*Fire management, climate change and their interacting effects on birds in complex Mediterranean landscapes: dynamic distribution modelling of an early-successional species—the near-threatened Dartford Warbler (*Sylvia undata*)*

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REVIEW

Fire management, climate change and their interacting effects on birds in complex Mediterranean landscapes: dynamic distribution modelling of an early-successional species—the near-threatened Dartford Warbler (*Sylvia undata*)

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Abstract The current challenge in a context of major environmental changes is to anticipate the responses of species to future landscape and climate scenarios. In the Mediterranean basin, climate change is one the most powerful driving forces of fire dynamics, with fire frequency and impact having markedly increased in recent years. Species distribution modelling plays a fundamental role in this challenge, but better integration of available ecological knowledge is needed to adequately guide conservation efforts. Here, we quantified changes in habitat suitability of an early-succession bird in Catalonia, the Dartford Warbler (*Sylvia undata*), which is globally evaluated as Near Threatened in the IUCN Red List. We assessed potential changes in species distributions between 2000 and 2050 under different fire management and climate change scenarios, and described landscape dynamics using a spatially-explicit fire-succession model that simulates fire impacts in the landscape and post-fire regeneration (MEDFIRE model). Dartford Warbler occurrence data were acquired at two different spatial scales from: (1) the Atlas of European Breeding Birds (EBCC) and (2) the Catalan Breeding Bird Atlas (CBBA). Habitat suitability was modelled using five widely-used modelling techniques in an ensemble forecasting framework. Our results indicated considerable habitat suitability losses (ranging between 47 and 57 % in baseline scenarios), which were modulated to a large extent by fire regime changes derived from fire management policies and climate changes. Such result highlighted the need for taking the spatial interaction between climate changes, fire-mediated landscape dynamics and fire management policies into account for coherently anticipating habitat suitability changes of early-succession bird species. We conclude that fire management programs need to be integrated into conservation plans to effectively preserve sparsely forested and early succession habitats and their associated species in the face of global environmental change.

Keywords Bird conservation · Global change scenarios · Multiscale hierarchical modelling · MEDFIRE model · Fire-prone ecosystems · Forest biomass extraction

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Introduction

The current challenge in a context of major environmental changes is to accurately forecast how the interaction

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between climate change and other ongoing human-induced threats affects biodiversity (De Chazal and Rounsevell 2009; Garcia et al. 2014; Stralberg et al. 2014). Species distribution models (SDMs) may play a fundamental role in this challenge, but we need to integrate more ecology in model building and develop a more coherent model validation before species distribution modelling may be of use in a dynamic ecological context (Guisan and Thuiller 2005; Elith et al. 2006; Guisan and Rahbek 2011).

Mediterranean landscapes are highly dynamic systems (Keeley et al. 2012). Climate change is one of the most powerful driving forces of these dynamics and, in the Mediterranean basin, its severity has markedly increased in recent years (IPCC 2007). However, climate change impacts on biodiversity are often also indirect through changes in disturbance regimes (Clavero et al. 2011; De Cáceres et al. 2013; Turco et al. 2014). Fire is a critical factor in the Mediterranean and is likely to drive landscape change effects over large areas. The description and analysis of landscape patterns associated to fire dynamics have received some attention (Lloret et al. 2002; Moreira et al. 2011, and references therein). However, knowledge about how the temporal and spatial arrangement of habitats arising from wildfires affects biodiversity in complex, human-dominated landscapes is astonishingly poor (Richards et al. 1999; De Cáceres et al. 2013; Kelly et al. 2014), with the exception of within-habitat succession-related recovery of communities after disturbance events (Loyn 1997; Zozaya et al. 2011; Nimmo et al. 2012; Santos et al. 2014; Lindenmayer et al. 2014; among others). In this work, we present recent advancements on habitat and bird modelling responses to fire and climate changes in Catalonia (north-east Iberian Peninsula) in which SDMs applications have played a major role. We focus on the spatial interactions among climate change, fire-conducted landscape dynamics and fire management actions with a future perspective. We used 'forecasting' techniques that identify the events leading from the current situation to a plausible future outcomes (Cook et al. 2014). Based on a storyline and simulation approach, we combined climate projections from global circulation models (GCMs) and fire simulation outcomes from a dynamic fire-succession model (MED-FIRE model) to develop a set of potential future trajectories.

Our main goal is to assess the effects of several fire management strategies on an early-succession bird species, the Dartford Warbler (*Sylvia undata*), as a 'model' study under a climate change context in order to provide insights into a conservation planning process aimed at preserving biodiversity in the face of global change. The Dartford Warbler was recently evaluated on a global scale as Near Threatened in the IUCN Red List, since it is declining at a moderately rapid rate (Birdlife International 2014). Declines in the core populations in Spain are largely responsible for the estimated overall decline of the species (Birdlife International 2004a, b). As a consequence, this species is considered of conservation concern in Europe (more than 95 % of the global population; Species of European Concern category 2 vulnerable, Annex 1 of the European Habitats Directive). The drivers of this population decline are not entirely clear but may include habitat degradation and modification (Van den Berg et al. 2001) and climate changes (Bibby 1978). In fact, climate-related changes in the species' Mediterranean stronghold could be particularly important, and the species could suffer a considerable range loss by the end of the century (Huntley et al. 2007). Changes in the pattern and frequency of wildfires may be a threat, although the species often colonises early successional habitat created by such fires (Pons and Prodon 1996; Herrando et al. 2001; Moreira et al. 2003; Pons et al. 2012). In particular, we ask the following questions: (1) how will climate change synergically with fire-conducted vegetation dynamics affect the distributional range of Dartford Warbler over the next 50 years?; and (2) can fire management offset distributional shifts caused by climate change and natural succession processes?

Methods

Study region and bird data

The study was conducted in Catalonia, a core region in the distribution of the genus *Sylvia* (Shirihai et al. 2001), dominated by a Mediterranean climate and located in north-eastern Spain (Fig. 1). Fire is a major landscape driver in the study region, with about 25 % of the wildland area affected by fires during 1975–2010 (Díaz-Delgado et al. 2004) (Fig. 1). Most fires in the region are severe, including crown fires that strongly affect both forest canopy and undergrowth, and cause widespread tree mortality (Rodrigo et al. 2004).

Dartford Warbler occurrence (presence/absence) data were acquired at two different spatial scales from: (1) the EBCC Atlas of European Breeding Birds (EBCC; Hagemeijer and Blair 1997); these data record the occurrence of breeding by each species in the 3,165 50-km^2 squares of a Universal Transverse Mercator (UTM) grid, largely during the late 1980s and early 1990s; and (2) the Catalan Breeding Bird Atlas (CBBA; Estrada et al. 2004). The CBBA resulted from a large-scale survey that between 1999 and 2002 covered the whole of the Catalonia using grid-based 10 km UTM squares. A total of 3,076 1 km^2 (approximately 9 % of the total area) were selected to conduct standardised intensive surveys of species presence

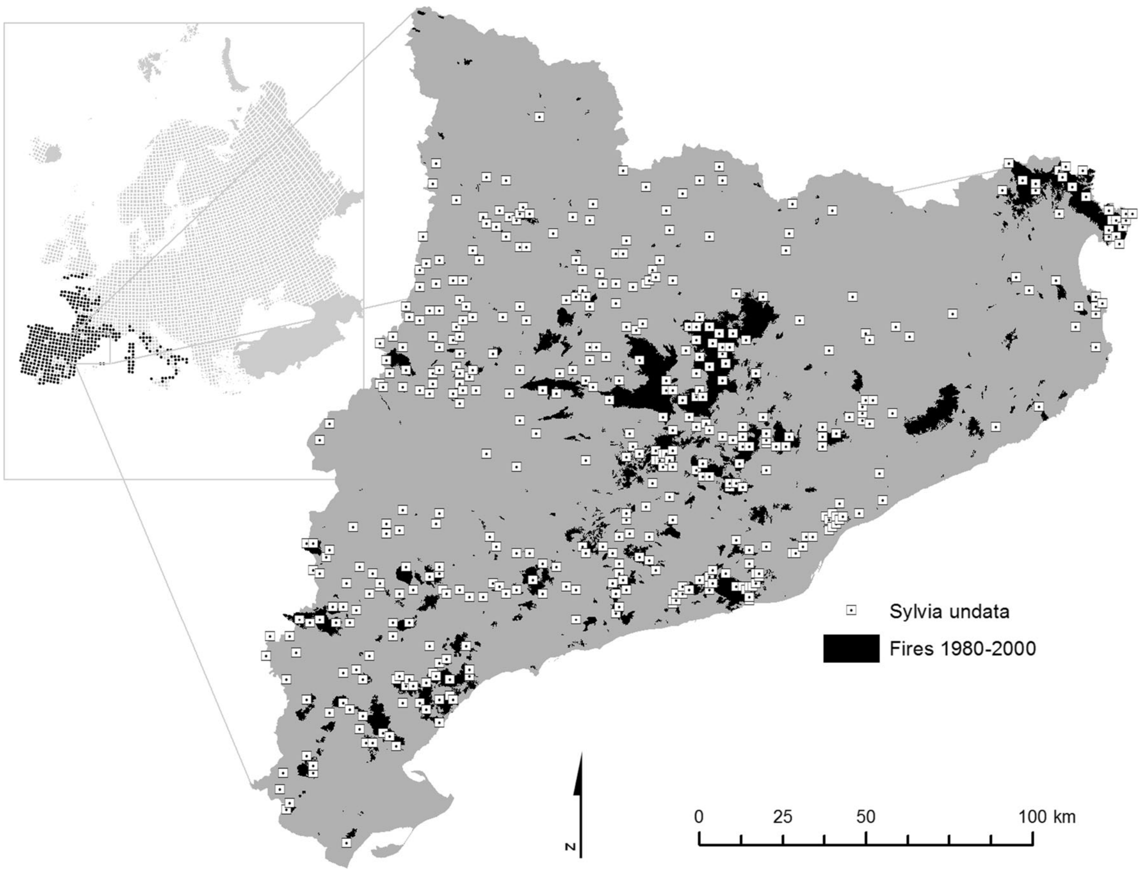

Fig. 1 Location of study region. Presence of Dartford Warbler (*Sylvia undata*) in Europe (*black dots*) at 50-km^2 resolution. Presence of Dartford Warbler in Catalonia (*white squares*) at 1-km^2 resolution and distribution of wildfires between 1980 and 2000

in a stratified fashion to cover the main habitat types present within each of the 10-km^2 squares (Hirzel and Guisan 2002).

Scenario design

We designed 12 future environmental scenarios by combining four strategies of potential fire management aimed at mitigating the impact of large fires in Mediterranean-type novel forest ecosystems and two IPCC climate change scenarios (see Table 1). A set of fire management scenarios assumes that forest biomass extraction would reduce the impact of wildfires in forested areas, while fires would freely burn the shrubland and cropland areas (Evans and Finkral 2009; Becker et al. 2009; Abbas et al. 2011). In particular, we developed four scenarios wherein the annual area treated for biomass extraction is changing in extent and allocation (for more details, see scenarios 1–4 in Table 1). Moreover, we also envisaged a set of four exploratory scenarios characterised by decreasing fire suppression levels in years with mild weather conditions (scenarios 5–8 in Table 1). Fire management options based on 'let-burn' fire suppression strategies in mild years were found to have the potential to substantially reshape fire regimes and decrease the amount of area burnt under undesired, extreme climate conditions (Houtman et al. 2013; Regos et al. 2014). Furthermore, we designed another set of two scenarios representing business-as-usual trajectories (baseline of current trends) including the fire suppression policies currently implemented in Catalonia (scenarios 9 and 10 in Table 1). Another set of exploratory scenarios was characterized by no suppression as an extreme reference trajectory to the current trend (scenarios 11 and 12 in Table 1). All scenarios were implemented under two climate baselines (A2a and B2a). Each fire management strategy supports particular fire mosaics that comprise different arrangements of fire age-classes in the landscape, also affecting land cover-type dynamics.

The modelling framework

To quantify changes in distributional range of Dartford Warbler under fire management and climate change scenarios, we used a multiscale hierarchical modelling approach. Climate and land cover variables at different scales were integrated into the same modelling framework in

Table 1 List of future scenarios designed for Catalonia

ID	Scenario	Storyline	IPCC	Incentive/constrains
1	BioFS + A2	Forest harvesting in optimal areas from an environmental and economic viewpoint (~39,000 ha extracted annually)	A2a	Forest biomass extraction is not allowed in protected areas
2	BioFS + B2		B2a	Forest biomass extraction is not allowed in protected areas
3	BioFS + A2 plus	Forest harvesting in optimal areas from a logistic and economic viewpoint (~62,000 ha extracted annually)	A2a	–
4	BioFS + B2 plus		B2a	–
5	UnFS + A2	An opportunistic fire suppression strategy based on low decreasing active firefighting efforts in controlled "mild" fire weather conditions to provide further firefighting opportunities in adverse years	A2a	6,500 ha/year to burn in climatically mild years
6	UnFS + B2		B2a	6,500 ha/year to burn in climatically mild years
7	UnFS + A2 plus	An opportunistic fire suppression strategy based on high decreasing active firefighting efforts in controlled "mild" fire weather conditions to provide further firefighting opportunities in adverse years	A2a	52,000 ha/year to burn in climatically mild years
8	UnFS + B2 plus		B2a	52,000 ha/year to burn in climatically mild years
9	Base + HighFS + A2	Strong active suppression corresponding to current fire suppression levels	A2a	–
10	Base + HighFS + B2		B2a	
11	NoFS + A2	No fire suppression	A2a	–
12	NoFS + B2		B2a	–

Each scenario is a combination of a climatic baseline (A2a and B2a) and fire management strategy (BioFS, UnFS, HighFS and NoFS)

three steps: (1) climate envelope models were calibrated at a European scale to capture the climate niche and physiological tolerance range of the species (Pearson et al. 2004) and then directly downscaled at the Catalan scale; (2) land-cover models were calibrated and projected at the Catalan scale; and (3) a final third set of models was performed using as predictors the outcomes of climate and land cover models developed in the two first steps.

Environmental data

Environmental predictors used in the distribution models for each scale (European and Catalan) were selected according to our research goals and the previous ecological knowledge available for Dartford Warbler (Pons and Prodon 1996; Herrando et al. 2001; Pons et al. 2012). We followed Pearson et al. (2004) and used climate variables to model the distribution of Dartford Warbler in the whole of Europe, as this extent encompasses more than 95 % of global distribution and thus allows us to capture the whole of the species' realized climatic niche. Climate predictors were selected by expert knowledge and according to previous scientific literature: (1) maximum temperature of warmest month; (2) minimum temperature of coldest month; and (3) annual precipitation. Three additional predictors were also considered after testing multicollinearity problems (Spearman's rho correlation coefficient <0.7); (4) mean diurnal range; (5) precipitation seasonality; and (6) precipitation in warmest quarter. The current climatic data were obtained from the WorldClim database (http://www.worldclim.org/current/) and future climatic projections from the International Center for Tropical Agriculture (ICTA) (http://ccafs-climate.org/) (IPCC 2007). These current climatic data were generated by interpolated climate data from the 1950–2000 period. Future climate change projections were computed from an average ensemble (ENS) model of four GCMs (CCCMA-CGCM2, CSIRO-MK2.0, HCCPR-HadCM3 and NIESS99) to account for the uncertainty arising from the inter-model variability. These projections were available at 30 arc-s (~1 km) resolution by the application of delta downscaling method on the original data from the IPCC Fourth Assessment Report (provided by ICTA) for time-slide 2050 (2040–2069).

Fire-mediated landscape dynamics were addressed at the Catalan scale using a landscape dynamic modelling approach. We used a MEDFIRE simulation model, a spatially-explicit dynamic fire-succession model designed to integrate climatic and anthropogenic drivers and allow the investigation of their combined effect on fire regimes and land cover at short- and medium-term time-scales in a Mediterranean context (Brotons et al. 2013). This model allows the prediction of changes in landscape properties and composition derived from spatial interactions between wildfire, vegetation dynamics and fire management strategies (a detailed description of the model can be found in

Brotons et al. 2013 and Regos et al. 2014). In the MEDFIRE, the potential burnt area and fire size distributions depend on the climatic severity of the year: (1) A2-IPCC scenarios: the probability of a year being adverse (characterized by higher proportion of large wildfires compared to the distribution corresponding to mild years) increases from 0.30 to 0.59 for time-slice 2050 (2040 and 2069); and (2) B2-IPCC: the probability of a year being adverse increases from 0.30 to 0.62 for time-slice (more details in supplementary Appendix 1). Initial landscape composition and properties are represented by means of two raster dynamic layers at 100-m resolution for year 2000: Land cover type (LCT) and time since last fire (TSF). Information of landscape composition is obtained from the land cover categories: (1) coniferous and (2) oak tree species, (3) shrubland as dynamic variables, and (4) cropland as a static variable. Detailed knowledge of the fire-mediated properties of landscapes is achieved through proportional extent of different three fire age-classes: (5) older vegetation (>30 years since fire) (6) mid-age vegetation (10–30 years since fire), and (7) recently burnt vegetation (<10 years since fire). All spatial layers were simulated 10-fold under each of the fire management scenarios for - year 2050 using the MEDFIRE model. The percentage of area covered by each variable was calculated within 1 km × 1 km cells to match them with the bird data resolution.

Model fitting and evaluation

Combining different modelling algorithms has been proposed as an approach to adjust inherent uncertainty of individual models, and to determine an optimal solution from an ensemble of predictions (Araújo and New 2007; Thuiller et al. 2009). Ensemble models, built on a series of competing models, each with a different combination of environmental predictors, may provide more informative and ecologically correct predictions (Thuiller 2003). We used the BIOMOD2 modelling tool (Thuiller et al. 2009; BIOMOD package is available at http://r-forge.r-project.org/projects/biomod/) for fitting ensemble models on the Dartford Warbler. We fitted models using five distinct techniques: (1) generalized linear models (GLM) (McCullagh and Nelder 1989); (2) generalized additive models (GAM) (Hastie and Tibshirani 1990); (3) classification tree algorithms (CTA) (Breiman et al. 1984); (4) generalized boosted regression Models (GBM) (Friedman et al. 2000); and (5) random forest (RF) (Breiman 2001). The area under the curve (AUC) of the receiver-operating characteristic (ROC) was used as a means to evaluate the performance of the models (Elith et al. 2006). We used a 10-fold split-sample procedure keeping 30 % of the initial data out of the calibration for the subsequent validation of the predictions. The European projections downscaled at the Catalan level were validated against the occurrence data of CBBA. We applied the weighted average approach for computing a consensus of any single model with AUC >0.7 using AUC values as model weights, which significantly increases the accuracy of species distribution forecasts (Araújo and New 2007; Marmion et al. 2009). Response curves for each algorithm used for building the final models were represented in three-dimensional plots using the Evaluation Strip method proposed by Elith et al. (2005). This method enabled us to compare the predicted responses from the different statistical approaches on the same data and to infer the importance of each predictor in the final model.

Boolean maps (presence/absence) were calculated from the probability layers to define two levels of habitat suitability (HS) for each projection, using two thresholds with applied ecological meaning: (1) we defined as species distribution areas (in terms of prevalence of the data used in the model development) those with habitat suitability values above the lowest 10 % HS percentile of available occurrences (Thresh1; hereafter "DIST"); and (2) within these distribution areas, we applied a second level threshold aimed at identifying optimal habitat suitability areas for the species. These were defined by setting a new threshold from the average of the suitable values within the DIST (Thresh2; hereafter "OpHS"). Optimal HS may be interpreted in the context of the European Birds directive as the best areas for the species and therefore those potentially to be included within Natura 2000 sites (Herrando et al. 2011; Arcos et al. 2012). In total, we projected 480 potential distribution maps for future environmental conditions (12 scenarios × 10 replicates × 2 steps × 2 thresholds).

Evaluation of potential changes

We counted the grid cells (100 ha) with probability values larger than each pre-specified presence threshold to estimate the extent of areas predicted as DIST and OpHS. We calculated the predicted gains and losses between 2000 and 2050 for each scenario from the models derived from land cover predictors (step 2) and from land cover and climate predictors (step 3) in order to infer the effect of climate in combination with fire-conducted landscape dynamics.

Results

The predictive accuracies of Dartford Warbler ensemble forecasts were good ($AUC_{LCT} = 0.898$). The inclusion of climate envelopes into the land cover ensemble models further improved their modelling performance ($AUC_{LCT+CLIM} = 0.947$). The high accuracy performance

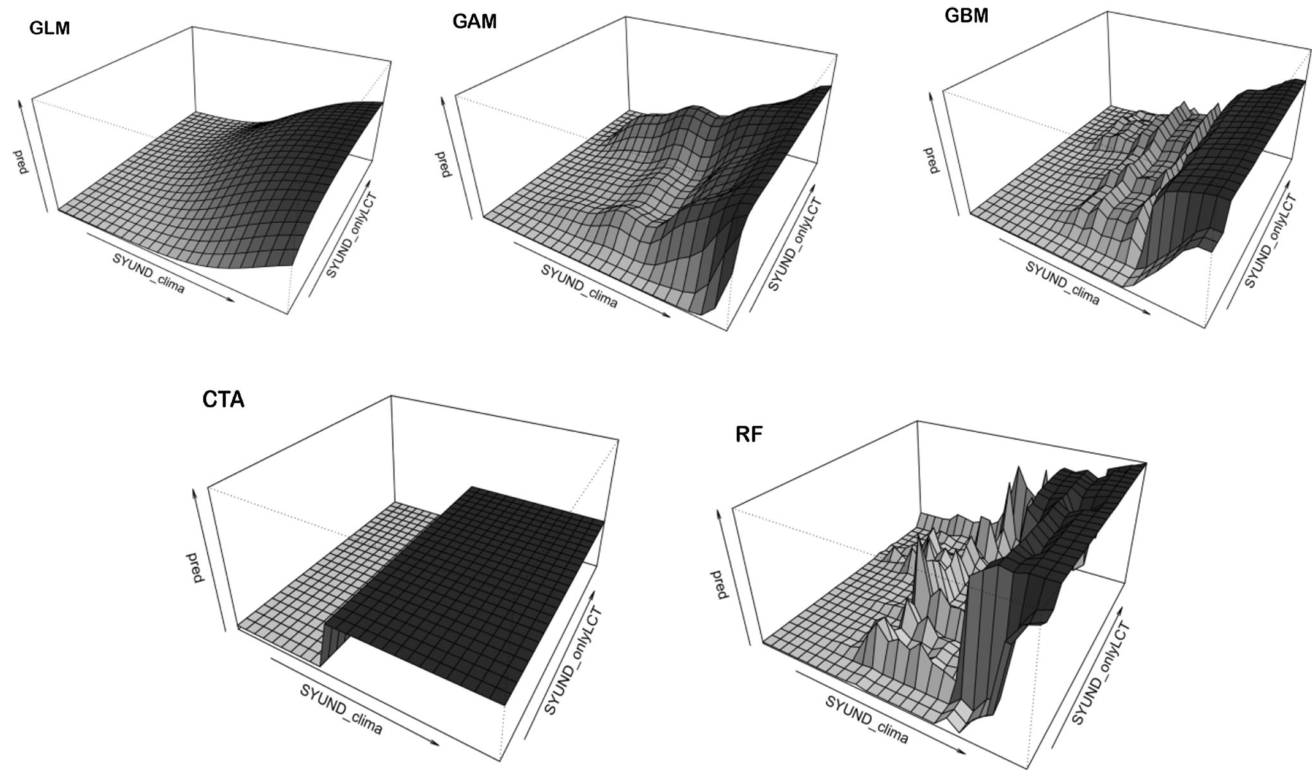

Fig. 2 Reponses to climate and land cover predictors at Catalan scale for the five algorithms considered: generalized linear models (GLM), generalized additive models (GAM), generalized boosted regression models (GBM), classification tree algorithms (CTA), and random forest (RF). Axes labels: the probability of occurrence (*pred*), climate (*SYUND_clima*) and land cover (*SYUND_onlyLCT*) predictors. The unit of measurements ranges between 0 and 1

obtained at the European scale ($AUC_{EU-CLIM} = 0.995$) shows a strong correlation between Dartford Warbler occurrence and the selected climate variables. However, the accuracy of climate models downscaled at a regional level was very low ($AUC_{CAT-CLIM} = 0.57$). This is in agreement with the importance of predictors in the final model (see response curves in Fig. 2) showing that landscape properties and composition are constraining the final Dartford Warbler distribution at finer scales.

The results derived from the analysis of different scenarios showed a strong effect of fire management strategy on Dartford Warbler potential distribution area. The DIST of Dartford Warbler decreased up to 40 % under the current fire suppression levels between 2000 and 2050 (see scenarios Base + HighFS in Figs. 3, 4). The optimal habitat suitability (OpHS) under these scenarios showed an average decrease of 56 %. The losses in habitat suitability decrease as fire suppression levels tend to be relaxed and annual burnt area increases (see scenarios Base + HighFS, UnFS and UnFS plus in Figs. 3, 4). Fire suppression strategies based on letting unplanned fires burn in mild weather conditions has the potential to create sparsely forested and early-succession habitats and increase the distribution range of the species (Figs. 3, 4), thus partially offsetting the overall trend of forest expansion recorded over the next 50 years in business-as-usual scenarios (Table 2). The decrease in optimal habitat suitability ranged between 20 and 43 % under biomass extraction scenarios (BioFS scenarios in Figs. 3, 4), thus slightly lower values than in scenarios with the current high fire suppression levels (Base + HighFS). Climate changes had a clear effect on Dartford Warbler distribution area (compare land cover and climate models with land cover models in Fig. 3). We found stronger declines in habitat suitability under IPCC scenario A2 than B2 (compare A2 and B2 scenarios in results of land cover and climate models; Fig. 3). The direct effect of climate change on Dartford Warbler distribution was clearly stronger than its indirect effect through the changes in fire regime (compare A2 and B2 scenarios of land cover and climate models with land cover models; Fig. 3).

Discussion

The European breeding population of the Dartford Warbler, which constitutes more than 95 % of the global population, was supposed to undergo a considerable

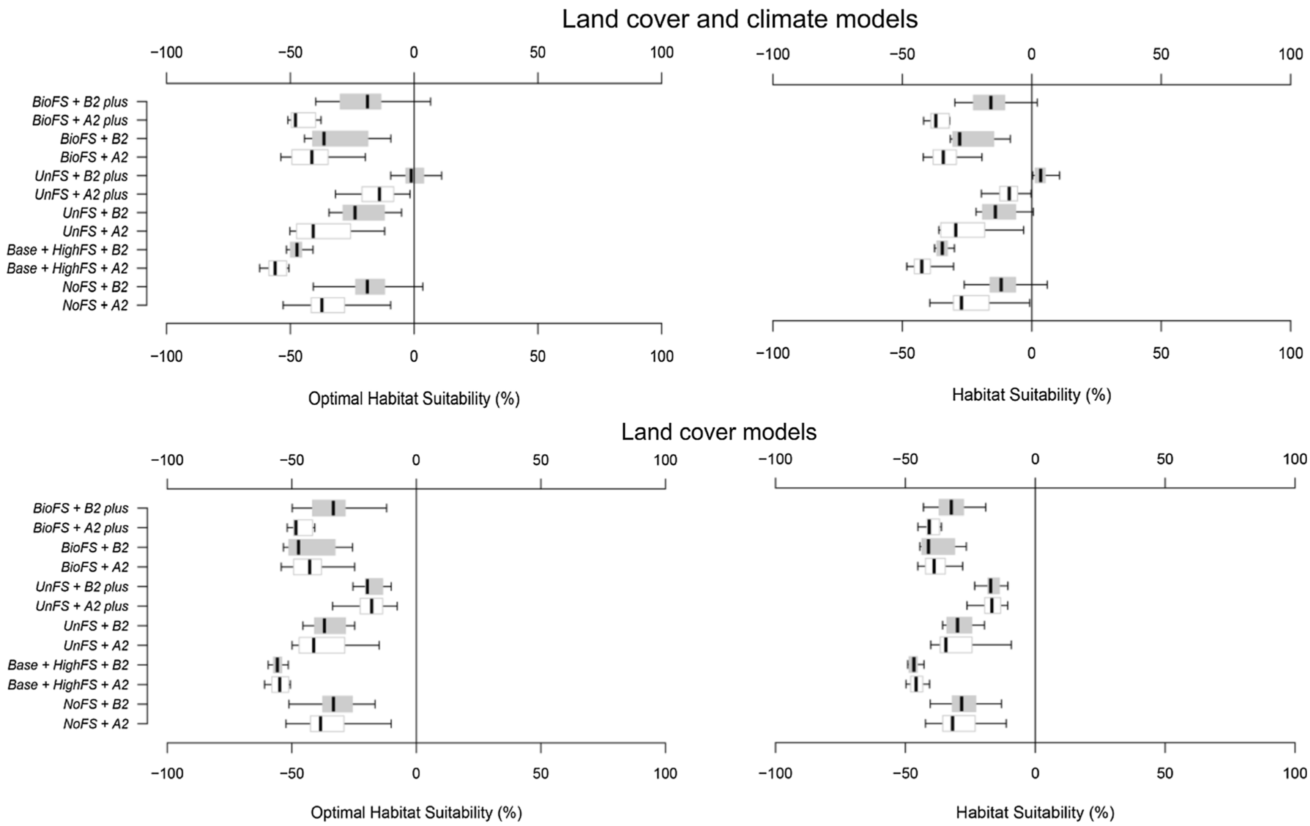

Fig. 3 Predicted changes (expressed in %) in optimal habitat suitability (calculated after applying Thresh2 to the probability layers) and habitat suitability (calculated after applying Thresh1) between 2000 and 2050 under each future scenario obtained from models exclusively performed with land cover variables (land cover models) or considering the interaction between climate and land cover change (land cover and climate models). The scenarios are described in Table 1

decline during the 1970–1990 period (Tucker and Heath 1994). The population trend for the species as shown by the Pan-European Common Bird Monitoring Scheme suggests that it declined by 17 % in the period 1998–2011 PECBMS (2013), so it has recently justified uplisting the species to a higher threat category (Birdlife International 2014). The stronghold of the species is located in Spain which holds 983,000–1,750,000 pairs (Martí and Del Moral 2003), but the populations there have declined by an average of 4.6 % (95 % CI: 6.2–3.1) per year during 1998–2011 according to the Spanish common bird monitoring scheme (SACRE) (SEO/BirdLife 2010). Our study also predicts large habitat suitability losses in Catalonia mainly derived from successional losses and land abandonment (ranging between 47 and 57 % in baseline scenarios), but these losses can be strongly modulated by fire regime shifts conducted by fire management, together with climate change. Our results thus highlight the need to take the spatial interaction among climate change, fire-mediated landscape dynamics and fire management policies in highly dynamic and fire-prone ecosystems into account to accurately predict habitat suitability changes of early-succession bird species in a context of global change.

The amount of area burnt by wildfires has decreased in Catalonia since the introduction of new fire suppression policies and the creation in 1999 of a specific technical fire brigades (GRAF) (Brotons et al. 2013). According to our projections, the habitat suitability of Dartford Warbler will strongly decrease between 2000 and 2050 due to pine and oak forest expansion caused by natural succession processes favoured by these high fire suppression levels (Fig. 3; Table 2). This decline could only be counterbalanced by a large-scale change in the use of forests and open habitats in the region or by progressive decrease in fire suppression levels and a subsequent increase in the annual burnt area (Figs. 3, 4). The use of unplanned fires resulting from decreasing suppression efforts are tactics that use fire as a tool to fight larger wildfires, and that aim to increase the effectiveness of fire suppression through fuel reduction (Regos et al. 2014). Unplanned fires increase landscape heterogeneity, offsetting the decade-long general trend towards homogenization due to land abandonment and the coalescence of natural vegetation patches (Table 2). Thus, early-successional species such as Dartford Warbler could be favoured in the future by this fire management policy, especially in those areas strongly affected by land

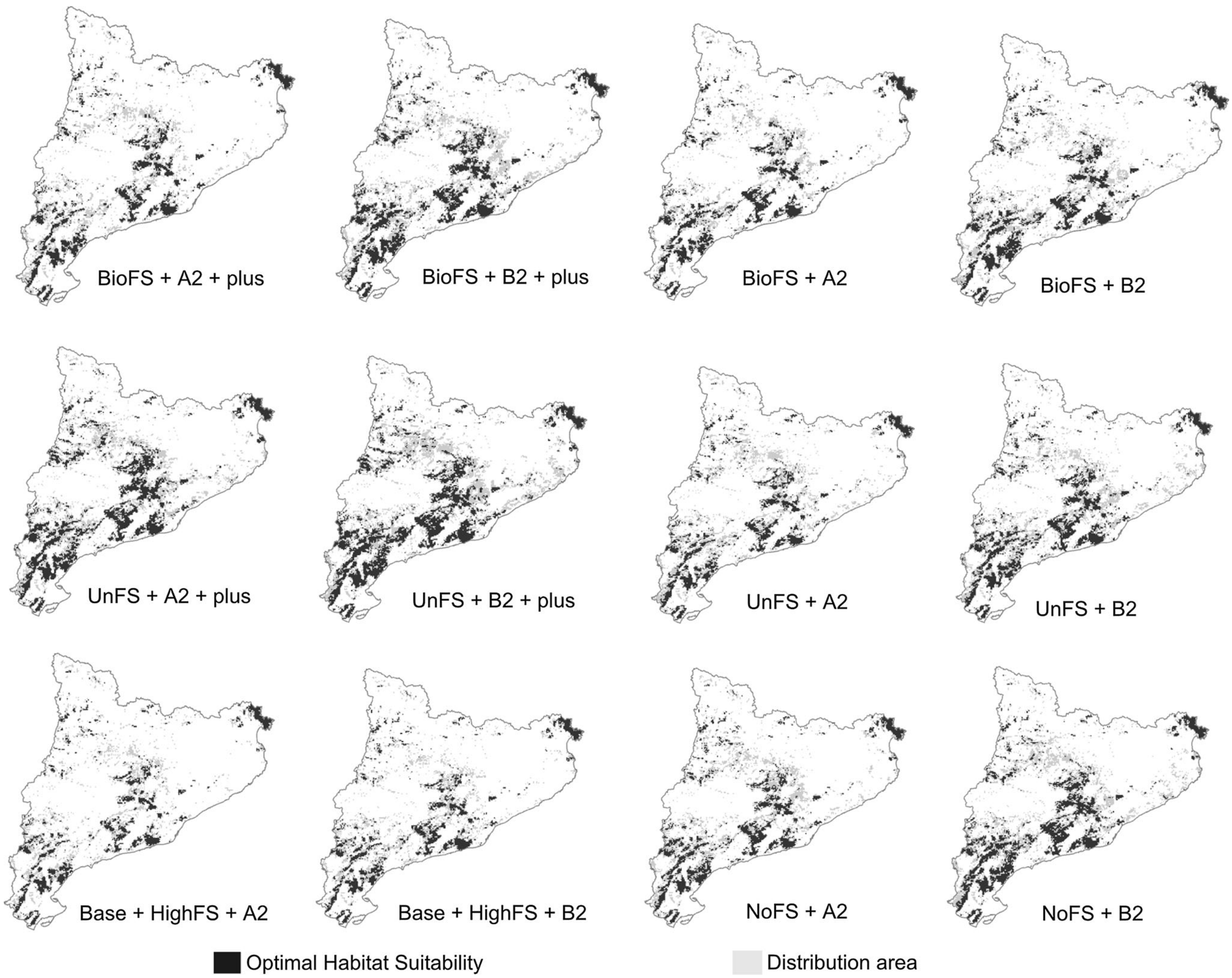

Fig. 4 The potential distribution areas (*grey*) and optimal habitat suitability (*black*) in 2050 under future scenarios. The maps were generated from averaging the probability layer and applying subsequent thresholds (Thresh1 and 2, respectively) for each 10 replicates performed in each scenario simulation. The scenarios are described in Table 1

abandonment processes. Forest biomass extraction for bioenergy purposes has also been proposed as a fuel-reduction treatment aimed at suppressing forest fires (Evans and Finkral 2009; Becker et al. 2009; Abbas et al. 2011). This forest management option may help in reducing the impact of wildfires in forested areas, while fires could burn the shrubland and cropland areas to a greater extent. Nevertheless, it is also important to note that forest biomass extraction (or logging) can increase the density of vegetation in lower forest layers, potentially increasing vegetation flammability but also providing temporary habitat for other shrubland species (Stephens 1998; Fenton et al. 2009; King et al. 2011). Our simulations showed that fire suppression strategies exclusively focused on forest areas have the potential to counterbalance the negative effect of shrub–forest succession on the distribution of the Dartford Warbler, but not to the same degree as those scenarios that include a larger number of fire events and a greater area burnt (Fig. 3). Landscape gradients induced by fire may potentially enhance the resilience of threatened open-habitat bird species by increasing the range of potential habitat used and their ability to colonize recently burnt areas (Brotons et al. 2005; Vallecillo et al. 2007). In particular, the Dartford Warbler can colonize burnt areas as soon as the second year after fire, even when it was absent before (Pons et al. 2012). However, the effects of wildfires on open-habitat-dwelling species hinge on the frequency and extent of burnt areas. If a fire regime characterized by small- and medium-sized fires prevails over the long term, local-scale heterogeneity introduced into the landscape may favour metapopulation dynamics for such species by maintaining a dynamic pool of suitable habitat patches that are colonized after perturbation from nearby suitable habitats. In contrast, a spread of extensive wildfires will

Table 2 Predicted changes (%) of different habitats and landscape properties in Catalonia (north-east Spain) under 12 future scenarios

	Coniferous	Oak	Shrub	Recently burnt	Mid-age	Old-age
BIOFS + A2	9.69	26.69	−44.53	−0.82	72.99	−2.31
BIOFS + B2	8.96	26.96	−43.86	4.51	73.70	−2.57
BIOFS + A2 PLUS	11.91	25.91	−46.59	−8.78	58.06	−1.47
BIOFS + B2 PLUS	8.98	26.61	−43.48	−12.61	133.10	−3.70
UNFS + A2	9.60	27.09	−44.87	9.68	110.07	−3.98
UNFS + B2	9.14	27.55	−44.81	3.21	120.71	−4.03
UNFS + A2 PLUS	−1.76	30.26	−33.36	71.87	266.16	−11.82
UNFS + B2 PLUS	−1.72	30.62	−33.84	28.88	298.96	−10.92
NOFS + A2	5.15	28.66	−40.76	27.53	138.19	−5.69
NOFS + B2	4.65	28.98	−40.45	34.71	136.35	−5.96
BASE + HIGHFS + A2	18.68	23.89	−53.30	−61.72	−22.51	3.53
BASE + HIGHFS + B2	18.57	24.06	−53.35	−61.16	−25.71	3.60

The habitats are: (1) coniferous and (2) oak tree species, and (3) shrubland; and the fire-mediated properties of landscapes: (4) recently burnt vegetation (<10 years since fire) (5) mid-age vegetation (10–30 years since fire), and (6) older vegetation (>30 years since fire). The scenarios are described in Table 1

initially favour open-habitat birds, but the habitat may soon turn unsuitable until new perturbations generate open habitats again (Brotons et al. 2005; Watson et al. 2012; Taylor et al. 2013; Kelly et al. 2014). This emphasises the importance that fire management might have on long-term preservation of these species associated with early-successional stages in highly dynamic environments. Besides, it is also important to keep in mind that wildfires could negatively affect forest-dwelling birds, which would have major implications for conservation for other threatened and endangered species. Previous studies have already proved that large-scale forest maturation and spread due to land abandonment processes have counteracted the potentially negative effects of fires on forest bird distributions in the Mediterranean Basin (Herrando and Brotons 2002; Gil-Tena et al. 2009). Since vegetation encroachment has been a major driving force for the avifauna in Catalonia over the last decade (Herrando et al. 2014), fire management programs aimed at effectively preserving open-habitat species could be reasonably integrated into current conservation plans without large negative impacts for forest species across the region. The removal of snags after a fire by extensive application of post-fire management practices such as salvage logging has negative impacts on forest birds in Mediterranean ecosystems, but also positive effects on a number of open-habitat species (Rost et al. 2012, 2013). On these grounds, we suggest that managers maintain some standing dead trees during post-fire logging operations to provide suitable habitat for the widest range of species (Rost et al. 2012). Nonetheless, further research considering a broader community perspective would be highly desirable in order to provide new insights that could help decision-making processes in conservation.

Regarding the effect of climate, our models showed that it is a main factor in determining the Dartford Warbler's distribution at large scales. Conversely, at regional scales, the species distribution is strongly constrained by landscape properties and composition (Figs. 2, 3). Nevertheless, the inclusion of climate at a regional scale also increased the predictive accuracies of the final model: the combined effect of both factors, climate and landscape, provides better predictive capabilities, as has already proved for other taxa, scales and regions (Pearson et al. 2004; Lomba et al. 2010; Cumming et al. 2013). Our simulations showed a larger loss in habitat suitability on Dartford Warbler distribution under IPCC scenario A2 than B2, mostly owing to the direct effect of climate change rather than to the indirect effect through the changes in the fire regime (Fig. 3).

In addition, an indirect effect of climate through the changes in natural succession could be affecting the response of the species to the newly burnt areas. In the driest areas of Catalonia, it has been found that the species colonises later, or remains confined to unburnt patches. The peak of highest abundance may occur as soon as the fourth year after fire or later, up to the ninth year (Pons and Clavero 2010). This delayed response was likely due to the slow plant regeneration resulting from a colder climate and higher grazing pressure in the mountain area (Pons et al. 2012). This mountain area is distributed across the northernmost part of Catalonia which is also the area less affected by fires (see Fig. 1; Díaz-Delgado et al. 2004). We suggest that, in addition to the fire management strategies discussed here, prescribed burning programs in mountain areas could help to maintain this species in the north of Catalonia.

Conclusions

Deeper insights on the temporal and spatial factors that interact to determine current landscape patterns and species responses are essential if we want to understand and manage the future outcome of biodiversity responses in Mediterranean systems. The generality of these constraints suggest that successful application of species distribution modelling to the prediction of species distribution dynamics in other conditions should be developed under a similar integrative, ecologically sound framework. In particular, our findings suggest that fire management programs must be integrated into conservation plans to effectively preserve sparsely forested and early-succession habitats and their associated species in the face of global change.

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