrium conditions between the species and the environment (Austin 2002). In this context, net habitat loss for our focal species, which was mainly related to the conversion of shrubland into forest and to decreases in nonirrigated herbaceous crops, could lead to a contraction of the species distribution range in future years if this trend is not compensated by newly appearing habitat patches generated by fire or other disturbances. Therefore, temporal and spatial scales of this study might be not adequate enough to allow a detailed assessment of factors behind species extinctions.

CONCLUSION

We have shown here that the successful evaluation of model projections with empirical data for two time periods does not necessarily involve confidence in the predictive ability of distribution dynamics under the new (in our case past) scenario. Consideration of processes behind changes when developing species distribution models may improve model performance. However, failing to capture the right processes leading to changes in species distributions may invalidate the interpretation of distribution model projections. In the context of global change, a better understanding of the ecological processes inducing changes in species distributions is

crucial and should be explicitly included when developing species distribution models aimed at predicting future species response to a changing environment.

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LITERATURE CITED

- Almeida, J., M. Díaz-Esteban, B. Hallman, F. Petretti, R. Prodon, and G. Rocamora. 1997. Mediterranean forest, shrubland and rocky habitats. Page 239 in G. M. Tucker and M. I. Evans, editors. *Habitats for birds in Europe: a conservation strategy for the wider environment*. BirdLife International, Cambridge, UK.
- Ambrosini, R., A. M. Bolzern, L. Canova, S. Arieni, A. P. Møller, and N. Saino. 2002. The distribution and colony size of barn swallows in relation to agricultural land use. *Journal of Applied Ecology* 39:524–534.
- Araújo, M. B., and A. Guisan. 2006. Five (or so) challenges for species distribution modeling. *Journal of Biogeography* 33: 1677–1688.
- Araújo, M. B., and M. New. 2007. Ensemble forecasting of species distributions. *Trends in Ecology and Evolution* 22: 42–47.
- Araújo, M. B., R. G. Pearson, W. Thuiller, and M. Erhard. 2005. Validation of species–climate impact models under climate change. *Global Change Biology* 11:1504–1513.
- Austin, M. P. 2002. Spatial prediction of species distribution: an interface between ecological theory and statistical modeling. *Ecological Modeling* 157:101–118.
- Beaumont, L. J., A. J. Pitman, M. Poulsen, and L. Hughes. 2007. Where will species go? Incorporating new advances in climate modeling into projections of species distributions. *Global Change Biology* 13:1368–1385.
- Bradstock, R. A., M. Bedward, A. M. Gill, and J. S. Cohn. 2005. Which mosaic? A landscape ecological approach for evaluating interactions between fire regimes, habitat and animals. *Wildlife Research* 32:409–423.
- Brawn, J. D., S. K. Robinson, and F. R. Thompson. 2001. The role of disturbance in the ecology and conservation of birds. *Annual Review Ecology and Systematics* 32:251–276.
- Broennimann, O., W. Thuiller, G. O. Hughes, G. F. Midgley, J. R. M. Alkamade, and A. Guisan. 2006. Do geographic distribution, niche property and life form explain plants' vulnerability to global change? *Global Change Biology* 12: 1079–1093.
- Brooks, M. B., and A. Balmford. 1999. Deforestation and bird extinctions in the Atlantic forest. *Animal Conservation* 2: 211–222.
- Brotons, L., S. Herrando, and P. Pons. 2008. Wildfires and the expansion of threatened farmland birds: the Ortolan Bunting (*Emberiza hortulana*) in Mediterranean landscapes. *Journal of Applied Ecology*, 45:1059–1066.
- Brotons, L., S. Mañosa, and J. Estrada. 2004. Modeling the effects of irrigation schemes on the distribution of steppe birds in Mediterranean farmland. *Biodiversity and Conservation* 13:1039–1058.
- Brotons, L., P. Pons, and S. Herrando. 2005. Colonization of dynamic Mediterranean landscapes: where do birds come from after fire? *Journal of Biogeography* 32:789–798.
- Burriel, J. A., C. Gracia, J. J. Ibáñez, T. Mata, and J. Vayreda. 2000–2004. *Inventari Ecològic i Forestal de Catalunya (IEFC)*. CREAf, Bellaterra. ISBN de la sèrie: 84-931323-0-6.
- Chatfield, C. 1995. Model uncertainty, data mining and statistical inference. *Journal of the Royal Statistical Society, Series A* 158:419–466.
- Dale, S., A. Lunde, and O. Steifetten. 2005. Longer breeding dispersal than natal dispersal in the Ortolan Bunting. *Behavioral Ecology* 16:20–24.
- DGMN (Direcció General del Medi Natural). 1994. *Plà General de Política Forestal*. DARP: Departament d'Agricultura, Ramaderia i Pesca, Barcelona, Spain.
- Diamond, J. M. 1972. Biogeographic kinetics: estimation of relaxation times for avifaunas of Southwest Pacific Islands. *Proceedings of the National Academy of Sciences (USA)* 69: 3199–3203.
- Díaz-Delgado, R., F. Lloret, and X. Pons. 2004. Statistical analysis of fire frequency models for Catalonia (NE Spain, 1975–1998) based on fire scar maps from Landsat MSS data. *International Journal of Wildland Fire* 13:89–99.
- Donald, P. F., and R. J. Fuller. 1998. Ornithological atlas data: a review of uses and limitations. *Bird Study* 45:129–145.
- Dormann, C. F. 2007. Promising the future? Global change projections of species distribution. *Basic and Applied Ecology* 8:387–397.
- Elith, J., et al. 2006. Novel methods improve prediction of species' distributions from occurrence data. *Ecography* 29: 129–151.
- Estrada, J., V. Pedrocchi, L. Brotons, and S. Herrando. 2004. *Catalan breeding bird atlas (1999–2002)*. Institut Català d'Ornitologia. Lynx, Barcelona, Spain.
- Fielding, A. H., and J. F. Bell. 1997. A review of methods for the assessment of prediction errors in conservation presence-absence models. *Environmental Conservation* 24:38–49.
- Guisan, A., and W. Thuiller. 2005. Predicting species distribution: offering more than simple habitat models. *Ecology Letters* 8:993–1009.
- Guisan, A., and N. E. Zimmermann. 2000. Predictive habitat distribution models in ecology. *Ecological Modeling* 135: 147–186.
- Heikkinen, R. K., M. Luoto, M. B. Araújo, R. Virkkala, W. Thuiller, and M. T. Sykes. 2006. Methods and uncertainties in bioclimatic envelope modeling under climate change. *Progress in Physical Geography* 30:751–777.
- Herrando, S., L. Brotons, R. Del Amo, and S. Llacuna. 2002. Bird community succession after fire in a dry Mediterranean shrubland. *Ardea* 90:303–310.
- Herrando, S., L. Brotons, and S. Llacuna. 2003. Does fire increase the spatial heterogeneity of bird communities in Mediterranean landscapes? *Ibis* 145:307–317.
- Hirzel, A., and A. Guisan. 2002. Which is the optimal sampling strategy for habitat suitability modeling. *Ecological Modeling* 157:331–341.
- Link, W. A., and J. R. Sauer. 1994. Estimating equations estimates of trend. *Bird Populations* 2:23–32.
- Lloret, F., E. Calvo, X. Pons, and R. Díaz-Delgado. 2002. Wildfires and landscape patterns in the Eastern Iberian Peninsula. *Landscape Ecology* 17:745–759.
- Lobo, J. M., A. Jiménez-Valverde, and R. Real. 2007. AUC: misleading measure of the performance of predictive distribution models. *Global Ecology and Biogeography* 17(2):145–151.

- MAPA (Ministerio de Agricultura, Pesca y Alimentación). 1980. Mapa de cultivos y aprovechamientos 1:50 000. Madrid, Spain.
- McCullagh, P., and J. A. Nelder. 1989. Generalized linear models. Chapman Hall, London, UK.
- McPherson, J. M., W. Jetz, and D. J. Rogers. 2004. The effects of species' range sizes on the accuracy of distribution models: ecological phenomenon or statistical artifacts? *Journal of Applied Ecology* 41:811–823.
- Moreira, F., P. G. Ferreira, F. C. Rego, and S. Bunting. 2001. Landscape changes and breeding bird assemblages in northwestern Portugal: the role of fire. *Landscape Ecology* 16:175–187.
- Moreno, J. M., and W. C. Oechel, editors. 1994. The role of fire in Mediterranean-type ecosystems. *Ecological Studies* No. 107. Springer-Verlag, New York, New York, USA.
- Muntaner, J., X. Ferrer, and A. Martínez-Vilalta. 1984. *Atlas dels ocells nidificants de Catalunya i Andorra*. Ketres, Barcelona, Spain.
- Ninyerola, M., X. Pons, and J. M. Roure. 2000. A methodological approach of climatological modeling of air temperature and precipitation through GIS techniques. *International Journal of Climatology* 20:1823–1841.
- Pearson, R. G., W. Thuiller, M. B. Araújo, E. Martínez-Mayer, L. Brotons, C. McClean, L. Miles, P. Segurado, T. P. Dawson, and D. C. Lees. 2006. Model-based uncertainty in species range prediction. *Journal of Biogeography* 33:1704–1711.
- Pickett, S. T. A., and P. S. White. 1985. *The ecology of natural disturbance and patch dynamics*. Academic Press, Orlando, Florida, USA.
- Pons, P., and R. Prodon. 1996. Short term temporal patterns in a Mediterranean shrubland bird community after wildfire. *Acta Oecologica* 17:29–41.
- Preiss, E., J. L. Martin, and M. Debussche. 1997. Rural depopulation and recent landscape changes in a Mediterranean region: consequences to the breeding avifauna. *Landscape Ecology* 12:51–61.
- R Development Core Team. 2007. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. (<http://www.R-project.org>)
- Sala, O. E., et al. 2000. Global biodiversity scenarios for the year 2100. *Science* 287:1770–1774.
- Sirami, C., L. Brotons, and J. L. Martin. 2007. Vegetation and songbird response to land abandonment: from landscape to census plot. *Diversity and Distributions* 13:42–52.
- Sirami, C., L. Brotons, and J. L. Martin. 2008. Spatial extent of bird species response to landscape changes: colonisation/extinction dynamics at the community-level in two contrasting habitats. *Ecography*. [doi: 10.1111/j.0906-7590.2008.05403.x]
- Suárez-Seoane, S., P. E. Osborne, and J. Baudry. 2002. Responses of birds of different biogeographic origins and habitat requirements to agricultural land abandonment in northern Spain. *Biological Conservation* 105:333–344.
- Thuiller, W. 2003. BIOMOD-optimizing predictions of species distributions and projecting potential future shifts under global change. *Global Change Biology* 9:1353–1362.
- Thuiller, W. 2004. Patterns and uncertainties of species' range shifts under climate change. *Global Change Biology* 10:2020–2027.
- Thuiller, W. 2007. Climate change and the ecologist. *Nature* 448:550–552.
- Thuiller, W., C. Albert, M. B. Araújo, P. M. Berry, M. Cabeza, A. Guisan, T. Hickler, G. F. Midgley, J. Paterson, F. M. Schurr, M. T. Sykes, and N. E. Zimmermann. 2008. Predicting global change impacts on plant species' distributions: future challenges. *Perspectives in Plant Ecology, Evolution and Systematics* 9:137–152.
- Thuiller, W., G. F. Midgley, G. O. Hughes, B. Bomhard, G. Drew, M. C. Rutherford, and F. I. Woodward. 2006. Endemic species and ecosystem vulnerability to climate change in Namibia. *Global Change Biology* 12:759–776.
- Vallecillo, S., L. Brotons, and S. Herrando. 2008. Assessing the response of open-habitat bird species to landscape changes in Mediterranean mosaics. *Biodiversity and Conservation* 17: 103–119.
- Vaughan, I., and S. Ormerod. 2005. The continuing challenges of testing species distribution models. *Journal of Applied Ecology* 42:720–730.
- Viñas, O., and X. Baulies. 1995. 1:250 000 Land-use map of Catalonia (32 000 km²) using multitemporal Landsat-TM data. *International Journal of Remote Sensing* 16:129–146.
- Westerhuis, J. A., T. Kourti, and J. F. MacGregor. 1998. Analysis of multiblock and hierarchical pca and pls methods. *Journal of Chemometrics* 12:463–482.
- Wiens, J. A. 2001. The landscape context of dispersal. Pages 96–109 in T. Clobert, E. Danchin, A. A. Dhondt, and J. D. Nichols, editors. *Dispersal*. Oxford University Press, Oxford, UK.

APPENDIX

The area under the curve (AUC) from calibration evaluation performed at the fine-grained scale for the current conditions, using 70% of the data set to calibrate the models and the remaining 30% for evaluation (calibration); and AUC from evaluation of model back-projections derived from single and ensemble forecasts (principal components analysis consensus and average projection) at the coarse-grained scale for all studied species (evaluation) (*Ecological Archives* A019-024-A1).