

Accounting for uncertainty in assessing the impact of climate change on biodiversity hotspots in Spain

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Abstract

Accounting for uncertainty in assessing the impact of climate change on biodiversity hotspots in Spain. Our limited understanding of the complexity of nature generates uncertainty in mathematical and cartographical models used to predict the effects of climate change on species' distributions. We developed predictive models of distributional range shifts of threatened vertebrate species in mainland Spain, and in their accumulation in biodiversity hotspots due to climate change. We considered two relevant sources of climatological uncertainty that affect predictions of future climate: general circulation models and socio-economic scenarios. We also examined the relative importance of climate as a driver of species' distribution and taxonomic uncertainty as additional biogeographical causes of uncertainty. Uncertainty was detected in all the forecasts derived from models in which climate was a significant explanatory factor, and in the species with taxonomic uncertainty. Uncertainty in forecasts was mainly located in areas not occupied by the species, and increased with time difference from the present. Mapping this uncertainty allowed us to assess the consistency of predictions regarding future changes in the distribution of hotspots of threatened vertebrates in Spain.

Key words: Climate change, Prediction accuracy, Taxonomic uncertainty, Threatened species, Uncertainty mapping

Resumen

Considerar la incertidumbre en la evaluación de los efectos del cambio climático en las zonas de gran diversidad de España. Nuestra comprensión incompleta de la complejidad de la naturaleza genera incertidumbre en los modelos matemáticos y cartográficos utilizados para predecir los efectos del cambio climático en la distribución de las especies. Se elaboraron modelos para predecir los cambios producidos por el cambio climático en la distribución de las especies de vertebrados amenazados en la España peninsular y en sus correspondientes zonas de alta biodiversidad. Se consideraron dos fuentes importantes de incertidumbre climática que afectan a las predicciones climáticas: los modelos de circulación general y el contexto socioeconómico. Asimismo, se analizó la importancia relativa del clima en cuanto factor determinante de la distribución de las especies y la incertidumbre taxonómica como causas biogeográficas añadidas de incertidumbre. Se detectó incertidumbre en todos los pronósticos realizados a partir de modelos en los que el clima era un factor explicativo significativo y en las especies con incertidumbre taxonómica. En los pronósticos, la incertidumbre se localizó principalmente en áreas no ocupadas por las especies y aumentó con el desfase temporal respecto al presente. La representación cartográfica de esta incertidumbre permitió evaluar la coherencia de las predicciones con respecto a los futuros cambios de la distribución de las zonas de alta biodiversidad de vertebrados amenazados de España.

Palabras clave: Cambio climático, Exactitud de las predicciones, Incertidumbre taxonómica, Especies amenazadas, Mapas de incertidumbre

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Introduction

Species distribution modelling (SDM) is useful to forecast the potential consequences of climate change on conservation of biodiversity (Dawson et al., 2011). A great deal of digital cartographic information has been produced related to observed and predicted climate, such as WorldClim (Hijmans et al., 2005; Fick and Hijmans, 2017), CliMond (Kriticos et al., 2012) and IPCC gas–emission scenarios (GESs) (Nakićenović et al., 2000). This large amount of information has significantly advanced predictive SDM. However, in SDMs and subsequent forecasts, uncertainties affect the reliability of predictions, leading to misconceptions and interpretation errors (Knutti, 2008), with critical consequences on the application of distribution forecasts to conservation policy (Real et al., 2010).

Identifying the geographic distribution of uncertainty associated with a predictive model is, consequently, as important as the model mapping itself (Beale and Lennon, 2012; Kujala et al., 2013). Several sources of uncertainty have been analysed, such as the variety of SDM methods (Carvalho et al., 2011; Beale and Lennon, 2012), the inherent imperfection of atmospheric circulation models (i.e. GCMs, Knutti, 2008; Real et al., 2010), alternative proposals on future GESs (Real et al., 2010, Carvalho et al., 2011), the resolution of climate data (McInerney and Purves, 2011), and survey design (Tessarolo et al., 2014). However, other sources of uncertainty in mapping species distributions have seldom been studied (Rocchini et al., 2011). Few studies have assessed the effects of taxonomic uncertainty (Lozier et al., 2009; Romero et al., 2013; McInerney and Purves, 2011; Tessarolo et al., 2017), diversity of sources for climate data (Fernández et al., 2013; García-López and Real, 2014), behavioural plasticity of species in their response to climate change (Muñoz et al., 2015), correlations between climate, and other environmental factors (Real et al., 2013). These causes of uncertainty can affect model accuracy more than the availability of GCMs and GESs.

The combination of models based on different species provides a dynamic measure of potential species' richness, as it can fill gaps in distribution knowledge mainly due to sampling bias (Estrada and Real, 2018). This combination is particularly useful for predicting future changes in the distribution of biodiversity hotspots (Estrada et al., 2008; Real, et al., 2017). When focused on endangered species, it can enable forecasts with important applications for conservation. However, combining models requires the use of SDM outputs based on a commensurate index that provides comparable measures of the importance of different localities for different species. This index is provided by the favourability function (Real et al., 2006; Acevedo and Real, 2012) as it removes the effect of prevalence from predicted probabilities, and therefore more accurately describes the environmental conditions that facilitate species presence, regardless of the proportion of presences in the dataset (Barbosa and Real, 2012; Acevedo and Real, 2012). Favourability models can be combined

through the application of fuzzy–logic operations (Estrada et al., 2008; Barbosa and Real, 2012; Romero et al., 2014; Olivero et al., 2017).

In this study, we took advantage of the properties of the favourability function regarding model combination to forecast how climate change may modify the location of biodiversity hotspots for threatened vertebrates in mainland Spain and to analyse the uncertainty associated with the resulting forecasts. We took into account the effect of alternative general circulation models, different gas–emission scenarios, the correlation between climate and other factors, and taxonomy on the forecasts. Specifically, we assessed the uncertainty associated with the identification of the areas where threatened species are most vulnerable to climate change. We also mapped the distribution of the degree of uncertainty, and quantified the reliability of forecasts across the study area.

Material and methods

Species and study area

Spain comprises 84 % of the Iberian peninsula, a biogeographically relevant area for the conservation of biodiversity hotspots (Maiorano et al., 2013). We analyzed all threatened vertebrate species in mainland Spain, where more than sixty percent of those with European distributions (in terms of extent of occurrence) are found. Only 14 species had less than 90 % of their European distribution within Spain, namely *Chioglossa lusitanica*, *Calotriton asper*, *Salamandra salamandra*, *Rana iberica*, *Iberolacerta bonnali*, *I. aranica*, *Mauremys leprosa*, *Cercotrichas galactotes*, *Emberiza schoeniclus*, *Tetrao urogallus*, *Tetrax tetrax*, *Arvicola sapidus*, *Microtus cabrere* y *Rhinolophos mehelyi*, which present significant populations in Portugal or France. We modelled seven amphibian, seven reptile, twelve bird and six mammal species (table 1s). We selected the threatened species according to the IUCN criteria (vulnerable, endangered and critically endangered), adapted to Spain by national red books (Madroño et al., 2004; Pleguezuelos et al., 2004; Palomo et al., 2007). Exceptions were: *Calotriton asper*, selected because some authors consider it is threatened (Montori and Llorente, 2008); *Salamandra salamandra*, because its subspecies (*S. s. longirostris*), which is proposed to be a separate species (Dubois and Raffaëli, 2009), is vulnerable; and *Tetrao urogallus* and *Emberiza schoeniclus*, as all their populations in Spain are threatened subspecies.

Presence in the 5,156 10x10–km UTM grid cells of mainland Spain were obtained from Pleguezuelos et al. (2004) for amphibians and reptiles, from Martí and del Moral (2003) for breeding birds, and from Palomo et al. (2007) for mammals. These data represent all or most of the distribution of the analysed species. Data of similar quality were partly unavailable from Portugal, which is why we restricted our analysis to Spain. In addition, the models were explicitly built to be helpful in conservation policy decisions, such as

the design of nature reserve networks, which is decided at a national level. The cells without presence according to the respective distribution atlas were considered as absences.

Although the number of presences was extremely low in a few cases (see table 1s), Proosdij et al. (2016) showed that the lower limit for presences needed to obtain good model performance depends on the species' prevalence in the dataset, with absolute minimum sample sizes extremely low for narrow-ranged species. In our case, all cases with an extremely low number of presences corresponded to endemic and narrow-ranging species, and included the whole range of the species. Lobo and Tognelli (2011) showed that the model performance also depends on the number of absences used to calibrate the models, with better performance when absences are numerous and unbiased. In our case, the number of absences was always very high and unbiased, particularly when modelling species with highly restricted ranges.

Predictors

Factors other than climate should be considered in SDMs constructed to forecast changes induced by climate in species distribution (Aragón et al., 2010; Márquez et al., 2011). We assessed four factors that had a potential impact on species distributions (Márquez et al., 2011): climate, space, topography, and human influence (table 2s). Climate is the main driver of species distribution to be analysed when assessing the effect of climate change on species distribution. The use of the spatial factor in the models accounts for geographical trends that cannot be explained by climate (Legendre, 1993). These spatial trends may arise from population dynamics, dispersal capacities, and historical events that affected species distributions (Legendre, 1993; Real et al., 2003). The topographic factor allows us to assess whether there is any relationship between the topographic structure of the territory and the distribution of the species, independently of the relationship between topography and climate. Finally, human activity may have an effect on the availability and quality of habitats of many species, possibly interfering with the effects of climate (Delibes-Mateos et al., 2009).

Table 2s shows the climatic, spatial, topographic and human variables and sources. The original resolution adopted for the variables was one km² per pixel; we computed average values for each 10 × 10-km square using ArcGIS 10.0 zonal statistic tools (ESRI, 2011). With the longitude and latitude of the original spatial variables we built a single spatial variable to be used as a spatial predictor for every species. For this, we made a trend surface analysis by performing a backward stepwise logistic regression of each species' presence/absence on nine spatial components that describe the spatial position of the data: X, Y, X², Y², X × Y, X³, Y³, X² × Y, Y² × X (X, latitude; Y, positive longitude). This produced a lineal combination of spatial components that we used as the single spatial predictor in the subsequent models. We used IBM SPSS statistics 21 (IBM, 2012) for this analysis.

Selection of variables and model building

Spearman correlation coefficients (*r*) were calculated to control the multicollinearity between independent variables. When a set of variables belonging to the same factor were correlated with *r* > 0.8, we selected just the variable with the most significant predictive power on the species presence; this was established by performing a logistic regression of presences/absences on the set of correlated variables separately and selecting the variable most significantly related with species presence/absence. This resulted in a reduced set of potential predictors that were tailored for each species.

We then performed logistic regressions of each species' presence/absence on the remaining variables separately. The false discovery rate (FDR) was used to control the increase in type I errors due to the number of remaining independent variables (Benjamini and Hochberg, 1995). The variables significantly related (*p* < 0.05) to the species distribution under a FDR < 0.05 were considered to be the further reduced subset of acceptable predictors.

We next performed a multivariate forward-backward stepwise logistic regression of presences/absences of each species on their corresponding reduced set of predictor variables to obtain probability values (*P*) of the species' presence in every square. Variables were included in the models according to the significance of their relationship with the species distribution while avoiding redundancy by checking at each step that the new variables added significant new information to the model. This was considered the current probability model for the species.

Then, we modelled the present and future favourability for the presence of each species using the favourability function (Real et al., 2006, 2017). Favourability (*F*) was calculated from *P* using the following equation (Real et al., 2006):

$$F = [P/(1 - P)] / [(n_1/n_0) + (P/[1 - P])]$$

where *n*₁ and *n*₀ are the number of presences and absences, respectively.

Climate in these models refers to the period 1961–1990; the models were later projected to the expected conditions of three future periods: 2011–2040, 2041–2070 and 2071–2100 in order to obtain the different future forecasts. To this end, we applied the following equation, using climate-variable values referring to the corresponding period:

$$F = e^y / [(n_1/n_0) + e^y]$$

where *e* is the base of the natural logarithm, and *y* is the logit function of the probability model obtained by multivariate logistic regression. We used IBM SPSS statistics 21 (IBM, 2012) for this analysis.

We evaluated the classification and discrimination capacity of the models using four indices: sensitivity, specificity, correct classification rate (CCR), and Cohen's Kappa (Fielding and Bell, 1997). These indices assessed classification based on the 0.5-favour-

rability threshold, which, in the favourability function, makes probability equal to overall prevalence. Discrimination capacity was evaluated using the area under the curve (AUC) of the receiver operating characteristic. Although discrimination cannot be considered an overall measure of model performance (Lobo et al., 2008), AUC provides a measure of the degree to which the modelled predictors allow separating presences from absences, which is informative when geographical extent, presence/absence dataset and modelling technique remain constant, as is the case here (Lobo et al., 2008).

Forecasting the future distribution of biodiversity hotspots

We considered four sources of uncertainty associated with future forecasts (fig. 1): (1) two alternative general circulation models (GCMs): CGCM2 (Canadian Climate Centre for Modeling and Analysis) and ECHAM4 (Max Planck Institut für Meteorologie) (IPCC, 2013), regionalized to Spain by the Spanish Meteorological Agency (AEMET) (Brunet et al., 2007); (2) two different Gas–Emission Scenarios or GESs for the 21st century from IPCC, (Nakićenović et al., 2000): A2 and B2, representing intermediate positions in the range of projected temperature changes, being medium–high and medium–low respectively (Brunet et al., 2007); (3) the degree to which climate affects distribution models, as a consequence of correlations between climate and other factors. We forecast distribution changes according to the spatial variation in the model that was exclusively explained by climate (pure effect); alternatively, we forecast changes according to the spatial variation potentially, although not exclusively, attributable to climate (apparent effect). We followed the method described in Real et al. (2013), which is based on variation partitioning (Legendre and Legendre, 1998); (4) taxonomic uncertainty, in those cases with taxonomic categorization under discussion. We constructed alternative models taking into account the taxonomic situations both before and after revision. This approach was used for: *Salamandra salamandra longirostris*, which is either considered a *S. salamandra* subspecies (García–Paris et al., 1998), or a species named *S. longirostris* (Dubois and Raffaëli, 2009); *Calotriton arnoldi*, recently separated from *Calotriton asper* (Carranza and Amat, 2005); *Iberolacerta monticola* (Pleguezuelos et al., 2004), recently categorised into *I. monticola*, *I. cyreni*, *I. martinezricai*, and *I. galani* (Arribas et al., 2006; Arribas and Carranza, 2004, 2015). Taxonomic alternatives resulted in two or more models for a single original species. On one hand, we considered a model for the species before the taxonomic revision; on the other hand, we considered a model performed by joining models for the species resulting from taxonomic revision using the fuzzy logic operator 'fuzzy union', which is equivalent to assigning the highest value observed in different models to each square (Zadeh, 1965). We calculated these fuzzy union values in each cell using the Max function from Microsoft Excel (version 2010).

We produced favourability models for each species according to each source of uncertainty. This resulted

in eight favourability models for species with no taxonomic uncertainty and eight further more favourability models for each taxonomic alternative (subspecies) for species with taxonomic uncertainty.

We applied the accumulated favourability to forecast the distribution of future diversity hotspots for threatened vertebrates in mainland Spain derived from these models. The accumulated favourability is a proxy for a diversity index (Estrada et al., 2008; Real et al., 2017), defined by the sum of favourability models of a group of species:

$$AF_j = \sum_{i=1}^n F_{ij}$$

where F_{ij} is the favourability value for species i in square j .

This index was applied to the 32 species analysed for 1961–1990 and for three future periods (2011–2040, 2041–2070, and 2071–2100) according to the four sources of uncertainty.

Uncertainty assessment

We used fuzzy logic operators to summarize the effect of the different sources of uncertainty on the predictive models (Zadeh, 1965). Fuzzy union represented the highest favourability value predicted for a species in each cell according to any of the four sources of uncertainty. Fuzzy intersection represented the lowest favourability value predicted for a species in each cell according to any of the four sources of uncertainty. Fuzzy intersection indicates the minimum consensus among the models (Romero et al., 2016). Average favourability predicted for a species in each cell according to any of the four sources of uncertainty was also computed as an indicator of a balanced consensus among the models. We calculated these values in each cell using the Microsoft Excel functions (version 2010): Max, Min and Average, respectively. We obtained the accumulated favourability values resulting from the fuzzy union, the fuzzy intersection and the average favourability of the models produced according to the four uncertainty sources, which summarized the effect of the different sources of uncertainty on the forecasted biodiversity hotspots.

We also calculated the fuzzy symmetric difference (Dubois and Prade, 1980) between all pairs of SDMs produced for the same species whose differences were based on a single source of uncertainty (i.e., a symmetric difference for each species, time period, and uncertainty source):

$$F_{A \nabla B}(j) = |F_A(j) - F_B(j)|$$

where F_A and F_B represent favourability values for a given j square according to two alternative SDMs for the same species. The degree of uncertainty in each j square (U_j) was calculated as the fuzzy union (the maximum value) of all the symmetric differences applying to a species in a given time period. The mapping of U_j indicated the geographic distribution of

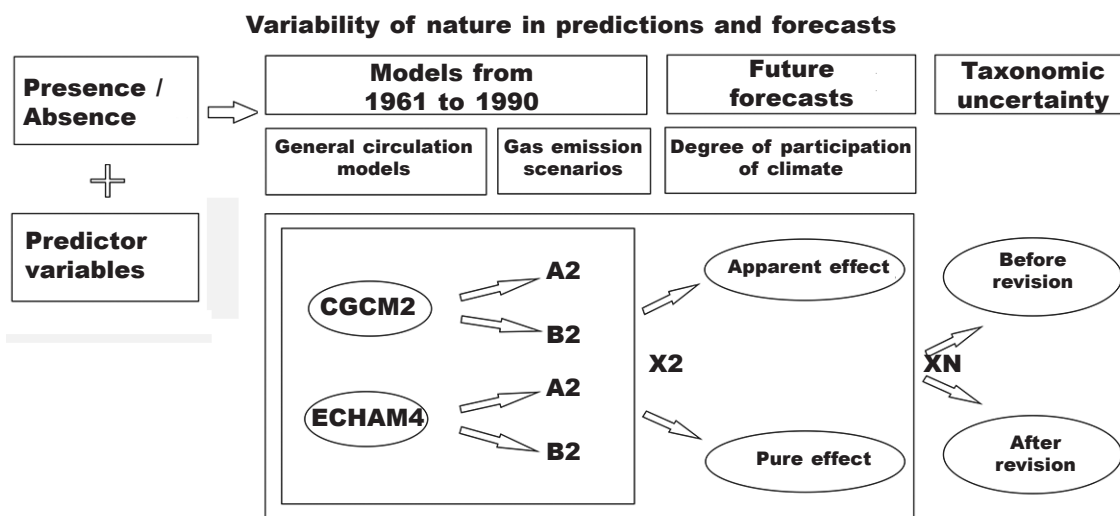


Fig. 1. Schematic representation of the model diversification caused by the different sources of uncertainty: N, number of species resulting from taxonomic revision in species with taxonomic uncertainty; X2, duplication of forecasts due to the different consideration of climate as a driver of species distribution; and XN, multiplication of models due to different taxonomic alternatives for species with taxonomy uncertainty.

Fig. 1. Esquema de la diversificación del modelo provocada por las distintas fuentes de incertidumbre: N, número de especies resultante de la revisión taxonómica en las especies de taxonomía incierta; X2, duplicación de los pronósticos debido a la diferente consideración del clima como factor determinante de la distribución de las especies; XN, multiplicación de modelos debido a las diferentes alternativas taxonómicas para las especies de taxonomía incierta.

the uncertainty associated to the predicted species distribution. Finally, we assessed the uncertainty associated to AF_j values using the accumulated uncertainty index:

$$AU_j = \sum_{i=1}^n (U_{ij})$$

where U_{ij} is the degree of uncertainty associated with the forecasts from different uncertainty sources obtained for species i in square j .

Results

Model assessment

We obtained significant favourability models for the 32 species considered. Figure 2 shows an example for one species, and all models can be seen in supplementary material. Classification and discrimination assessments generally obtained high scores. On a scale ranging from 0 to 1, sensitivity was always higher than 0.6 (average 0.93); specificity was higher than 0.66 (average 0.88); CCR was higher than 0.69 (average 0.89); and Cohen's Kappa was higher than 0.1, with an average 0.42 or 'good' according to Fielding and Bell (1997). On a scale ranging from 0 to 1,

the AUC was always higher than 0.70 or 'acceptable' according to Hosmer and Lemeshow (2000), with an average of 0.95 or 'outstanding'.

Relative importance of climate and other explanatory factors

The pure effect of climate explained more than 40% of the environmental favourability for 17.5% of the species analysed: 27% of reptiles, 25% of birds, 9% of amphibians, but 0% of mammals (see Supplementary material, in fig. 1s, pictures 1–32). When the apparent effect of climate was considered, it explained more than 40% of the environmental favourability in 72.5% of the species: 83% of mammals, 81% of amphibians, 67% of birds, and 64% of reptiles. In contrast, non-climatic variables explained more than 40% of the environmental favourability in 42.5% of the species: 68% of mammals, 64% of amphibians, 36% of reptiles, and 17% of birds (see supplementary material, in fig. 1s, pictures 1–32).

Effect of climate change on Spanish threatened vertebrates

Eight different forecasts per species and future period were calculated, varying according to the sources of ambiguity considered in every case (see

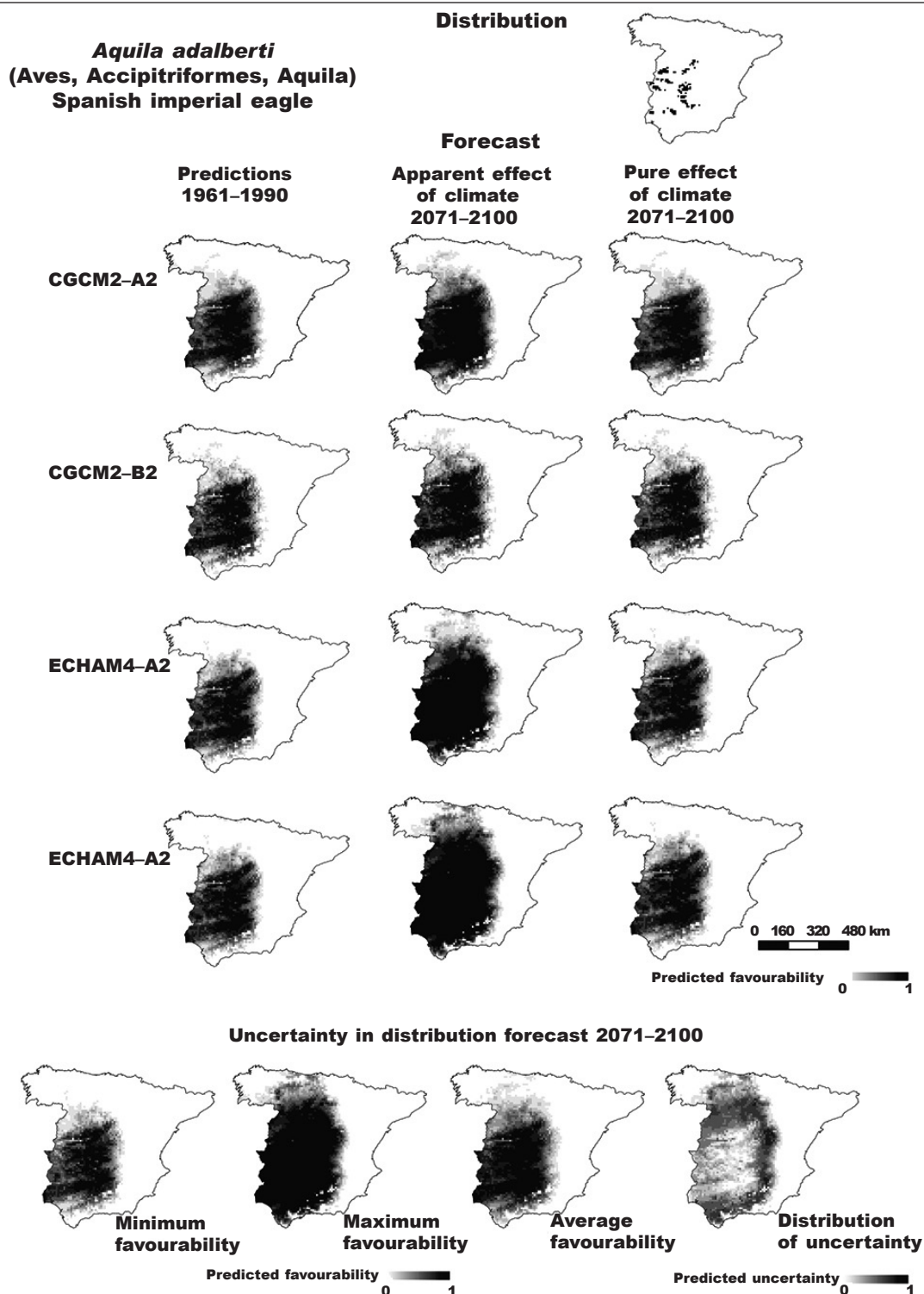


Fig. 2. Example of the methodology modelling for *Aquila adalberti* with the forecasts according to: two general circulation models, two gas–emissions scenarios and the different contribution of climate. Below, the consensual favourability values (minimum, maximum and average), and the uncertainty distribution in 2071–2100.

Fig. 2. Ejemplo de la metodología de elaboración de modelos para *Aquila adalberti* con los pronósticos según: dos modelos generales de circulación, dos situaciones hipotéticas de emisiones de gases y la diferente contribución del clima. Abajo, los valores consensuados de favorabilidad (mínimo, máximo y promedio) y la distribución de la incertidumbre en el período 2071–2100.

supplementary material, in fig. 1s, pictures 1–32), with eight more forecasts for each taxonomic alternative (subspecies) in the species with taxonomy uncertainty. When the apparent effect of climate was considered, the increment in favourability (Real et al., 2010) was positive for 48.8% of the species, negative for 39.6% of the species, and nearly zero (< 1%) for 12% of the species. The average change between 1961–1990 and 2071–2100 for all models was 26%. However, distributions forecasted according to the pure effect of climate were predicted to experience lower changes (average 7.3%): favourability increased in 26.8% of species, decreased in 27.4%, and remained unchanged in 45.7% (see supplementary material, in fig. 1s, pictures 1–32).

A decrease in favourability over time was forecast for 60.4% of the studied endemic mammals, 57.3% of birds, 29.6% of amphibians, and 27.1% of reptiles. Opposite trends depending on the GCM considered were predicted only for five species (*Alytes dickhilleni*, *Algyroides marchi*, *Chioglossa lusitanica*, *Lepus castroviejoi*, and *Pterocles alchata*). Our SDMs forecast an exceptionally large decrease of favourability (> 50% according to at least two methodological options), for another five species (*Rana pyrenaica*, *Iberolacerta monticola*, *Chersophilus duponti*, *Pterocles alchata*, and *Tetrao urogallo*). All the methodological options explored forecast a decrease in favourability in three species only (*Iberolacerta bonnali*, *Iberolacerta monticola*, and *Chersophilus duponti*). For seven more species (*Chioglossa lusitanica*, *Triton pygmaeus*, *Mauremys leprosa*, *Arvicola sapidus*, *Galemys pyrenaicus*, *Microtus cabrerai*, and *Rhinolophus meleis*), a decrease in favourability was predicted according to all the forecasts based on the apparent effect of climate.

Forecasted biodiversity hotspots and associated uncertainty

Figure 3 shows the accumulated favourability (AF) of all species, representing the biodiversity hotspots. The accumulated favourability showed a general positive increase over time in the centre and south–west of Spain (fig. 3). In contrast, the lowest accumulated favourability values were detected in the north–east (see fig. 3, 4).

The uncertainty associated to AF values can be seen in figure 4. Uncertainty was detected in all the forecasts involving climate variables and in the species subject to taxonomic uncertainty. Favourability forecasts showed low and highly localized uncertainty values for most species, with high uncertainty values generally aggregated at the edges of species distributions. In 87.5% of the forecasts, the area affected by uncertainty increased as a function of the time elapsed from the present (fig. 4; and fig. 2s, pictures 1–32); a decrease was detected only in the case of *Chersophilus duponti* (fig. 2s, picture 19). Our models showed an aggregation of the highest uncertainty values in the eastern half of the Iberian peninsula, including the Pyrenees and some southern mountains (fig. 4). In the north–eastern Pyrenees, some species, such as *Iberolacerta monticola*,

showed high discrepancies in future favourability values forecasted by alternative models (fig. 1s, picture 10.1), and therefore high uncertainty (fig 2s, picture 10.1).

Discussion

Effects of uncertainty in distribution models

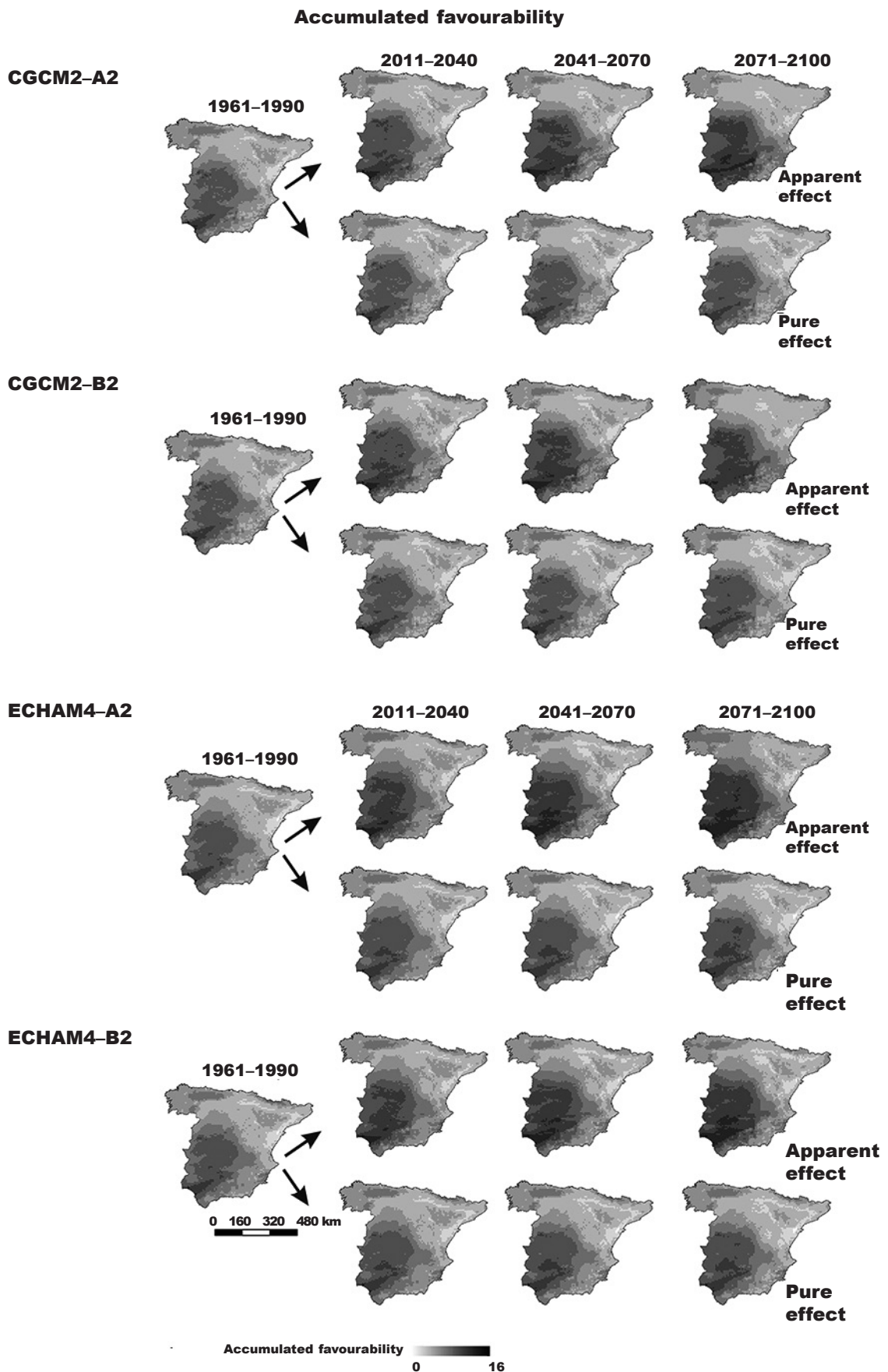
Several authors have indicated the importance of taking into account the different sources of uncertainty in species distribution models (Knutti, 2008; Real et al., 2010; Rocchini et al., 2011; Beale and Lennon, 2012). Our results also highlight that the implementation of the different uncertainty measures in SDMs is key for obtaining reliable results. Specifically, our analysis allowed us to identify the areas where the models from different uncertainty sources are consistent and the areas where the uncertainty was mainly located (Beale and Lennon, 2012; Kujala et al., 2013). The comparison between the consensus in the predictions between the different models and the associated uncertainty may thus be useful to locate the forecast important territories for conservation of species and the degree of reliability of these predictions (Beale and Lennon, 2012).

Relative importance of climate as a driver of species distribution

Climate was the most important factor influencing the distribution of birds and reptiles, whereas other factors were more influential for mammals and amphibians. This is probably a consequence of the greater dispersal ability of birds, which makes them less tied to regional influences such as historical events, geographic barriers, and local human influences (Cumming et al., 2012), and of the high dependence of reptiles on temperature (Adolph and Porter, 1993). However, much of the role of climate in explaining distributions fell on the intersection with other variables, in which the role of climate cannot be distinguished from the role of other factors (Real et al., 2013). In our models, climate not only had different degrees of influence depending on the species and the general circulation models (GCMs) and gas–emission scenarios (GES) analysed, but the relative contribution of climate was also responsible for the largest differences between forecasts. Thus, the analysis of this source of uncertainty is of great relevance for qualifying and geographically locating the reliability of distribution forecasts based on climate change.

Climate change and predicted changes in favourability

The concern about the negative impact of climate change on biodiversity was behind many of the studies on distribution forecasts in climate change scenarios (Bellard et al., 2012). Assessments of the positive impacts of climate change on species distributions are nevertheless accumulating (e.g. Araújo et al., 2006; Romero et al., 2013; Sorte et al., 2013; García–Valdés et al., 2015). We found positive, neutral, and negative effects depending on the species



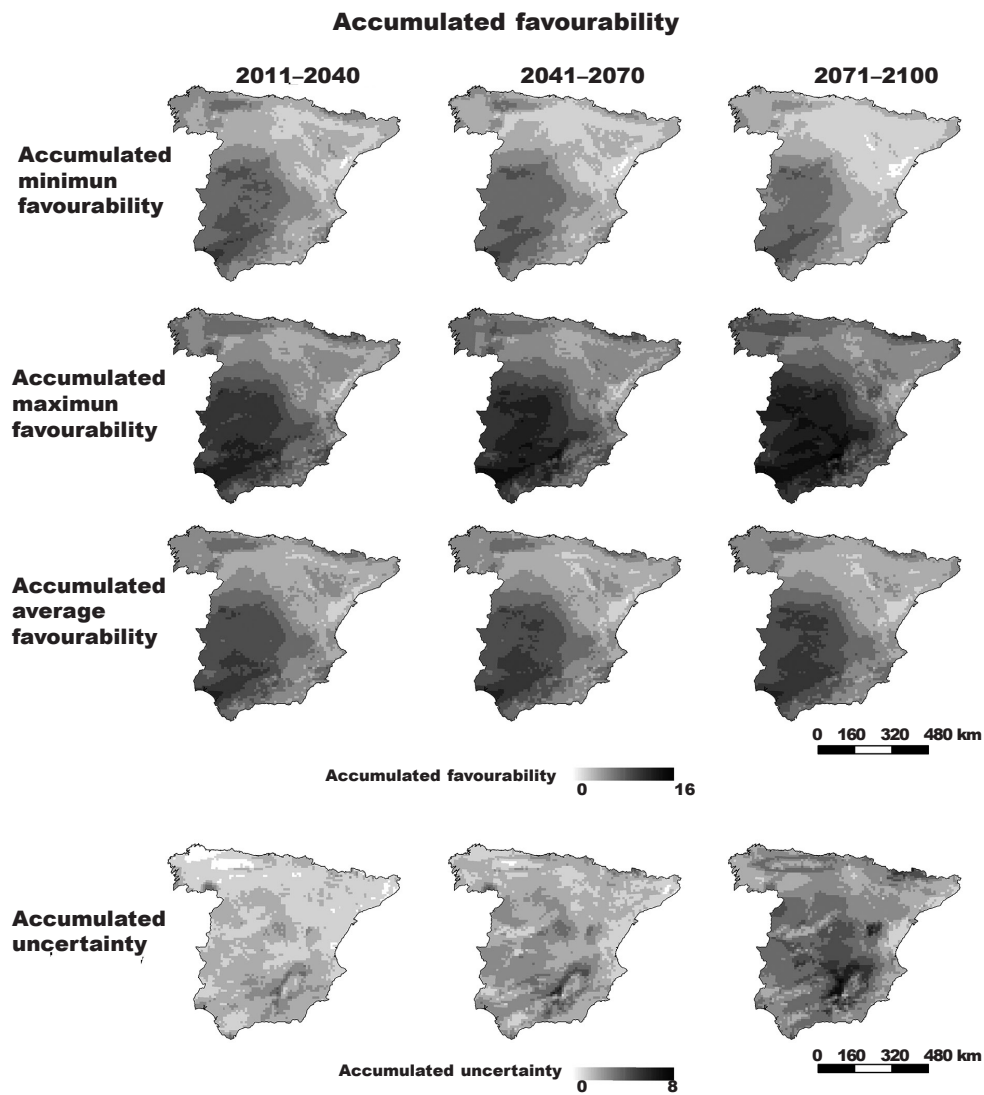


Fig. 4. Consensual accumulated favourability values (minimum, maximum, and average) and accumulated uncertainty taking into account the 32 species analysed for the three time periods.

Fig. 4. Valores consensuados de favorabilidad acumulada (mínimo, máximo y promedio) e incertidumbre acumulada teniendo en cuenta las 32 especies analizadas en los tres periodos de tiempo.

Fig. 3. Accumulated favourability for the 32 species analysed from 1961–1990 and for three future periods (2011–2040, 2041–2070, and 2071–2100) according to four sources of uncertainty: two general circulation models, two emissions scenarios, and the different contribution of climate to the species distribution (apparent or pure effect).

Fig. 3. Favorabilidad acumulada de las 32 especies analizadas en el período 1961–1990 y en tres periodos futuros (2011–2040, 2041–2070 y 2071–2100) según las cuatro fuentes de incertidumbre: dos modelos de circulación general, dos situaciones hipotéticas de emisiones de gases y la diferente contribución del clima a la distribución de las especies (efecto aparente o efecto puro).

considered. Consequently, our results suggest that climate change could harm many species by altering the local conditions they are adapted to, whereas it could contrarily move the environmental conditions closer to the optimal requirements of some other species. Furthermore, species can adapt to new climatic conditions by modifying their phenology (Parmesan, 2007) and physiology (Johansen and Jones, 2011), not only by changing their distribution ranges (Moreno–Rueda et al., 2011).

Several authors have predicted that reptiles and amphibians have the highest susceptibility to climate change (Araújo et al., 2006; Maiorano et al., 2013). However, our results suggest that some bird species could experience the highest decrease in favourability values (around 30%), whereas this decrease could be about half (around 15%) in the case of amphibians, reptiles, and mammals. This discrepancy could be due to the fact that we forecast on the basis of different degrees of participation of climate in the models. For a large number of birds, the highest proportion of explanatory power in the models was due to climate, regardless of whether the pure effect or the apparent effect of this factor was considered (non-climatic factors had more explanatory power only in the models of 17% bird species). In all cases, the proportion of change over time was higher when the apparent effect of climate was taken into account than when its pure effect was considered (average difference, 25%).

According to our forecasts, there are two groups of species for which conservation measures should be reinforced. The first group includes already endangered species (*Iberolacerta bonnali*, *Iberolacerta monticola*, and *Chersophilus duponti*), for which there were consensus on a predicted decrease in environmental favourability. We consider that these are good examples of reliable predictions that highlighted the suitable territories to incorporate in the decision-making framework for the conservation of these species (Beale and Lennon, 2012; Estrada and Real, 2018). Priority actions should therefore be implemented for these species in the territories with reliable forecasts of range contraction in order to prevent strong negative impacts due to climate change (Pleguezuelos et al., 2004; Madroño et al., 2004; Dawson et al., 2011).

The second group includes species whose predicted trends are seriously affected by uncertainty, but for which a decrease in favourability is forecast by some of the models: *Rana pyrenaica*, *Salamandra longirostris*, *Pterocles alchata*, *Tetrao urugallo*, *Arvicola sapidus*, *Galemys pyrenaicus*, and *Microtus cabreræ*. For some of these species, we detected areas where the decrease in favourability was not affected by uncertainty: some squares at the southern limit of the *Rana pyrenaica* distribution; the core squares of the north–western populations of *Tetrao urugallo*, that is home to a large part of the genetic stock of populations at the southern limit of its global distribution, essential for the conservation of the genetic biodiversity of the species (Alda et al., 2013); the southern half of the Iberian peninsula, where the presence of *Arvicola sapidus* is scattered (Palomo et al., 2007); and the mid–western populations of

Microtus cabreræ, for which climate was not the main driver of its distribution or possible decline (Alagador and Cerdeira, 2018). Anyway, for this group of species our results highlighted territories to monitor the populations and evaluate the possibility of applying conservation measures (Dawson et al., 2011).

Areas most vulnerable to climate change

We found that a large part of western peninsular Spain has areas with favourable environmental conditions for a great majority of threatened vertebrates, an area that includes five Spanish National Parks (Estrada and Real, 2018). In contrast, the areas with the lowest favourability values and the highest uncertainty are located in some eastern areas. Wildlife managers will have to decide whether conservation priorities should focus on areas with the highest favourable environmental conditions for a greater number of species, or on areas with less favourable conditions but in which some species are present (Real et al., 2017). Management efforts could also be prioritized according to present or to future environmental conditions (Dawson et al., 2011; Beale and Lennon, 2012; Kujala et al., 2013). Our study contributes to this issue by identifying the areas in which environmental favourability is currently high, but in which a future decrease in favourability is predicted. Conservation measures should be reinforced, for example, by adapting the location and extension of protected spaces within the network of protected areas taking into account the dynamics of climate change (Estrada and Real, 2018), especially when the affected species are endemic or are narrowly distributed within the Iberian peninsula (e.g., *Alytes dickhilleni*, *Iberolacerta monticola*, *Aquila adalberti*, or *Lynx pardinus*).

It is also important to monitor areas that could become favourable for some species in the future under the effect of climate change, especially areas in which the accumulated favourability could reach high values and uncertainty is low; these areas might act as refuges for species vulnerable to climate change. This is the situation of the following species: *Salamandra salamandra* in the northernmost ridge of the Iberian peninsula, the Duero and Guadalquivir valleys, and in southern Spain (Romero et al., 2012; Tejado et al., 2003); *Algyroides marchi* in the southeast of the Iberian peninsula (Pleguezuelos et al., 2004); *Emberiza schoeniclus* in the Pyrenees and the northwest corner and eastern edge of the Iberian peninsula (Madroño et al., 2004); and *Rhinolophus mehelyi* in southwestern Spain (Palomo et al., 2007).

Concluding remarks

Based on SDMs, climate change could have both positive and negative impacts on biodiversity. These effects will probably affect the distribution of species to different extents, and predictions will be more or less accurate in different locations according to each individual case. Advances in SDM cannot claim to eliminate the uncertainty involved in predictions, because uncertainty is often a result of the complexity

of nature and of our incomplete knowledge about how it works, and therefore about how to forecast its changes. The method used in this study takes into account a wide range of possible variations according to a range of sources of uncertainty, and also takes uncertainty into account to identify spatial overlap between alternative forecasts. Although climate was the most important factor influencing the distribution of threatened birds and reptiles, other factors were more influential than climate for threatened mammals and amphibians; moreover, climate not only had different degrees of influence depending on the vertebrate group, but correlations between climate and other factors were responsible for the largest differences between alternative forecasts. Besides, imprecision in forecasts increased as predictions move forward in time. Acknowledging, identifying, and quantifying the degree of imprecision in equally probable models for the same species generate more accurate predictions and serve to assess reliability in forecasts based on climate change.

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Supplementary material

Table 1s. Endangered vertebrate species analysed, IUCN threatened categories adapted to Spain (IUCN), and number of 10 x 10 UTM squares in Spain with species presences: N, number of species; -0 and -1, species names before and after being divided into the current species, respectively.

Tabla 1s. Especies analizadas de vertebrados amenazados, categorías de la UICN adaptadas para España y número de cuadrículas UTM de 10 x 10 km con presencia de la especie en España: N, número de especies; -0 y -1, nombre de las especies antes y después de dividirse en las especies actuales.

ID	Species	Abbr.	Vernacular name	IUCN	N
Amphibians					
1	<i>Chioglossa lusitanica</i>	Chiolus	Golden-striped salamander	VU	167
2	<i>Calotriton asper</i> -0	Calasp-0	Pyrenean brook salamander	NT	186
2.1	<i>Calotriton asper</i> -1	Calasp-1	Pyrenean brook salamander	NT	184
2.2	<i>Calotriton arnoldi</i> -1	Calarn-1	Montseny brook newt	CR	2
3	<i>Salamandra salamandra</i> -0	Salsal-0	Common fire salamander	LC	1,409
3.1	<i>Salamandra salamandra</i> -1	Salsal-1	Common fire salamander	LC	1,315
3.2	<i>Salamandra longirostris</i> -1	Sallong-1	Salamandra penibética	VU	94
4	<i>Triturus pygmaeus</i>	Tripyg	Southern marbled newt	VU	466
5	<i>Alytes dickhilleni</i>	Alydic	Betic midwife toad	VU	135
6	<i>Rana iberica</i>	Ranibe	Iberian frog	VU	473
7	<i>Rana pyrenaica</i>	Ranpyr	Pyrenean frog	VU	24
Reptiles					
8	<i>Algyroides marchi</i>	Algmar	Spanish algyroides	VU	30
9	<i>Iberolacerta bonnali</i>	Ibebon	Pyrenean rock lizard	VU	25
10	<i>Iberolacerta monticola</i> -0	Ibemon-0	Iberian rock lizard	VU	169
10.1	<i>Iberolacerta monticola</i> -1	Ibemon-1	Iberian rock lizard	VU	128
10.2	<i>Iberolacerta cyreni</i> -1	Ibecyr-1	Cyren's rock lizard	VU	39
10.3	<i>Iberolacerta galani</i> -1	Ibegal-1	Galan's rock lizard	NT	10
10.4	<i>Iberolacerta matinezricai</i> -1	Ibemar-1	Peña de Francia rock lizard	CR	2
11	<i>Iberolacerta aranica</i>	Ibeara	Aran rock lizard	EN	3
12	<i>Iberolacerta aurelio</i>	Ibeaur	Aurelio's rock lizard	EN	5
13	<i>Mauremys leprosa</i>	Maulep	Mediterranean turtle	VU	1,427
14	<i>Testudo graeca</i>	Tesgra	Moorish tortoise	EN	38
Birds					
15	<i>Aquila adalberti</i>	Aquada	Spanish imperial eagle	EN	163
16	<i>Aegypius monachus</i>	Aegmon	Eurasian black vulture	VU	151
17	<i>Apus caffer</i>	Apucaf	White-rumped swift	VU	62
18	<i>Cercotrichas galactotes</i>	Cergal	Rufous-tailed scrub-robin	EN	414
19	<i>Chersophilus duponti</i>	Chedup	Dupont's lark	EN	233
20	<i>Emberiza schoeniclus</i>	Embsho	Common reed bunting	LC	118
21	<i>Pterocles alchata</i>	Ptealc	Pin-tailed sandgrouse	VU	477
22	<i>Pterocles orientalis</i>	Pteori	Black-bellied sandgrouse	VU	864
23	<i>Tetrao urogallus</i>	Teturo	Western capercaillie	LC	141
24	<i>Tetrax tetrax</i>	Tettet	Little bustard	VU	1,339
25	<i>Fulica cristata</i>	Fulcri	Crested coot	CR	26
26	<i>Oxyura leucocephala</i>	Oxyleu	White-headed duck	EN	57

Tabla 1s. (Cont.)

ID	Species	Abbr.	Vernacular name	IUCN	N
Mammals					
27	<i>Arvicola sapidus</i>	Arvsap	Southern water vole	VU	1,498
28	<i>Microtus cabreræ</i>	Miccab	Cabrera's vole	VU	220
29	<i>Galemys pyrenaicus</i>	Galpyr	Pyrenean desman	VU	429
30	<i>Lepus castroviejoi</i>	Lepcas	Broom hare	VU	63
31	<i>Lynx pardinus</i>	Lynpar	Iberian lynx	CR	27
32	<i>Rhinolophus mehelyi</i>	Rhimeh	Mehely's horseshoe bat	EN	165

Table 2s. Predictor variables that have a potential influence on threatened vertebrate distributions in Spain and are taken into account in the species distribution models. Variable sources: (1) IGN, Instituto Geográfico Nacional, 1999, Road map, Iberian Peninsula, Balearics and Canary Island, National Geographic Institute, Ministry of Development, Madrid, Spain. (2) United States Geological Survey, 1996, GTOPO30, Land Processes Distributed Active Archive Center, EROS Data Center, <https://lta.cr.usgs.gov/GTOPO30>. (3) Farr T. G., Kobrick, M., 2000. Shuttle Radar Topography Mission produces a wealth of data. *EOS Transactions, American Geophysical Union*, 81: 583–585. (4) AEMET, Agencia Estatal de Meteorología, Spanish Ministry of Agriculture, Food and Environment. <http://escenarios.inm.es/> (Accessed on June 2007). (5) Pearson, R. G., Dawson, T. P., Berry, P. M., Harrison, P. A., 2002. SPECIES: A Spatial Evaluation of Climate Impact on the Envelope of Species. *Ecological Modelling*, 154: 289–300. (6) López Fernández, M. L., López, F. M. S., 2008. Artículo 1: Ideas básicas de "Global Bioclimatics", del profesor Rivas–Martínez. Guía para reconocer y clasificar las unidades bioclimáticas. *Publicaciones de Biología de la Universidad de Navarra, Serie Botánica*, 17: 3–188. (7) Supan, 1884, Oceanity map of the earth. Continental Index. (8) Oak Ridge National Laboratory, LandScan 2000 Global Population Database, Tennessee, USA, Oak Ridge National Laboratory, 2001.

Tabla 2s. Variables predictivas que pueden influir en la distribución de los vertebrados amenazados en España y que se toman en cuenta en los modelos de distribución de las especies. (Para la información sobre las fuentes variables, véase arriba).

Abbr	Variable	Abbr	Variable
Spatial situation			
La	Latitude (°N) (1)	Lo	Longitude (°E) (1)
Topography			
A	Mean altitude (m) (2)	S	Slope (°) (calculated from altitude)
WE	Westward exposure degree (°) (3)	SE	Southward exposure degree 3 (3)
Climate			
Climatic variables			
Temp	Mean annual temperature (°C) (4)	TWin	Mean temperature in winter (°C) (4)
TJan	Mean temperature in January (°C) (4)	Prec	Mean annual precipitation (mm) (4)
TJul	Mean temperature in July (°C) (4)	PreSpr	Mean precipitation in spring (mm)(4)
TSpr	Mean temperature in spring (°C) (4)	PreSum	Mean precipitation in summer (mm) (4)
TSum	Mean temperature in summer (°C) (4)	PreAut	Mean precipitation in autumn (mm) (4)
TAut	Mean temperature in autumn (°C) (4)	PreWin	Mean precipitation in winter (mm) (4)
Bioclimatic variables			
MinT	Minimum temperature (°C) (5)	ConI	Continental Index (°C) (7)
Tp0	Mean temperatures annual of days above 0°C (6)	GDD0	Growing degree–days when annual temperature sum > 0°C (5)
Tp5	Mean temperatures annual of days above 5°C (6)	GDD5	Growing degree–days when annual temperature sum > 5°C (5)
Pp0	Mean precipitation annual of days with temperatures > 0°C (mm) (6)	OI0	Ombrothermic index of days with temperatures > 0°C (mm/°C) (6)
Pp5	Mean precipitation annual of days with temperatures > 5°C (mm) (6)	OI5	Ombrothermic index of days with temperatures > 5°C (mm/°C) (6)
Other human activities			
Dhi	Distance to the nearest highway (km) (1)	U500	Distance to the nearest urban centre with > 500,000 inhabitants (km) (1)
U100	Distance to the nearest urban centre with > 100,000 inhabitants (km) (1)	HPd	Human population density in 2000 (number of inhabitants/km ²) (8)

Fig. 1s. Models according to the overall sources of ambiguity analyzed, and variation partitioning from each General Circulation Model and emission scenarios for the species analyzed. The number above each picture (from 1 to 32) indicates the ID of the species corresponding to table 1s.

Fig. 1s. Modelos según las fuentes generales de ambigüedad analizadas y partición de la variación de cada modelo de circulación general y situación hipotética de emisiones para la especie analizada. El número de cada imagen (del 1 al 32) es el número de identificación de las especie que figura en la columna ID de la tabla 1s.

Fig. 2s. Minimum, maximum and average consensus measures of the coinciding and non-coinciding territories from among the various alternatives proposed, and the degree of uncertainty in the periods 2011–2040, 2041–2070 and 2071–2100 for the species analyzed. The number above each picture (from 1 to 32) indicates the ID of the species corresponding to table 1s.

Fig. 2s. Medidas consensuadas mínima, máxima y media de los territorios coincidentes y no coincidentes entre las distintas alternativas propuestas y grado de incertidumbre en los periodos 2011–2040, 2041–2070 y 2071–2100, para las especies analizadas. El número de cada imagen (del 1 al 32) es el número de identificación de las especies, que figura en la columna ID de la tabla 1s.

Fig. 3s. Consensual favourability and the degree of uncertainty according to taxonomy uncertainty. Suffixes –0 and –1 indicate species before and after being split into the current species, respectively. The number above each picture (2, 3 and 10) indicates the ID of the species with taxonomy uncertainty corresponding to table 1s.

Fig. 3s. Valores consensuados de favorabilidad y grado de incertidumbre según la incertidumbre taxonómica. Los sufijos –0 y –1 indican el nombre de las especies antes y después de dividirse en las especies actuales, respectivamente. El número de cada imagen (2, 3 y 10) indica el número de identificación de las especies con incertidumbre taxonómica, que coincide con el de la columna ID de la tabla 1s.