



# Predicting the future effectiveness of protected areas for bird conservation in Mediterranean ecosystems under climate change and novel fire regime scenarios

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## ABSTRACT

**Aim** Global environmental changes challenge traditional conservation approaches based on the selection of static protected areas due to their limited ability to deal with the dynamic nature of driving forces relevant to biodiversity. The Natura 2000 network (N2000) constitutes a major milestone in biodiversity conservation in Europe, but the degree to which this static network will be able to reach its long-term conservation objectives raises concern. We assessed the changes in the effectiveness of N2000 in a Mediterranean ecosystem between 2000 and 2050 under different combinations of climate and land cover change scenarios.

**Location** Catalonia, Spain.

**Methods** Potential distribution changes of several terrestrial bird species of conservation interest included in the European Union's Birds Directive were predicted within an ensemble-forecasting framework that hierarchically integrated climate change and land cover change scenarios. Land cover changes were simulated using a spatially explicit fire-succession model that integrates fire management strategies and vegetation encroachment after the abandonment of cultivated areas as the main drivers of landscape dynamics in Mediterranean ecosystems.

**Results** Our results suggest that the amount of suitable habitats for the target species will strongly decrease both inside and outside N2000. However, the effectiveness of N2000 is expected to increase in the next decades because the amount of suitable habitats is predicted to decrease less inside than outside this network.

**Main conclusions** Such predictions shed light on the key role that the current N2000 may play in the near future and emphasize the need for an integrative conservation perspective wherein agricultural, forest and fire management policies should be considered to effectively preserve key habitats for threatened birds in fire-prone, highly dynamic Mediterranean ecosystems. Results also show the importance of considering landscape dynamics and the synergies between different driving forces when assessing the long-term effectiveness of protected areas for biodiversity conservation.

## Keywords

biodiversity management, bird conservation, hierarchical approach, land abandonment, land cover change, MEDFIRE model, multiscale modelling, species distribution models, vegetation dynamics.

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## INTRODUCTION

Global change poses a daunting challenge to any large-scale planning effort, such as the implementation of biodiversity conservation and management strategies (Kukkala & Moilanen, 2013). In a dynamic socio-ecological system, traditional conservation approaches based on the selection of static protected areas (hereafter PAs) are increasingly questioned due to their limited ability to incorporate the future impact of changing conditions (e.g. climate change, land cover change) on biodiversity (Rayfield *et al.*, 2008; Le Saout *et al.*, 2013; Leroux & Rayfield, 2014). Although protected areas have proven to be effective for the protection of species against ongoing human threats, many species might shift their distributions outside existing protected areas under climate change scenarios (Araújo *et al.*, 2004, 2011; Alagador *et al.*, 2014). This issue may raise particular concern in highly dynamic environments such as fire-prone ecosystems where climate change could act in synergy with vegetation encroachment following land abandonment and move natural fire regimes out of their historical range (Pausas & Fernández-Muñoz, 2011; Batllori *et al.*, 2013).

Wildland fires are a major component of disturbance regimes in Mediterranean-type ecosystems world-wide (Keeley *et al.*, 2012). Current global circulation models (GCMs) and climate change scenarios forecast higher burning frequencies and larger burnt areas due to greater severity of weather conditions in the future (Piñol *et al.*, 1998; De Groot *et al.*, 2013; Flannigan *et al.*, 2013). Current fire suppression policies will be challenged in the future and alternative fire management strategies will likely be applied to achieve the stand structure and fuel reduction objectives required to minimize the impact of undesired fires (Liu *et al.*, 2010; McIver *et al.*, 2012; Moritz *et al.*, 2014). However, it is still largely unknown how these new fire management strategies could impact on ecosystems and biodiversity. In particular, the effectiveness of PAs for biodiversity conservation in a medium-term future has never been evaluated under novel fire regime scenarios and fire management strategies.

In Europe, Natura 2000 (hereafter N2000) is a network of PAs that constitutes the backbone of biodiversity conservation. N2000 is, however, implemented in a static manner and the degree to which it will be able to meet its conservation objectives under changing conditions in the future remains a major question (Hole *et al.*, 2009; Trouwborst, 2011; Van Teeffelen *et al.*, 2014). N2000 is based on the Birds Directive (79/409/EEC, amended in 2009: 2009/147/EC) and the Habitats Directive (92/43/EEC, consolidated in 2007) of the European Union. This network is targeted at ensuring the long-term survival of Europe's most valuable and threatened species and habitats listed in the annexes of these two directives. N2000 is not a system of strict nature reserves where all human activities are excluded: the emphasis of the system relies on the sustainability of future

management within the PAs, both from ecological and socio-economical perspectives. Therefore, a better understanding of the interactions between climate change and large-scale future land management and of their future effects in terms of biodiversity conservation inside these PAs is needed at the earliest (Le Saout *et al.*, 2013; Virkkala *et al.*, 2013; Coetzee *et al.*, 2014).

Comparing changes in biodiversity inside and outside PAs has proved to be an efficient option in assessing the protection effectiveness and reporting on the initial status of biodiversity (Johnston *et al.*, 2013; Barnes *et al.*, 2015). Such an approach may help assess whether N2000 is fulfilling the requirements of European Commission's conservation policy goals and to provide a starting point for future evaluations of the network. The future effectiveness of the PAs has been already evaluated under climate change (Araújo *et al.*, 2007; D'Amen *et al.*, 2011; Johnston *et al.*, 2013) and land use change (Pouzols *et al.*, 2014) scenarios at large scales for a variety of species groups, but their interactions at fine scale in dynamic landscapes have not been considered yet. In fire-prone ecosystems like in the Mediterranean region, the effect of wildfires and fire suppression policies should be explicitly considered as they are expected to interact closely with climate change and to produce a range of positive and negative effects on biodiversity (Taylor *et al.*, 2013; Vallecillo *et al.*, 2013; Kelly *et al.*, 2014). In this respect, forest management practices and vegetation encroachment in previously abandoned cultivated areas are key driving forces as they may affect natural fire regimes and, in turn, land cover dynamics in the short to medium term (e.g. James *et al.*, 2007; De Cáceres *et al.*, 2013; Herrando *et al.*, 2014).

Here we integrated climate change scenarios at continental scale with simulations of vegetation dynamics at regional scale in a hierarchical manner to evaluate the future combined effect of multiple driving forces on a sample of conservation interest bird species. We used a storyline-and-simulation approach (De Chazal & Rounsevell, 2009) where storylines describe potential fire suppression and land management policies in a Mediterranean-type ecosystem, and simulations reinforce storylines with numerical estimates of future environmental changes. We predicted changes in the distribution of 23 bird species of conservation interest included in the Birds Directive under climate change and novel fire regime scenarios between 2000 and 2050. We focused on the distribution changes in bird species that are expected to respond to fire, vegetation encroachment and climate change in the future. Based on the future predictions, we assessed the long-term effectiveness of N2000 in allowing the future persistence of relevant habitats for these target species in Catalonia. To evaluate whether N2000 will ensure its key conservation role in the next decades, we tested the hypothesis that relevant habitats for the target bird species will be more efficiently preserved within this network of PAs than in areas without such a European protection status.

## METHODS

### Study area

The study was conducted in Catalonia, a region located in north-eastern Spain with a typical Mediterranean climate (Fig. 1). Its complex topography induces an important geographical variability in climate and weather conditions. The vegetation mainly includes forest and shrubland (CORINE, 2006), two land cover types that are most affected by fire (Díaz-Delgado *et al.*, 2004). Land abandonment due to the cessation of agricultural activities over the last decades has been followed by the conversion from abandoned open land (i.e. shrublands) to forest habitats (Herrando *et al.*, 2014). The interaction among such vegetation encroachment, fire suppression and climate change induces important modifications of the fire disturbance regime in this Mediterranean study region (Brotons *et al.*, 2013).

There are 115 Sites of Community Importance (SCIs) designed for the protection of habitats and species of Community interest (Habitats Directive) and 73 Special Protection Areas (SPAs) designed for the protection of birds of Community interest (Birds Directive) in Catalonia (Fig. 1). SCIs and SPAs cover 32% and 28% of the region, respectively, and their total combined extent is 10,624 km<sup>2</sup>, 87% of which is covered by both SCIs and SPAs (GENCAT, 2013).

### Bird data

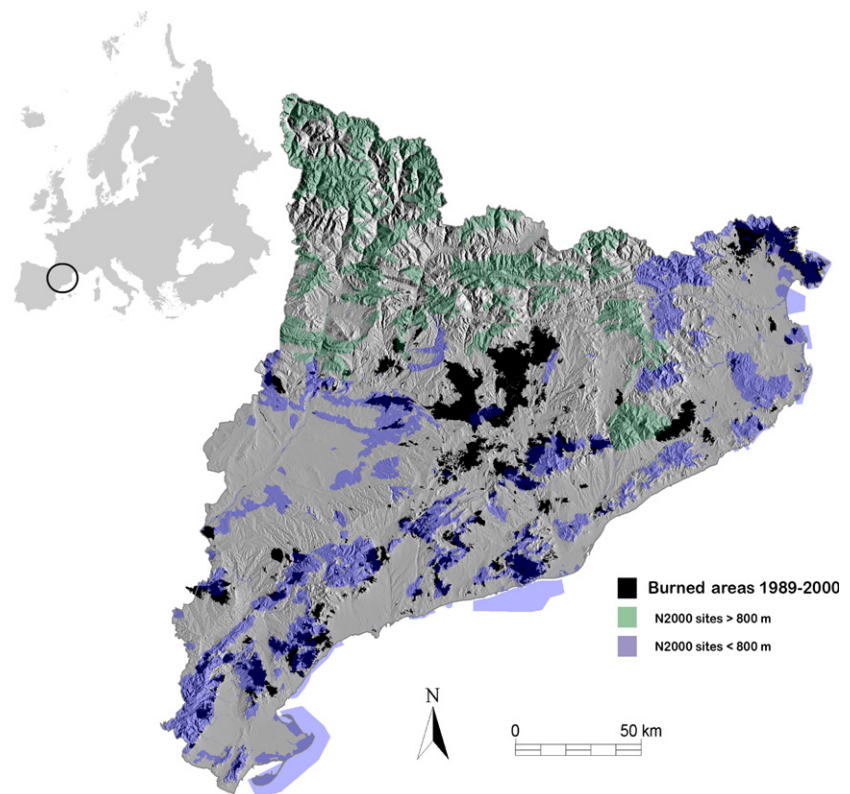
We used presence/absence data for breeding bird species at two different spatial extents and resolutions: (1) European

extent at a 50 km resolution and (2) Catalan extent at a 1 km resolution.

At the European level, bird data were obtained from the *EBCC Atlas of European Breeding Birds* (EBCC; Hagemeyer & Blair, 1997, available at <http://s1.sovon.nl/ebcc/eoa/>). This dataset documents the occurrence of breeding bird species in the 3165 50 km resolution squares in Europe according to a Universal Transverse Mercator (UTM) grid. Field data were mostly collected during the late 1980s and early 1990s.

At the Catalan level, bird data were obtained from the *Catalan Breeding Bird Atlas* (CBBA; Estrada *et al.*, 2004, available at <http://www.sioc.cat/atles.php>). The CBBA resulted from a large-scale survey conducted between 1999 and 2002 to cover the whole of the Catalonia using a grid system with 10 km resolution UTM squares. A total of 3076 1 km resolution squares (*c.* 9% of the total area) were selected to conduct standardized intensive surveys of species presence in a stratified fashion to cover the main habitat types present within each of the 10 km resolution squares (Hirzel & Guisan, 2002).

Among the 214 bird species that commonly breed in Catalonia, we only selected those included in the Annex I from the Birds Directive (European Parliament, 2010). We chose this set of species as indicators of conservation value at the European level, as they have a legal conservation status in Europe. From this set, we removed those species with < 30 occupied 1 km squares in Catalonia to ensure sufficient information is available for further analyses. As we focused here on the combined effect of climate change, vegetation encroachment due to land abandonment and fire regime on



**Figure 1** Location of the study area in Europe (black circle) and spatial distribution of the N2000 sites and wildfires occurred in Catalonia between 1989 and 2000.

birds, we also excluded those species that are not breeding in habitat types along the gradient from abandoned open land to forest. Hence, we focused on 23 species exhibiting different degrees of specialization from open habitats (i.e. early-successional stages and sparsely vegetated areas) to forest.

### Climate data

We obtained current climate data (period 1950–2000; hereafter 2000s) from the WorldClim database ([www.worldclim.org/current](http://www.worldclim.org/current)) and future climate scenarios (period 2040–2069; hereafter 2050s) from International Center for Tropical Agriculture (CIAT) (<http://www.ccafs-climate.org>). Future climate change projections were computed for A2 and B2 IPCC-SRES scenarios from an average ensemble model of four GCMs (CCCMA-CGCM2, CSIRO-MK2.0, HCCPR-HadCM3 and NIESS99) to account for the uncertainty arising from the intermodel variability (see Appendix S1). These four GCMs were selected as they provide a range of variability with respect to annual temperature and cumulative precipitation predictions (Naujokaitis-Lewis *et al.*, 2013). These projections were available at 30 arc seconds (*c.* 1 km) resolution and were resampled by estimating mean value within the specified grid cell to match the resolution of bird data in Europe and in Catalonia.

### Landscape data

We used the MEDFIRE model to simulate future land cover changes derived from spatial interactions among fire regime, vegetation dynamics and fire management policies (Brotons *et al.*, 2013; De Cáceres *et al.*, 2013; Regos *et al.*, 2014). MEDFIRE is based on observed time series to simulate the future effect of primary processes driving vegetation dynamics and fire regime in the landscape (see Appendix S2). Vegetation encroachment due to land abandonment (hereafter land abandonment) is explicitly integrated into MEDFIRE to simulate the succession from abandoned open land to forest and its interaction with fire regime. To deal with the stochastic nature of wildfires, the land cover layers were then simulated 10 times (hereafter runs) for 2050 under the different combinations of six fire management scenarios and two climate change scenarios (Table 1, Appendix S2). To describe predicted vegetation changes under each scenario, we used the outputs of the simulation runs and we calculated the area occupied by each land cover type. Some land cover types do not influence fire dynamics (i.e. water, rocks and urban areas), whereas farmland was assumed to be static but to allow fire to spread through it. Fire can affect farmlands, but they do not directly shift to other habitat types after fire unless an additional land use change occurs.

### Modelling framework

To estimate potential changes in habitat suitability for the target species between 2000 and 2050, we used a hierarchical

approach integrating climate and land cover change scenarios at different scales in the same modelling framework (more details in Appendix S3). This approach required the following steps:

#### *Step 1. – Climate models at the European level*

We fitted species distribution models from EBCC bird data and climate variables at the European scale (hereafter climate models) to estimate the bioclimatic envelope of each species (Araújo *et al.*, 2005a; Barbet-Massin *et al.*, 2012). Model predictions under both current and future climate conditions were directly downscaled (Araújo *et al.*, 2005b; McPherson *et al.*, 2006) within the 1 km resolution squares in Catalonia.

#### *Step 2. – Land cover models at the Catalan level*

Higher resolution models for the target species were built from the CBBA bird data and land cover variables derived from the MEDFIRE model at the Catalonia level (hereafter land cover models). We predicted the probability of occurrence within each 1 km resolution square in Catalonia under current and future land cover scenarios.

#### *Step 3. – Combined models at the Catalan level*

Combined climate and land cover models (hereafter combined models) were built using the same dependent variables (bird occurrence from CBBA) and the same resolution (1 km) and extent (Catalonia) as in *Step 2*. They were developed using two predictors: (1) the outcomes of the climate model at 1 km resolution (*Step 1*) and (2) the outcomes of the land cover model at 1 km resolution (*Step 2*).

All the models were trained using five widely used algorithms (GLM, GAM, CTA, GBM and RF) implemented in the BIOMOD2 library in R (Thuiller *et al.*, 2009). We used a repeated (10 times) split-sample approach to produce predictions independent of the training data. Each model was fitted using 70% of the data and evaluated using the area under the curve (AUC) of a receiver operating characteristics (ROC) (Fielding & Bell, 1997) calculated on the remaining 30%. We applied an ensemble-forecasting framework by computing a consensus of single-model projections (from models with AUC > 0.7 using AUC values as model weights) using a weighted average approach (Araújo & New, 2007; Marmion *et al.*, 2009).

To quantify the changes in the effectiveness of N2000 between 2000 and 2050, high-quality habitats (hereafter optimal habitats) for the species need to be firstly identified. Probability outputs were hierarchically ranked in two levels of increasing suitability (Herrando *et al.*, 2011; Arcos *et al.*, 2012) (see Appendix S4 for a sensitivity analysis in selecting thresholds). These optimal habitat areas can be interpreted as critical habitats for our study species in line with the conservation mandate of the European directives.



**Table 1** List of fire regime scenarios simulating future land cover changes in the study area. Each scenario is a combination of a climate (A2 and B2) and a fire management (BioFS, UnFS or HighFS) treatment. Asterisks indicate the business-as-usual scenarios. For more details, see Regos *et al.* (2015) and Appendix S2

ID	Scenario acronym	Scenario description	Storyline	Incentives/Constrains
1	BioFS + A2	Forest harvesting in optimal areas from an environmental and economic viewpoint (c. 39,000 hectares annually extracted) + climate trend according to the A2 IPCC-SRES climate scenario	Forest biomass extraction	Forest biomass extraction is prohibited in protected areas
2	BioFS + B2	Forest harvesting in optimal areas from an environmental and economic viewpoint (c. 39,000 hectares annually extracted) + climate trend according to the B2 IPCC-SRES climate scenario	Forest biomass extraction	Forest biomass extraction is prohibited in protected areas
3	BioFS + A2 plus	Forest harvesting in optimal areas from a logistic and economic viewpoint (c. 62,000 hectares annually extracted) + climate trend according to the A2 IPCC-SRES climate scenario	Forest biomass extraction	Forest biomass extraction is allowed in protected areas
4	BioFS + B2 plus	Forest harvesting in optimal areas from a logistic and economic viewpoint (c. 62,000 hectares annually extracted) + climate trend according to the B2 IPCC-SRES climate scenario	Forest biomass extraction	Forest biomass extraction is allowed in protected areas
5	UnFS + A2	An opportunistic fire suppression strategy based on lowly decreasing active firefighting efforts in controlled 'mild' fire weather conditions to provide further firefighting opportunities in adverse years + climate trend according to the A2 IPCC-SRES climate scenario	Let-burn	6500 hectares annually burnt in climatically mild years
6	UnFS + B2	An opportunistic fire suppression strategy based on lowly decreasing active firefighting efforts in controlled 'mild' fire weather conditions to provide further firefighting opportunities in adverse years + climate trend according to the B2 IPCC-SRES climate scenario	Let-burn	6500 hectares annually burnt in climatically mild years
7	UnFS + A2 plus	An opportunistic fire suppression strategy based on highly decreasing active firefighting efforts in controlled 'mild' fire weather conditions to provide further firefighting opportunities in adverse years + climate trend according to the A2 IPCC-SRES climate scenario	Let-burn	52,000 hectares annually burnt in climatically mild years
8	UnFS + B2 plus	An opportunistic fire suppression strategy based on highly decreasing active firefighting efforts in controlled 'mild' fire weather conditions to provide further firefighting opportunities in adverse years + climate trend according to the B2 IPCC-SRES climate scenario	Let-burn	52,000 hectares annually burnt in climatically mild years
9*	Base + HighFS + A2	Strong active fire suppression management corresponding to currently implemented strategy + climate trend according to the A2 IPCC-SRES climate scenario	Stop all fires	–
10*	Base + HighFS + B2	Strong active fire suppression management corresponding to currently implemented strategy + climate trend according to the B2 IPCC-SRES climate scenario	Stop all fires	–
11	NoFS + A2	No fire suppression strategy + climate trend according to the A2 IPCC-SRES climate scenario	No suppression	–
12	NoFS + B2	No fire suppression strategy + climate trend according to the B2 IPCC-SRES climate scenario	No suppression	–

### Evaluation of simulation outcomes

To disentangle the relative role of climate change and land cover change in shaping the future distribution of the target species, we categorized the distribution change of the different species to each of these driving forces as positive, negative or neutral. To do so, we first estimated for each species the number of squares with optimal habitats in 2000 and for each scenario in 2050 according to the climate, land cover and combined models. Second, we calculated the relative changes in this number of squares between 2000 and 2050 (see Appendix S5). The number of species expected to be

potentially affected by fire-induced land cover changes within a general context of climate change and land abandonment was estimated using generalized linear models (GLMs) with a Gaussian error distribution and 'identity' link function (Guisan *et al.*, 2002) (see Fig. S5.2). The effects were considered as significant at  $P < 0.05$ , and the number of species associated with a significant effect of fire suppression strategies in these GLMs was counted.

To summarize the response of bird species assemblages under each scenario, we counted the number of species predicted to gain or lose < 20%, between 20 and 50%, or more than 50% of squares with optimal habitats between 2000 and

2050, inside and outside N2000. To assess the extent to which N2000 will likely be able to maintain its role to ensure the persistence of key habitats for the target species under climate and land cover change scenarios, we first calculated the percentage of squares with optimal habitats inside N2000 relative to those in the whole study area and we used this percentage as a measure of effectiveness of N2000 in 2000 ( $Eff_{2000}$ ) and in 2050 ( $Eff_{2050}$ ). We tested whether the results inside and outside N2000 were significantly different using a Wilcoxon signed rank test for paired samples. Second, increase or decrease in effectiveness was estimated from the difference between  $Eff_{2050}$  and  $Eff_{2000}$  for each species under each scenario (Appendix S6). Third, we calculated the number of species for which N2000 is expected to increase or decrease in effectiveness by < 5%, by 5% to 10% and by more than 10% between 2000 and 2050.

In addition to a global analysis of the results over the whole N2000 network, we also explored the geographical variation in the decrease/increase of the number of squares with optimal habitats for the species and in the effectiveness of N2000 along the latitudinal/altitudinal gradient in Catalonia. We split the N2000 sites into two sets of PAs associated with different elevation ranges: (1) above 800 metres (> 800 m) and (2) below 800 metres (< 800 m) (Fig. 1). This elevation threshold was used to distinguish between PAs

predominantly located in mountain areas (north of Catalonia) from those in the lowlands (south). The results obtained above and below 800 m were compared through a Wilcoxon signed rank test for paired samples.

## RESULTS

### Model accuracy

Climate models calibrated at the European scale efficiently captured the climate envelope of the species (mean  $AUC_{EU-CLIM} = 0.97$ ), but when they were compared to the known distribution of the species in Catalonia, they fit only weakly because of low specificity values (mean  $AUC_{CAT-CLIM} = 0.54$ , Table 2). At such resolution, the distribution of the species is also constrained by land cover related factors, but down-scaled climate models were considered as useful as they were able to capture the broad climate envelope of the species (mean sensitivity values above 0.70). The predictions based on climate variables could be subsequently refined with the inclusion of land cover variables at the Catalan level, as indicated by the higher predictive accuracy of the combined models (mean  $AUC_{CLIM+LCT} = 0.93$ ) than that of the models based on land cover variables only (mean  $AUC_{LCT} = 0.89$ ) (Table 2).

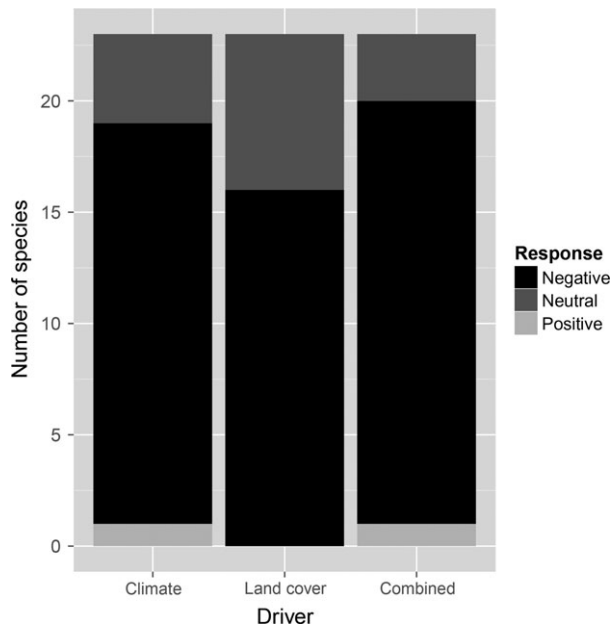
**Table 2** Evaluation of predictive performance for ensemble models built with land cover variables only (Land cover), climate variables only downscaled from the European to the Catalan level (Climate) and with climate and land cover variables according to a multiscale hierarchical integration approach (Combined) for each bird species. AUC values are calculated for land cover, climate and combined models, whereas sensitivity and specificity are given only for climate models

Species	Acronym	AUC			Sensitivity Climate	Specificity Climate
		Land cover	Climate	Combined		
<i>Anthus campestris</i>	ANCAM	0.912	0.590	0.957	0.91	0.18
<i>Aquila chrysaetos</i>	AQCHR	0.863	0.800	0.952	0.56	0.79
<i>Bubo bubo</i>	BUBUB	0.838	0.550	0.891	0.25	0.65
<i>Caprimulgus europaeus</i>	CAEUR	0.701	0.610	0.727	0.95	0.20
<i>Circaetus gallicus</i>	CIGAL	0.676	0.580	0.708	0.84	0.25
<i>Dryocopus martius</i>	DRMAR	0.913	0.910	0.98	0.89	0.84
<i>Emberiza hortulana</i>	EMHOR	0.926	0.600	0.969	0.66	0.54
<i>Falco peregrinus</i>	FAPER	0.818	0.540	0.859	0.99	0.00
<i>Galerida theklae</i>	GATHE	0.919	0.790	0.958	0.90	0.53
<i>Gypaetus barbatus</i>	GYBAR	0.926	0.840	0.984	0.25	0.96
<i>Gyps fulvus</i>	GYFUL	0.868	0.560	0.941	0.32	0.80
<i>Hieraaetus fasciatus</i>	HIFAS	0.98	0.750	0.997	0.91	0.39
<i>Hieraaetus pennatus</i>	HIPEN	0.901	0.650	0.971	0.61	0.68
<i>Lanius collurio</i>	LACOL	0.898	0.870	0.969	0.98	0.52
<i>Lullula arborea</i>	LUARB	0.76	0.670	0.883	0.94	0.14
<i>Milvus migrans</i>	MIMIG	0.811	0.550	0.866	0.60	0.38
<i>Milvus milvus</i>	MIMIL	0.936	0.750	0.991	0.82	0.68
<i>Neophron percnopterus</i>	NEPER	0.905	0.580	0.968	0.21	0.76
<i>Oenanthe leucura</i>	OEURA	0.997	0.770	0.999	0.77	0.62
<i>Pernis apivorus</i>	PEAPI	0.868	0.730	0.926	0.63	0.69
<i>Pyrrhocorax pyrrhocorax</i>	PYRAX	0.91	0.660	0.963	0.64	0.64
<i>Sylvia undata</i>	SYUND	0.898	0.570	0.947	0.81	0.29
<i>Tetrao urogallus</i>	TEURO	0.976	0.960	0.997	0.88	0.90
Mean		0.878	0.690	0.930	0.71	0.54

### Predicted changes in habitat suitability for birds

A wide range of bird responses to climate change, to land cover change and to their combined effect were found. Overall, a larger number of species were predicted to show a negative than a positive response to climate change and to land cover changes (see effects of both drivers on Fig. 2 and Table S5.1). The combined effect of climate and land cover change in the future was therefore predicted to be negative for most of the target species (Fig. 2): only 3 and 1 species were predicted to show a neutral or positive response, respectively. For most species, a stronger effect (either positive or negative) of climate change was expected under the A2 than under the B2 scenario (Fig. 3 and Table S5.2). According to the results of the GLMs, 18 species of the 23 studied ones will potentially be affected by decisions in relation to the implementation of future fire suppression strategies within the general context of climate change and land abandonment, especially in lowland areas below an average elevation of 800 metres (Fig. S5.1 and S5.2).

Overall, the amount of optimal habitat in N2000 was significantly larger than non-protected areas in 2000 (Wilcoxon signed rank test,  $P < 0.05$ ) and especially in 2050 ( $P < 0.001$ ). Our results showed a strong decrease in the number of squares with optimal habitats for the target species between 2000 and 2050, both inside and outside N2000 (Fig. 3a,b). Inside N2000, although the amount of optimal habitat above and below 800 metres was not found to be significantly different ( $P > 0.05$ ), the largest decreases were predicted in PAs below 800 metres, indicating a latitudinal/altitudinal gradient in the expected changes (Fig. 3c,d). Changes in the amount of



**Figure 2** Number of species predicted to have a positive, negative or neutral response across the alternative climate, land use or combined models between 2000 and 2050. See detailed results for each species in Table S5.1.

optimal habitats largely varied among species and scenarios (see details in Appendix S5). The smallest decreases were predicted under scenarios of fire suppression strategies based on letting unplanned fires burn during mild weather conditions (UnFS plus in Fig. 3). This strategy is predicted to be particularly effective to counterbalance the negative effect of land abandonment in areas below 800 metres for open-habitat bird species such as the Ortolan Bunting (*Emberiza hortulana*) or the Dartford Warbler (*Sylvia undata*) (Fig. S5.1). The greatest number of species with decreasing amount of optimal habitats was found under business-as-usual scenarios (Base + HighFS scenarios in Fig. 3a,b). A great number of species were also predicted to undergo a decrease in the amount of optimal habitats outside PAs under forest biomass extraction scenarios (Fig. 3b), but this decrease is expected to be slightly smaller inside PAs (Fig. 3a).

### Predicted changes in N2000 effectiveness

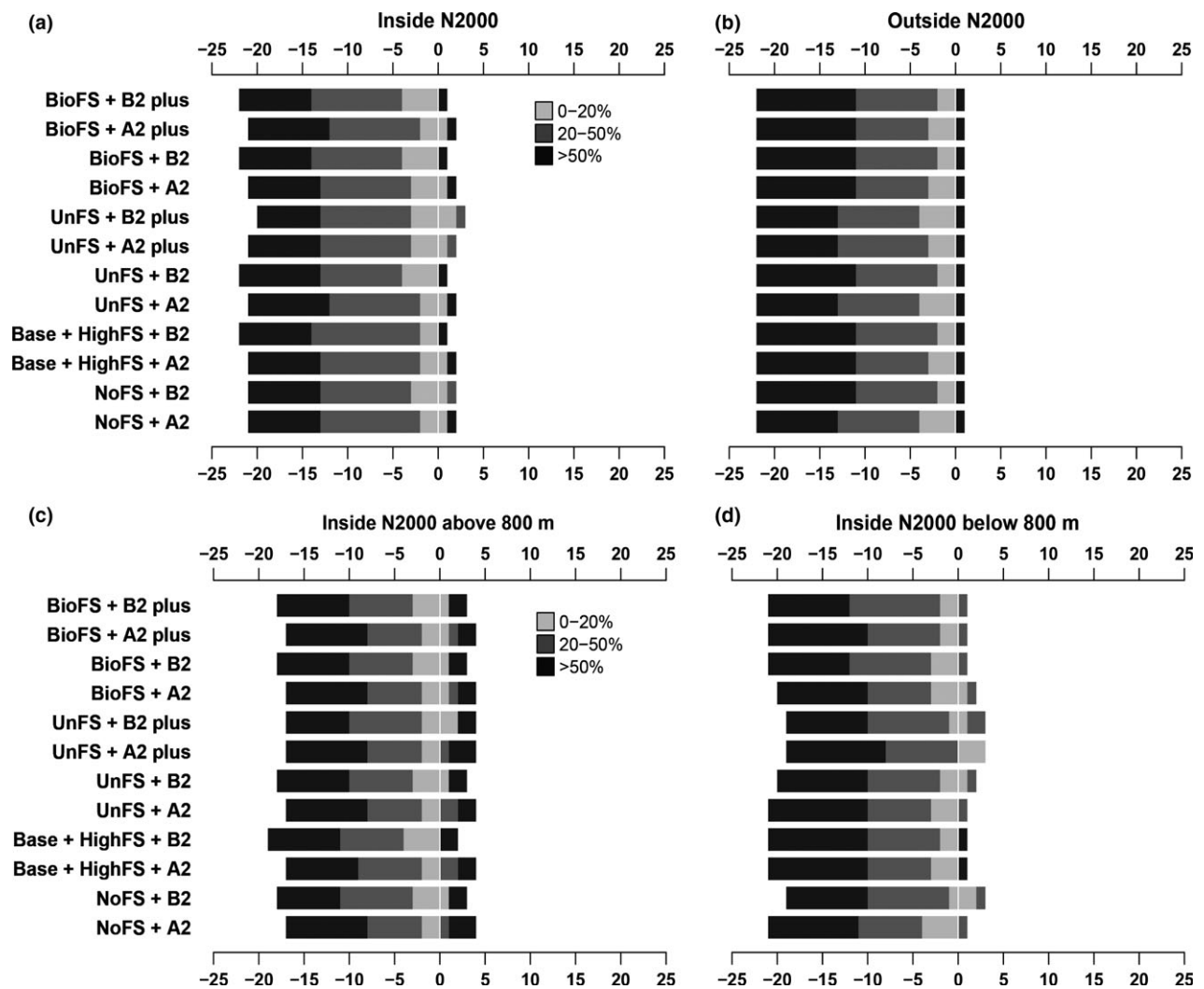
The future effectiveness of N2000 was expected to largely depend on the target species and the scenario of environmental change (Fig. 4a). Overall, the number of squares with optimal habitats for the target species is predicted to decrease less inside than outside N2000 (Fig. 4a,b). Hence, the effectiveness of N2000 will likely increase between 2000 and 2050, especially at elevations higher than 800 m (Fig. 4b). The potential of fire management policies to indirectly affect this effectiveness through fire-induced changes in the amount of optimal habitats will be higher in areas below 800 m (Figs 4c and S3).

## DISCUSSION

### Losses and gains in habitat suitability

To our knowledge, the present study is one of the most ambitious attempts so far to forecast biodiversity changes (i.e. multispecies responses) based on simulations of future vegetation dynamics and fire disturbance under climate change in a fire-prone Mediterranean region. The multiscale approach we implemented allowed us to predict the future changes in habitat suitability for conservation-concern bird species as a response to climate change and vegetation dynamics driven by fire-related disturbance regime and land abandonment. Our findings show that although the future response of the species to these changes is species specific, large decreases in the amount of optimal habitats are expected for most of the species (Fig. 3). In addition, our results also indicate that such a decrease in habitat suitability will be driven by both climate and land cover changes (Fig. 2). Interestingly, the response of a high number of species to these changes is predicted to vary substantially depending on the fire management practices that will be implemented in the future (Fig S5.2).

Despite the huge resources invested in fire suppression over the last decades in the Mediterranean region, wildfires



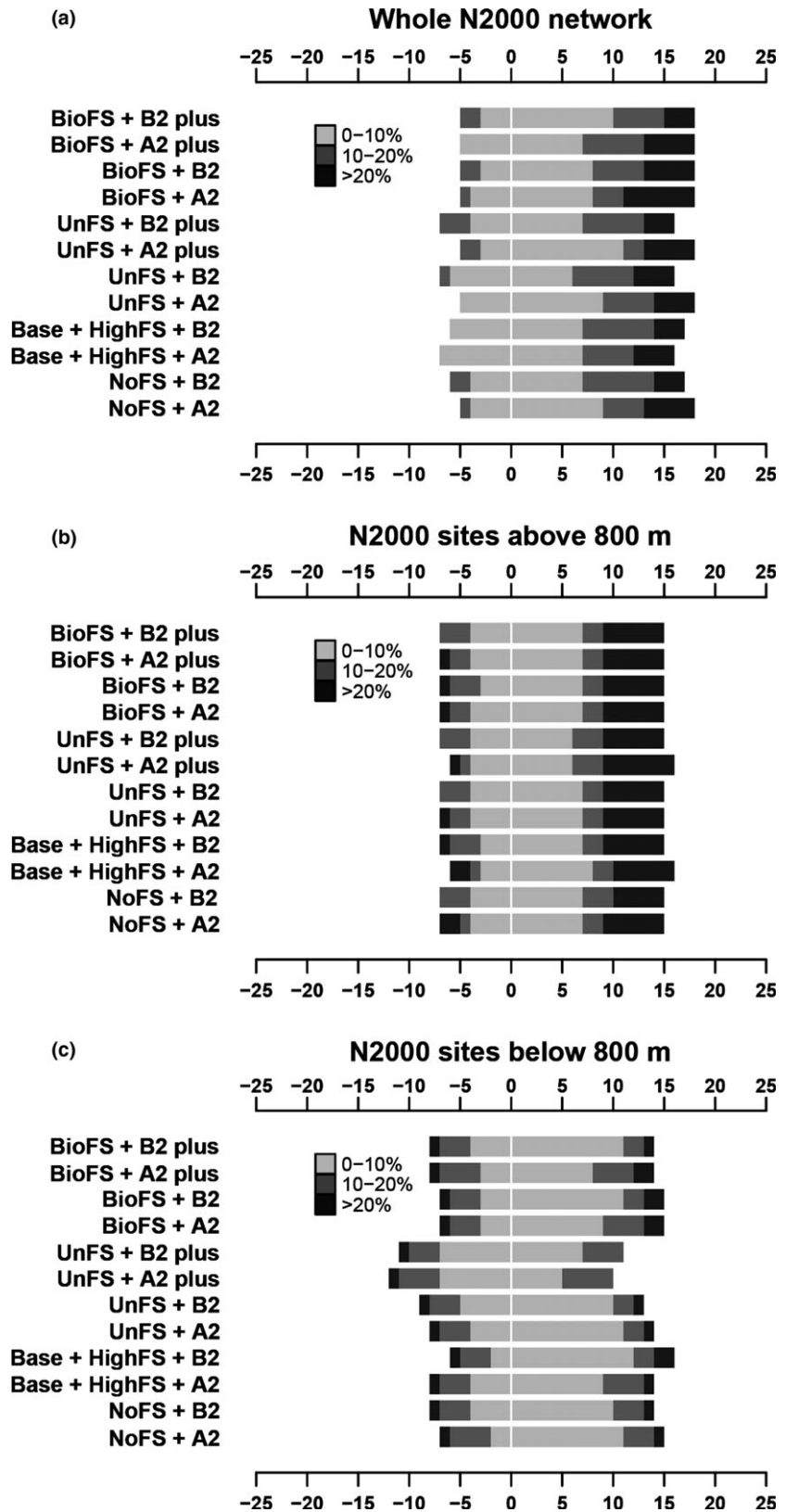
**Figure 3** Number of species predicted to gain (positive values) or lose (negative values) < 20% (low-light grey), between 20 and 50% (medium-light grey) and more than 50% (dark grey) of their optimal habitats between 2000 and 2050 under each future scenario (see Table 1 for acronyms): (a) inside N2000, (b) outside N2000, (c) inside N2000 above 800 m and (d) inside N2000 below 800 m. Bar length reflects mean number of species across the different MEDFIRE runs simulating land cover changes.

are expected to increase their impact as a result of an interaction between vegetation encroachment due to land abandonment (Loefer *et al.*, 2010; Moreira *et al.*, 2011) and harsher (i.e. drier and/or warmer) climate conditions (Piñol *et al.*, 1998; Turco *et al.*, 2014). The fire management option that is typically implemented in the study area involves large fire suppression efforts regardless of the climatic severity of the year. It is expected that this strategy will continue to be applied in a near future. According to our simulations, the greatest number of species with a decreasing amount of optimal habitats in the future is predicted under these business-as-usual scenarios (Base + HighFS scenarios). This pattern results from a combination between a negative effect of land abandonment and fire suppression strategies on open-habitat species and a negative impact of climate change on cold-dwelling forest species (Fig. 3 and Table S5.1).

Reducing fire suppression efforts in mild weather conditions is an alternative but hotly debated strategy that consists

in using unplanned fires and associated fuel reduction to create opportunities for suppression of large fires in future adverse weather conditions (Regos *et al.*, 2014). Our projections revealed that the negative impact of land cover change on open-habitat bird species such as the Ortolan Bunting or the Dartford Warbler (De Cáceres *et al.*, 2013; Regos *et al.*, 2015) is expected to be significantly less important when projecting species distribution changes under such a novel fire management strategy (Fig. S5.2). There are more opportunities to create new open habitats for these species through changes in fire regime below than above 800 metres elevation (Figs 3d and S5.1), where a larger number of fire events are predicted. These findings are consistent with previous studies suggesting that heterogeneous landscapes induced by fire management aimed at creating uneven shrubland patches may potentially enhance the resilience of threatened open-habitat species in an overall land abandonment context (Brotons *et al.*, 2005; Vallecillo *et al.*, 2007; Zozaya *et al.*, 2010).





**Figure 4** Number of species for which N2000 effectiveness is predicted to increase (positive values) and decrease (negative values) by < 5% (low-light grey), by 5–10% (medium-light grey) and by more than 20% (dark grey) between 2000 and 2050 for each future scenario (see Table 1 for acronyms): (a) whole N2000 network, (b) N2000 sites above 800 m and (c) N2000 sites below 800 m. Bar length reflects mean number of species across the different MEDFIRE runs simulating land cover changes.

The obtained projections and the relative roles of the various drivers were different for forest-dwelling birds. For this group of species, climate change was predicted to override the effect of fire management in the future. Scenarios based

on forest biomass extraction for energy purposes (Evans & Finkral, 2009) were included in the analysis because we expected forest birds to benefit from such fire management strategy in the future through a reduction in the impacts of

wildfires in forested areas. However, for those species, the decrease in habitat suitability under biomass extraction scenarios was only slightly, and not significantly, lower than in business-as-usual scenarios (Base + HighFS scenarios in Fig. 3). In addition, when the direct impact of climate change is taken into account in our multiscale combined models, forest specialist species, such as the Western Capercaillie (*Tetrao urogallus*) or the Black Woodpecker (*Dryocopus martius*), were predicted to be almost insensitive to the different fire suppression strategies (Fig. S5.2). Those species are distributed in the northernmost areas, that is the least fire-affected areas in Catalonia (Díaz-Delgado *et al.*, 2004 and Fig. 1), and climate change is therefore expected to have the strongest effect in determining their future distribution. As a result, such forest species are predicted to undergo decreases in the amount of their optimal habitats over the next decades primarily due to climate-induced north- and upward shifts in their distribution. It is not surprising to find large decrease in habitat suitability for cold-dwelling forest species in a context of climate warming (Huntley *et al.*, 2008), especially for those species that have in north of Spain the southern margin of their distributional range (e.g. Black woodpecker; Hagemeyer & Blair, 1997).

Overall, our projections suggest that fire management practices aimed at decreasing fire impact through the creation of new early-successional stages and sparsely vegetated areas by letting unplanned fires burn during mild weather conditions are the best option to help reduce the decline of open-habitat species in a context of land abandonment. At the same time, such strategy is not expected to have negative side effects on forest specialist species: future habitat suitability for these species is mostly driven by climate change (negative effect) and forest expansion under land abandonment (positive effect) (see also Gil-Tena *et al.*, 2009). Conservation efforts for these forest specialist species should focus on increasing the resilience of key forest habitats (*Pinus sylvestris* and *P. uncinata*) to climate change. Such regional objectives may be potentially achieved through adaptive forest management (Gil-Tena *et al.*, 2010; Keskkitalo, 2011; Kolström *et al.*, 2011).

### The role of N2000 in the near future

Our results provide the first assessment of the future effectiveness of the currently established protected areas for the conservation of bird species targeted by N2000 under different combinations of climate and novel fire regime scenarios. The effectiveness of N2000 for the protection of the target conservation interest bird species will likely increase over the next decades as the proportion of optimal habitats within N2000 relative to the whole of Catalonia is predicted to increase (Fig. 3). This result highlights the key role that the current N2000 network will play in the near future to maintain suitable habitats for open-habitat and forest bird species of European conservation interest in fire-prone, highly dynamic Mediterranean ecosystems. In a context of climate change and especially in lowland areas, this effectiveness may

be considerably improved through the implementation of novel fire management strategies that are not in line with those that have been typically implemented so far (Fig. 4c).

Our results suggest that climate-induced north- and upward shifts in the geographical distribution of a large sample of species will take place in the region. As it has also been shown at the European level (Araújo *et al.*, 2011; Thomas & Gillingham, 2015), mountain areas will therefore likely remain a stronghold for most of the cold-dwelling species in Catalonia. As mountains are well covered with protected areas in Catalonia, this could explain that the effectiveness of N2000 is predicted to be higher at sites above 800 metres for these species. As for warm-dwelling bird species, they were predicted to mostly benefit from climate change but, above all, such open-habitat species were expected to undergo strong declines due to land abandonment processes in lowland areas. For the conservation of their suitable habitats in the future, N2000 is predicted to be less efficient and novel fire management policies would be particularly relevant.

Recent studies assessing present and future effectiveness of PAs for biodiversity conservation under climate change have found discrepancies among taxa (Maiorano *et al.*, 2006; Araújo *et al.*, 2007; Lisón *et al.*, 2013). For instance, while some studies reported larger decrease in suitable habitats for birds outside than inside PAs (Araújo *et al.*, 2011; Virkkala *et al.*, 2013; Gillingham *et al.*, 2015), other authors drew attention to the limited effectiveness of PAs in protecting amphibians and lichen species (D'Amen *et al.*, 2011; Rubio-Salcedo *et al.*, 2013). This pattern might be explained by the lack of consideration for non-charismatic species groups in the design of PAs. The bird-targeted SPAs in Catalonia cover 87% of the whole of N2000, which indicates a large overlap with SCIs and contributes to explaining the important role that N2000 will likely play for bird conservation in the near future in Catalonia. Besides, SCIs are indirectly protecting relevant habitats for most of the target species. A multitaxa approach is now warranted to address the impact of global change on a variety of species associated with a range of ecological requirements and life history traits, as birds may perform only fairly as surrogates of biodiversity (Larsen *et al.*, 2012).

Although the effectiveness of N2000 is expected to increase in the future (Fig. 4), the total amount of optimal habitats for conservation interest birds will strongly decrease both inside and outside the network. First, this sheds light on the need to implement proactive conservation strategies inside N2000 so as to maintain and improve biodiversity conservation under changing environmental conditions (Heller & Zavaleta, 2009; Bush *et al.*, 2014). Second, our simulations showed an even more important decrease in habitat suitability in the unprotected areas surrounding the PAs (Fig. 3b). Population viability can decline considerably as a result of large losses on temporal availability of optimal habitats due to the loss of connectivity between patches, often exacerbated by dispersal constraints (Gil-Tena *et al.*, 2012; Mazaris *et al.*, 2013; Saura *et al.*, 2014). Such habitat loss outside PAs could

compromise the future chances to ensure species conservation status within the conservation network (Cabeza, 2003; Cabeza & Moilanen, 2003; Rayfield *et al.*, 2008). Biodiversity management actions should also focus on maintaining suitable habitats in unprotected areas if we are to guarantee the medium- and long-term conservation of bird diversity (Brambilla *et al.*, 2014).

This study offers novel insights into how fire management policies in interaction with land abandonment and climate change might strongly impact on future biodiversity conservation in fire-prone Mediterranean ecosystems. Based on a hierarchical modelling approach integrating climate and land cover change scenarios at different scales, we draw attention to the key role that the current N2000 network might play in the near future. We also emphasize the need for an integrative and proactive conservation perspective wherein agricultural, forest and fire management policies should be considered inside and outside N2000 to effectively maintain key habitats for threatened birds in these types of ecosystems. In the light of our results, we underline the need for an explicit consideration of landscape dynamics when forecasting the future effectiveness of a network of protected areas in a context of global change.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Appendix S1.** Detailed information on climate scenarios: degree of similarity among the four GCMs and the multimodel mean consensus GCM.

**Table S1.** The Pearson correlation quantifies the similarities in spatial patterns between each individual general circulation model (GCM) variable and the multimodel mean ensemble for the same variable for the 2050 for two emission scenarios (A2a and B2a).

**Appendix S2.** Detailed information on land cover scenarios: storylines and simulations.

**Appendix S3.** Complete description of the modelling framework —uncertainties and limitations.

**Appendix S4.** Complete description of binary conversion procedure: Sensitivity analysis in selecting thresholds.

**Figure S4.** Predicted percentage of change in the effectiveness of N2000 for preserving the optimal habitats for the target species between 2000 and 2050 from different thresholds in binary conversion.

**Appendix S5.** Changes in habitat suitability for each bird species under climate and/or land cover change scenarios.

**Table S5.1.** Predicted percentage of gains and losses in the amount of optimal habitats for the target species between 2000 and 2050 averaged across the different scenarios of future environmental changes.

**Table S5.2.** Predicted percentage of gains and losses in the amount of optimal habitats for the target species between 2000 and 2050 under A2 and B2 climate change scenarios.

**Figure S5.1.** Predicted percentage of gains and losses in the amount of optimal habitats for the target species between 2000 and 2050 in N2000 sites above and below an average elevation of 800 metres under each scenario of future change according to the combined models.

**Figure S5.2.** Predicted percentage of gains and losses in the amount of optimal habitats for the target species between 2000 and 2050 inside N2000 under each scenarios of future change and according to the combined models and the land cover models.

**Appendix S6.** Changes in the effectiveness of N2000 for the conservation each bird species under climate and land cover change scenarios.

**Figure S6.** Predicted percentage of change in the effectiveness of N2000 for preserving the optimal habitats for the target species between 2000 and 2050 under each scenario of future environmental changes according to the combined models.

## BIOSKETCH

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