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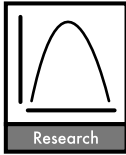


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Species distribution models in climate change scenarios are still not useful for informing policy planning: an uncertainty assessment using fuzzy logic

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We compared the effect of general circulation models and greenhouse gas emission scenarios on the uncertainty associated with models predicting changes in areas favourable to animal species. Given that mountain species are particularly at risk due to climate warming, we selected one amphibian (Baetic midwife toad), one reptile (Lataste's viper), one bird (Bonelli's eagle), and one mammal (Iberian wild goat) present in Spanish mountains to model their distributional response to climate change during this century. Climate forecasts for the whole century were provided by the Agencia Estatal de Meteorología (AEMET; National Meteorological Agency) of Spain, which adapted the general circulation models CGCM2 and ECHAM4 and produced expected temperature and precipitation values for Spain according to the A2 and B2 emission scenarios. We constructed separate models of the species response to spatial, topographic, human, and climate variables using current values of the corresponding variables. We predicted future areas favourable to the species by replacing the current climate values with those expected according to each climate change scenario, while keeping spatial, topographic and human variables constant. Fuzzy logic was used to compute the coincidence between predictions for different emission scenarios in the same global circulation model, and the consistency between predictions for the same emission scenario applying different general circulation models. In general, coincidences were higher than consistencies and, thus, discrepancies between predictions were more attributable to uncertainty in global circulation models, i.e. our insufficient knowledge concerning the effect of the oceans and atmosphere on climate, than to the putative effect of different emission scenarios on future climates. Our conclusion is that species distribution models in climate warming scenarios are still not useful for informing emission policy planning, although they have great potential as tools once consistencies become higher than coincidences.

Species distribution models are usually employed to assess the potential changes in the distribution of species in response to different factors (Barbosa et al. 2003, Muñoz et al. 2005, Muñoz and Real 2006, Farfán et al. 2008, Luoto and Heikkinen 2008). Several studies have focused on modelling species distribution shifts in response to climate change (Beaumont et al. 2005, Levinsky et al. 2007, Foody 2008) to monitor the effects of the increase in global average temperature recorded over the last century and predicted for the present century (IPCC 2007). One of the main aims of modelling biogeographical responses to climate change is to inform policy planning by providing a kind of virtual feedback on greenhouse gas emissions. This kind of modelling uses future climates, which are predicted according to the combination of Atmosphere-Ocean General Circulation Models (AOGCMs) and special reports on emission scenarios (SRESs).

This procedure incorporates several sources of uncertainty, some of them related to the existence of different

AOGCMs (over 20 models available), characterized by different hypotheses on the effect of the oceans and the atmosphere on climate, and SRESs (40 scenarios of future emissions developed by the Intergovernmental Panel on Climate Change), characterized by different storylines of future socio-economic and technological development (Beaumont et al. 2008). The use of different AOGCMs may produce conflicting projected distributions of a species (Xu and Yan 2001). Nevertheless, species distribution models in climate-warming scenarios (which include the effects of AOGCMs and SRESs) will be useful for informing emission policy planning if differences in predicted effects due to differences in SRES are significantly higher than those due to differences in AOGCMs. Fuzzy set theory may be applied to the analysis of species distribution modelling (Robertson et al. 2004, Gevrey et al. 2006, van der Broekhoven et al. 2006, Estrada et al. 2008, Real et al. 2009), and may be used to assess the models' projections

to the future and the different kinds of uncertainty associated with them.

The Mediterranean region is considered to be highly responsive to climate change, because of its geographical situation between temperate central Europe and arid northern Africa (Sánchez et al. 2004, Giorgi and Lionello 2008). Mountain ecosystems seem to be particularly sensitive to global warming and are of particular concern to policy planners (Foster 2001, Nogués-Bravo et al. 2007, Trivedi et al. 2008), especially in the Mediterranean region (Nogués-Bravo et al. 2008). Mountain species ranges might shift more rapidly in response to climate change, as mountains often retain more natural habitats than lowlands do, and because in mountains the microclimate varies with elevation and the species may track climate change over shorter distances (Wilson et al. 2007). Several mountain species have indeed shifted to higher altitudes across European mountains (Grabherr 1994, Klanderud and Birks 2003, Peñuelas and Boada 2003, Wilson et al. 2005, Pauli et al. 2007, Wilson et al. 2007). Mountain species are, therefore, especially suited to evaluating the potential effects of future climate change on distributions.

We used fuzzy logic to compare the effect of AOGCMs and SRESs on the uncertainty associated with models predicting changes in areas favourable to four mountain species in mainland Spain during the 21st century.

Methods

Species and study area

We selected four mountain species in mainland Spain: Baetic midwife toad *Alytes dickhilleni*, Lataste's viper *Vipera latasti*, Bonelli's eagle *Aquila fasciata*, and Iberian wild goat *Capra pyrenaica* to model their distributional responses to climate change during this century. Distribution data were extracted from Martí and del Moral (2003), Pleguezuelos et al. (2004), and Palomo et al. (2007) and are taken to represent the species distributions in 1990. The study area was located in the Mediterranean region, a transition zone between the temperate climate of central Europe and the arid climate of northern Africa. As small changes in the processes that control those climates can lead to important changes in the Mediterranean climate, this area is important to analyse the effect of future climate changes on biodiversity (Giorgi and Lionello 2008, Nogués-Bravo et al. 2008).

Climatic data

The climatic variables were the result of regionalizing the general circulation models, which combined AOGCMs and SRESs, to Spain. This regionalization was done by the Agencia Estatal de Meteorología (AEMET; National Meteorological Agency <www.aemet.es/es/elclima/cambio_climat/escenarios>) of Spain (Brunet et al. 2007), which used two AOGCMs: CGCM2 from the Canadian Climate Centre for Modelling and Analysis, and ECHAM4 from the Max Planck Inst. für Meteorologie; and two SRESs: A2 and B2 (Nakicenovic et al. 2000). These SRESs represent an intermediate position regarding the wide range of

projected shifts in temperature and precipitation (Brunet et al. 2007).

Distribution modelling

We modelled the distribution of each species in 10 × 10 km UTM cells with variables related to four explanatory factors taken separately: spatial situation, topography, human activity, and climate (Table 1). For climate we used the values for the period 1961–1990. Real et al. (2008b) showed that while in the north of Europe energy availability is the main factor limiting species distribution, in the south their distribution seems to be more affected by climatic stress due to an excess of environmental energy. We used maximum temperatures because this variable is more representative of this type of climatic stress; in the Iberian Peninsula an increase in maximum temperatures may be potentially more detrimental to species distributions than an increase in minimum temperatures. Non-climatic factors such as topography, human activity, history and population dynamics may have an effect on species distributions (Real et al. 2008a, 2009). As the species may show differential responses to these factors (De Frene et al. 2009), their relative importance should be assessed together with climate before projecting species distribution models to the future. The inclusion of spatial variables in a model can reveal a geographical trend in distribution that could be associated with historical events or with the species population dynamics (Legendre 1993, Real et al. 2003). On the other hand, latitude and longitude also affect the climatic variables (Márquez et al. 2004). Consequently, the true

Table 1. Explanatory factors and associated variables used to model the species distributions.

Factors	Code	Variables
Spatial situation	La	Latitude (°N) ⁽¹⁾
	Lo	Longitude (°E) ⁽¹⁾
Topography	A	Mean altitude (m) ⁽²⁾
	S	Slope (°) (calculated from altitude)
	SE	Southward exposure degree ⁽³⁾
	WE	Westward exposure degree ⁽³⁾
Human activity	DHi	Distance to the nearest highway (km) ⁽¹⁾
	U100	Distance to the nearest urban centre with > 100 000 inhabitants (km) ⁽¹⁾
	U500	Distance to the nearest urban centre with > 500 000 inhabitants (km) ⁽¹⁾
	HPd	Human population density in 2000 (number of inhabitants km ⁻²) ⁽⁴⁾
Climatic	PAn	Annual precipitation (mm) ⁽⁵⁾
	PSp	Spring precipitation (mm) ⁽⁵⁾
	PSu	Summer precipitation (mm) ⁽⁵⁾
	PAu	Autumn precipitation (mm) ⁽⁵⁾
	PWi	Winter precipitation (mm) ⁽⁵⁾
	TAn	Annual maximum temperature ⁽⁵⁾
	TJa	January maximum temperature ⁽⁵⁾
	TJu	July maximum temperature ⁽⁵⁾
	TSp	Spring maximum temperature ⁽⁵⁾
TSu	Summer maximum temperature ⁽⁵⁾	
TAu	Autumn maximum temperature ⁽⁵⁾	
TWi	Winter maximum temperature ⁽⁵⁾	

Sources: ⁽¹⁾I.G.N. (1999); ⁽²⁾US Geological Survey (1996); ⁽³⁾Shuttle Radar Topography Mission (SRTM), Farr and Kobrick (2000); ⁽⁴⁾ORNL (2001); ⁽⁵⁾Agencia Estatal de Meteorología of Spain (AEMET), Ministerio de Medio Ambiente <www.aemet.es/es/elclima/cambio_climat/escenarios>.

effect of climate should be assessed in the context of the spatial influences on the species distribution and on climate. As for the human variables, major urban centres and population density, although referring to 1999 and 2000, respectively, do not differ greatly from the situation in 1990, whereas the highways built after 1990 were already major roads in this year. Therefore, all these variables are representative of the general pattern in effect in 1990.

For each species and factor (spatial situation, topography, human activity, and climate) we performed logistic regression of presence/absence with each variable related to the factor separately. To control for the increase in type I errors due to multiple tests (Benjamini and Hochberg 1995, García 2003), we controlled the false discovery rate (FDR) using the procedure proposed by Benjamini and Hochberg (1995), only accepting the variables that were significant under an FDR of $q < 0.05$. We then performed forward-backward stepwise logistic regression of presence/absence data on each subset of significant predictor variables related to the factor. In this way we obtained for each species four multivariate models, one for each factor considered. These factor models show the response of the species to spatial, topographic, human, and climatic variables, separately.

We obtained a combined model performing forward-backward stepwise selection of the variables that were involved in any factor model. We then applied the favourability function (Real et al. 2006), which allows direct comparison of favourability values for species differing in their prevalence. In biological terms, this function has proven to be able to reflect species abundance (Real et al. 2009) and performs correctly when transferring models between different geographical areas (Barbosa et al. 2009). We assessed the discrimination power of these models by calculating Cohen's kappa, sensitivity, specificity, and their Correct Classification Rate (CCR), using the favourability value of $F=0.5$ as classification threshold, and the Area Under the Curve (AUC) of the Receiver Operating Characteristic, which is independent of any favourability threshold (Hosmer and Lemeshow 2000). Lobo et al. (2008) recommended not using AUC as a comparative measure of accuracy between model results when the occupancy of the species in the territory differ, which is the case here. We used AUC because it provides a measure of the degree to which a species is restricted to a part of the variation range of the modelled predictors, which is valuable information in models intended to predict the response of the species to changes in these predictors. The goodness-of-fit of the models was assessed using the Hosmer and Lemeshow test (Hosmer and Lemeshow 2000).

Models of this kind are inductively obtained from current distribution data following certain induction rules that guarantee agreement with them and, thus, do not require validation with the training data. Models should be validated according to, and specifically for, the specific purpose they are built for. Although true validation of models built to be transferred to the future is not possible at present (Araújo et al. 2005), we determined whether the models were at least spatially transferable within the study area, by assessing if, after recalibrating them using a training dataset, they perform similarly well in a pseudovalidation dataset. We subsequently divided our whole dataset in a randomly distributed recalibration set and a remaining pseudovalidation set. The proportion of the whole dataset used to constitute the recalibration set was determined by the expression: $[1 + (p - 1)^{1/2}]^{-1}$, where p is the number of predictor variables in each distribution model (Fielding and Bell 1997). In each model we assessed the agreement between the results of the recalibration and pseudovalidation by comparing their corresponding Cohen's kappa, sensitivity, specificity, CCR, and AUC, taking into account that unsatisfactory coherence between recalibration and pseudovalidation results does not imply that the recalibrated model is wrong (Araújo et al. 2005), and even less that the whole model is wrong. We projected to the future the models based on the whole datasets, as they usually perform better than those based on a subset (Fielding and Bell 1997, Araújo et al. 2005).

Future projection assessment using fuzzy set theory

Areas favourable to each species were projected to the future by replacing the current (1961–1990) climatic values in the favourability models with those expected according to each AOGCM and SRES for the following time periods (2011–2040, 2041–2070, 2071–2100). Values of the spatial, topographic and human variables were not modified.

The process of environmental modelling can be understood as the identification of the fuzzy set of areas favourable to each species (Estrada et al. 2008). In the favourability models, the favourability values represent the degrees of membership of each area to the fuzzy set of areas favourable to the species. We used various fuzzy logic operations (Kuncheva 2001) to calculate, for each future projection, several features of the predicted impact of climate change on the species favourability, namely the favourability overlap (O), the favourability maintenance (M), the predicted shift in favourability (S), and the increment in favourability (I) with respect to the 1961–1990 period:

Table 2. Variables included in the favourability models for each species and combination of AOGCM and SRES. Variables codes as in Table 1.

	<i>A. dickhilleni</i>	<i>V. latasti</i>	<i>A. fasciata</i>	<i>C. pyrenaica</i>
CGCM2-A2	Lo, La, A, S, PAn, PSu, TSp, Tau	Lo, La, A, U100, U500, PSp, TJa, TWi	Lo, A, S, PSu, TJu	Lo, A, S, Dhi, U100, PSp, PSu, PAu, Twi
CGCM2-B2	Lo, La, A, S, PAn, PSu, TSp, TAu	A, Dhi, U100, U500, PSp, TJa, TWi	A, S, PAn, TJu	Lo, A, S, Dhi, U100, PSp, PSu, PAu, Twi
ECHAM4-A2/B2	Lo, La, A, S, U500, PAn, PSp	Lo, La, A, PAn, PWi	Lo, A, S, PSu, TJu, TSu, TAu	Lo, La, A, S, Dhi, PAn, PAu, TJa

Table 3. Values obtained for different discrimination assessment measures of the favourability models obtained for the period 1961–1990. Cohen's kappa, sensitivity, specificity and Correct Classification Rate (CCR) have been calculated using the favourability value of $F=0.5$ as a classification threshold. AUC: Area Under the Curve of the Receiver Operating Characteristic. Goodness-of-fit was assessed with the Hosmer and Lemeshow test (H-L). * = $p < 0.01$, n.s. = $p > 0.05$. cF_p is the cardinality of the fuzzy set of favourable areas modelled for each species and referring to the 1961–1990 period. Pre: prevalence.

	Pre			cF_p	Kappa	Sensitivity	Specificity	CCR	AUC	H-L
<i>A. dickhilleni</i>	0.031	CGCM2	A2	480.61	0.43	0.971	0.928	0.929	0.986	1.696 n.s.
			B2	480.45	0.429	0.971	0.927	0.928	0.986	1.65 n.s.
		ECHAM4	A2/B2	455.09	0.456	0.978	0.934	0.935	0.987	0.586 n.s.
<i>V. latasti</i>	0.179	CGCM2	A2	2235.89	0.234	0.643	0.689	0.681	0.737	12.59 n.s.
			B2	2234.29	0.211	0.618	0.682	0.67	0.731	33.66*
		ECHAM4	A2/B2	2116.79	0.276	0.719	0.683	0.689	0.768	16.29 n.s.
<i>A. fasciata</i>	0.164	CGCM2	A2	1930.27	0.422	0.808	0.775	0.781	0.853	16.20 n.s.
			B2	1935.98	0.414	0.803	0.772	0.777	0.847	8.06 n.s.
		ECHAM4	A2/B2	1912.35	0.406	0.799	0.768	0.773	0.861	11.12 n.s.
<i>C. pyrenaica</i>	0.138	CGCM2	A2	1505.59	0.487	0.875	0.818	0.826	0.916	10.66 n.s.
			B2	1507.66	0.489	0.878	0.818	0.826	0.916	9.79 n.s.
		ECHAM4	A2/B2	1488.95	0.498	0.889	0.82	0.83	0.92	16.50 n.s.

$$O = \frac{c(F_f \cap F_p)}{c(F_f \cup F_p)} \quad M = \frac{c(F_f \cap F_p)}{c(F_p)}$$

$$S = \frac{\text{Min}[c(F_p) - c(F_f \cap F_p), c(F_f) - c(F_f \cap F_p)]}{c(F_p)}$$

$$I = \frac{c(F_f) - c(F_p)}{c(F_p)}$$

where, $c(X)$ is the cardinality of the X fuzzy set, that is, the sum of all cells' degrees of membership in the fuzzy set X . F_f is the fuzzy set of future areas favourable to the species, and the degree of membership of each cell to F_f is defined by the future favourability value for the species in the cell. F_p is the fuzzy set of present areas favourable to the species, and the degree of membership of each cell to F_p is defined by the present favourability value for the species in the cell. $F_f \cap F_p$ is the intersection between future and present favourabilities, and the degree of membership of each cell to $F_f \cap F_p$ is defined by the minimum of the two favourability values for the species in the cell. $F_f \cup F_p$ is the union between future and present favourabilities, and the degree of membership of each cell to $F_f \cup F_p$ is defined by the maximum of the two favourability values for the species in the cell.

Positive values of increment (I) indicate the expansion in favourability for the species ($E = \text{Max}[0, I]$), that is, a gain

in favourable areas, whereas negative values of I mean a net loss of areas favourable to the species ($L = \text{Min}[0, I]$). These features of the predicted impact of climate change on species favourability would be informative for policy planning if the coincidence between predictions for different SRESs using the same AOGCM is lower than the consistency between predictions for the same SRES applying different AOGCMs. Coincidence is here defined as the concurrence between predictions according to two SRESs for a given AOGCM and time period. These are computed as follows:

$$\text{Coincidence} = \frac{c(F_{A2} \cap F_{B2})}{c(F_{A2} \cup F_{B2})}$$

where, F_{A2} is the predicted future favourability according to the AOGCM and the scenario A2, and F_{B2} is the predicted future favourability according to the AOGCM and the scenario B2.

Consistence is defined here as the agreement between predictions for a given SRES applying different AOGCMs, and is computed as follows:

$$\text{Consistence} = \frac{c(F_C \cap F_E)}{c(F_C \cup F_E)}$$

where, F_C is the predicted future favourability according to the circulation model CGCM2, and F_E is the predicted

Table 4. Values obtained for Cohen's kappa (K), Correct Classification Rate (CCR) and Area Under the Curve (AUC) of the Receiver Operating Characteristic for each model on the recalibration set (rc) and on the pseudovalidation set (va). SE: standard error of Kappa.

			K_{rc}	SE	K_{va}	SE	CCR_{rc}	CCR_{va}	AUC_{rc}	AUC_{va}
<i>A. dickhilleni</i>	CGCM2	A2	0.423	0.051	0.457	0.063	0.933	0.920	0.987	0.982
		B2	0.422	0.051	0.454	0.062	0.933	0.919	0.987	0.982
	ECHAM4	A2/B2	0.453	0.052	0.469	0.063	0.939	0.923	0.988	0.982
<i>V. latasti</i>	CGCM2	A2	0.241	0.021	0.204	0.033	0.689	0.665	0.746	0.710
		B2	0.227	0.021	0.196	0.032	0.681	0.655	0.739	0.706
	ECHAM4	A2/B2	0.275	0.020	0.261	0.032	0.687	0.681	0.775	0.749
<i>A. fasciata</i>	CGCM2	A2	0.423	0.024	0.346	0.034	0.786	0.758	0.862	0.836
		B2	0.467	0.024	0.365	0.034	0.808	0.763	0.853	0.835
	ECHAM4	A2/B2	0.509	0.024	0.371	0.033	0.822	0.762	0.872	0.839
<i>C. pyrenaica</i>	CGCM2	A2	0.477	0.024	0.488	0.041	0.822	0.815	0.914	0.922
		B2	0.476	0.024	0.490	0.035	0.821	0.816	0.914	0.921
	ECHAM4	A2/B2	0.371	0.034	0.421	0.048	0.873	0.868	0.916	0.929

future favourability according to the circulation model ECHAM4.

Mean coincidences and consistencies were compared using ANOVA after controlling for the normality of their distributions using the Kolmogorov-Smirnov test.

Results

Scenarios A2 and B2 applied to the circulation model ECHAM4 produced the same values for the period 1961–1990, both for precipitation and temperature, which is why there is only one favourability model for this AOGCM in the initial period (Table 2 and 3).

The recalibrated models' performances were similar in the recalibration and the pseudovalidation datasets (Table 4). The Cohen's kappa and AUC values for the favourability models based on the whole dataset were intermediate between the corresponding values obtained on the recalibration and pseudovalidation datasets (Table 3 and 4).

For *A. dickhilleni* and *V. latasti*, the predicted maintenance rate of the favourability was, in most cases, medium-high (>0.70) and with slight shifts of the favourable areas (the maximum shift rate being 0.145) (Table 5, Fig. 1 and 2). However, for these species a clear loss of favourable areas was sometimes predicted, reaching net favourability loss values >0.25. For *A. dickhilleni* a net expansion was predicted for the beginning and middle of

Table 5. Values of the rates of overlap (*O*), maintenance (*M*), shifting (*S*), increment (*I*), expansion (*E*) and net loss (*L*) of favourability predicted for each future projection with respect to the 1961–1990 period. cF_f is the cardinality of the fuzzy set of areas favourable predicted for the respective future period; $c(F_f \cap F_p)$ is the cardinality of the intersection between future and present favourability; and $c(F_f \cup F_p)$ is the cardinality of the union between future and present favourability.

Species	CGM-SRES	Period	<i>O</i>	<i>M</i>	<i>S</i>	<i>I</i>	<i>E</i>	<i>L</i>	cF_f
<i>A. dickhilleni</i>	CGCM2-A2	2011–2040	0.807	0.993	0.007	0.224	0.224	0	588.19
		2041–2070	0.655	0.706	0.079	–0.215	0	0.215	377.10
		2071–2100	0.223	0.225	0.008	–0.768	0	0.768	111.81
	CGCM2-B2	2011–2040	0.736	0.976	0.024	0.302	0.302	0	625.66
		2041–2070	0.777	0.904	0.096	0.067	0.067	0	512.71
		2071–2100	0.517	0.522	0.010	–0.468	0	0.468	255.57
	ECHAM4-A2	2011–2040	0.622	0.987	0.013	0.573	0.573	0	715.86
		2041–2070	0.53	0.899	0.101	0.597	0.597	0	726.60
		2071–2100	0.506	0.579	0.145	–0.276	0	0.276	329.57
	ECHAM4-B2	2011–2040	0.515	0.98	0.020	0.881	0.881	0	856.17
		2041–2070	0.636	0.719	0.131	–0.15	0	0.15	386.75
		2071–2100	0.625	0.859	0.141	0.233	0.233	0	561.30
<i>V. latasti</i>	CGCM2-A2	2011–2040	0.433	0.433	0.000	–0.567	0	0.567	968.14
		2041–2070	0.451	0.451	0.099	–0.451	0	0.451	1229.02
		2071–2100	0.648	0.649	0.002	–0.348	0	0.348	1456.61
	CGCM2-B2	2011–2040	0.8	0.805	0.006	–0.189	0	0.189	1811.27
		2041–2070	0.583	0.583	0.000	–0.417	0	0.417	1302.59
		2071–2100	0.75	0.997	0.003	0.326	0.326	0	2962.84
	ECHAM4-A2	2011–2040	0.698	0.705	0.010	–0.286	0	0.286	1513.02
		2041–2070	0.661	0.674	0.020	–0.306	0	0.306	1469.10
		2071–2100	0.784	0.985	0.015	0.241	0.241	0	2627.95
	ECHAM4-B2	2011–2040	0.729	0.754	0.035	–0.212	0	0.212	1669.30
		2041–2070	0.856	0.938	0.062	0.033	0.033	0	2187.16
		2071–2100	0.773	0.932	0.068	0.138	0.138	0	2407.90
<i>A. fasciata</i>	CGCM2-A2	2011–2040	0.858	1	0.000	0.166	0.166	0	2251.11
		2041–2070	0.741	1	0.000	0.35	0.35	0	2605.87
		2071–2100	0.689	1	0.000	0.45	0.45	0	2798.89
	CGCM2-B2	2011–2040	0.799	1	0.000	0.252	0.252	0	2423.85
		2041–2070	0.731	1	0.000	0.368	0.368	0	2648.42
		2071–2100	0.684	1	0.000	0.462	0.462	0	2830.40
	ECHAM4-A2	2011–2040	0.77	0.97	0.030	0.229	0.229	0	2351.00
		2041–2070	0.462	1	0.000	1.166	1.166	0	4142.15
		2071–2100	0.678	0.931	0.069	0.305	0.305	0	2495.49
	ECHAM4-B2	2011–2040	0.713	1	0.000	0.403	0.403	0	2683.03
		2041–2070	0.533	1	0.000	0.878	0.878	0	3591.39
		2071–2100	0.586	1	0.000	0.705	0.705	0	3260.56
<i>C. pyrenaica</i>	CGCM2-A2	2011–2040	0.731	0.999	0.001	0.366	0.366	0	2056.25
		2041–2070	0.588	1	0.000	0.701	0.701	0	2561.38
		2071–2100	0.365	1	0.000	1.742	1.742	0	4128.31
	CGCM2-B2	2011–2040	0.742	0.999	0.001	0.345	0.345	0	2027.69
		2041–2070	0.652	1	0.000	0.533	0.533	0	2311.26
		2071–2100	0.648	0.999	0.001	0.543	0.543	0	2325.79
	ECHAM4-A2	2011–2040	0.818	0.993	0.007	0.206	0.206	0	1796.22
		2041–2070	0.705	0.996	0.004	0.408	0.408	0	2096.12
		2071–2100	0.522	1	0.000	0.916	0.916	0	2852.83
	ECHAM4-B2	2011–2040	0.797	0.988	0.012	0.227	0.227	0	1826.95
		2041–2070	0.643	1	0.000	0.555	0.555	0	2315.32
		2071–2100	0.561	1	0.000	0.781	0.781	0	2651.99

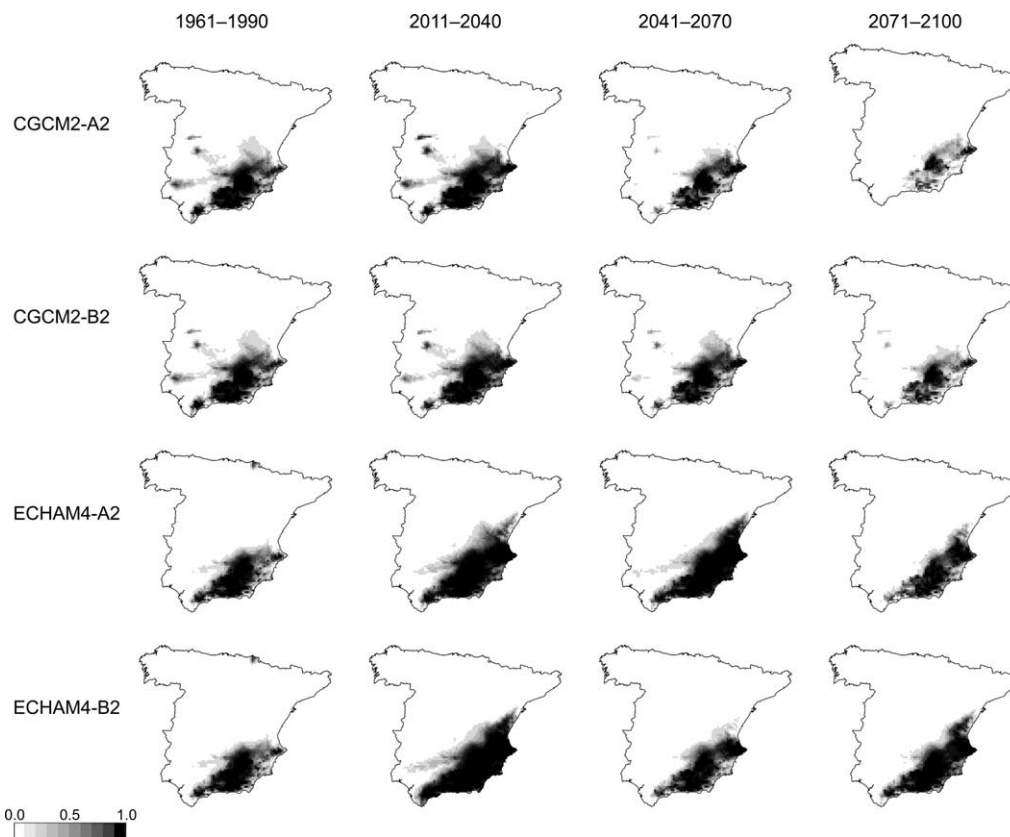


Figure 1. Favourability predicted at each 10×10 km UTM square of mainland Spain for *A. dickhilleni* according to each climatic model and for each period.

the century with a net favourability loss during the final three decades, whereas the opposite occurs with *V. latasti* (Table 5).

For *A. fasciata* and *C. pyrenaica*, predicted maintenance rates of the favourable areas were very high (>0.93) and shifting rates were very low for all the AOGCMs and SRESs used (Table 5, Fig. 3 and 4). No net loss of favourable areas was detected for them, but important favourability expansions were frequently predicted.

Table 6 shows the coincidences between predictions for different SRESs using the same AOGCM, and the consistencies of results derived from different AOGCMs assuming the same SRES. Coincidence values did not differ significantly when using different AOGCMs, nor did consistence values differ significantly when using different SRESs. However, coincidences (mean = 0.768, $n = 24$) were higher than consistencies (mean = 0.668, $n = 24$) and these differences were statistically significant ($t = 2.29$, $gl = 46$, $p = 0.027$). This difference could not be attributed to the different sets of climatic variables selected in the different AOGCM-SRES combinations, because after using the same variables in all the models (those obtained in the ECHAM4-A2/B2 combination) differences between coincidences (mean = 0.838, $n = 24$) and consistencies (mean = 0.679, $n = 24$) were even higher and more significant ($t = 4.405$, $gl = 46$, $p < 0.001$).

Coincidences were significantly lower in ectotherms when compared with endotherms ($t = -2.996$, $gl = 22$, $p = 0.007$) and consistence values were also significantly lower in ectotherms ($t = -5.811$, $gl = 22$, $p < 0.001$).

Discussion

Our results show that discrepancies between predictions were more attributable to the lack of knowledge concerning the effect of oceans and atmosphere on climate (general circulation models) than to the putative effect of different emission scenarios on future climate. Uncertainty is inherent to the climate system and to nature in general and, thus, cannot be avoided (Beaumont et al. 2008, Baer and Risbey 2009). However, it can be, and should be, assessed and taken into account when modelling biodiversity responses to climate change (Araújo et al. 2005). Numerous factors contribute to the emergence of uncertainties at each step of the process leading to modelling the species response to climate change (Dormann et al. 2008), and they are transmitted to the following steps (Beaumont et al. 2007). Thus, we are addressing a kind of uncertainty which arises at the final stage of the favourability modelling procedure, but whose source resides in a previous step, namely, in the depth of our knowledge about the effects on global climate of oceans and the atmosphere, on the one hand, and greenhouse gasses, on the other. Both consistence and coincidence are inversely proportional to uncertainty. Consistence provides information about the uncertainty associated with our understanding of the basic principles governing global climate, and uncertainty should be kept low, that is, higher values of consistence are to be preferred. However, it is not the case that every kind of uncertainty is unhelpful, because that associated with the existence of different SRESs is the kind of uncertainty we, as a human

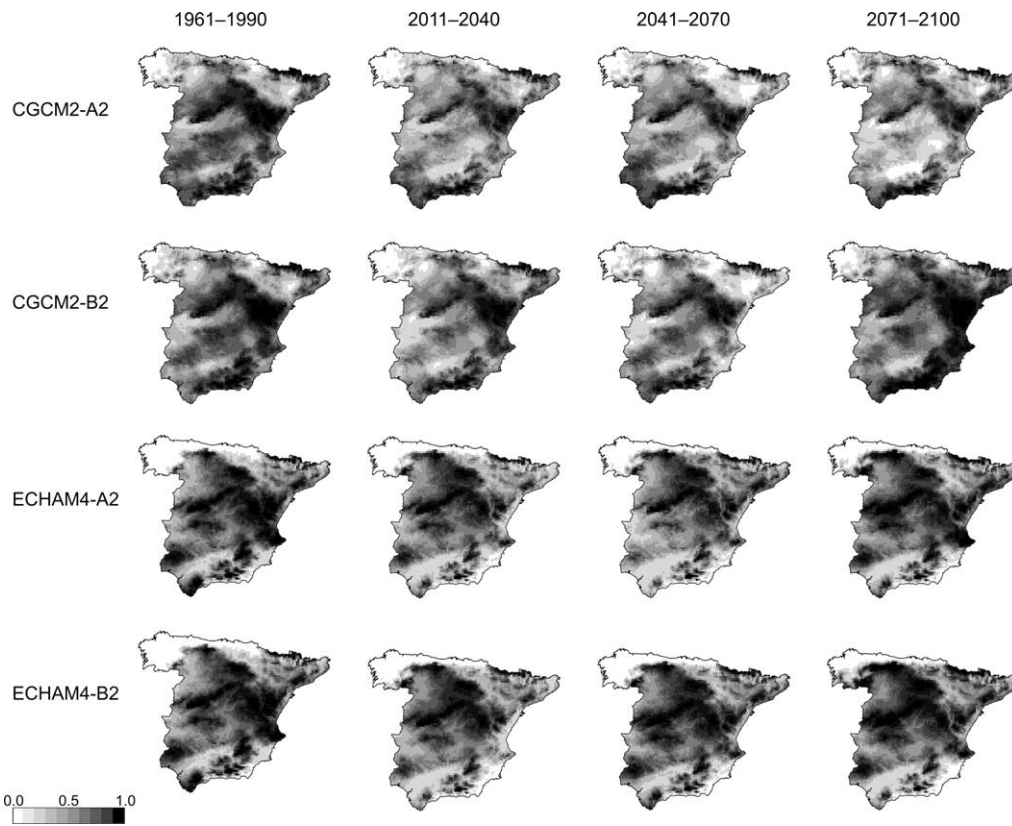


Figure 2. Favourability predicted at each 10×10 km UTM square of mainland Spain for *V. latasti* according to each climatic model and for each period.

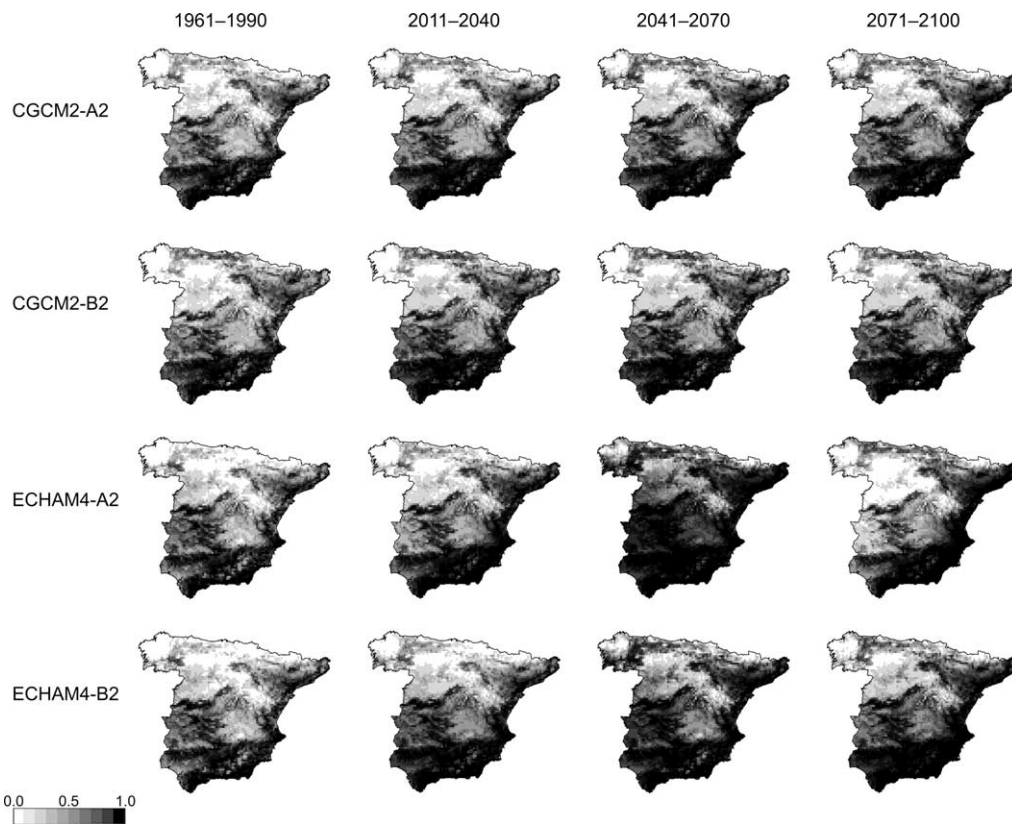


Figure 3. Favourability predicted at each 10×10 km UTM square of mainland Spain for *A. fasciata* according to each climatic model and for each period.

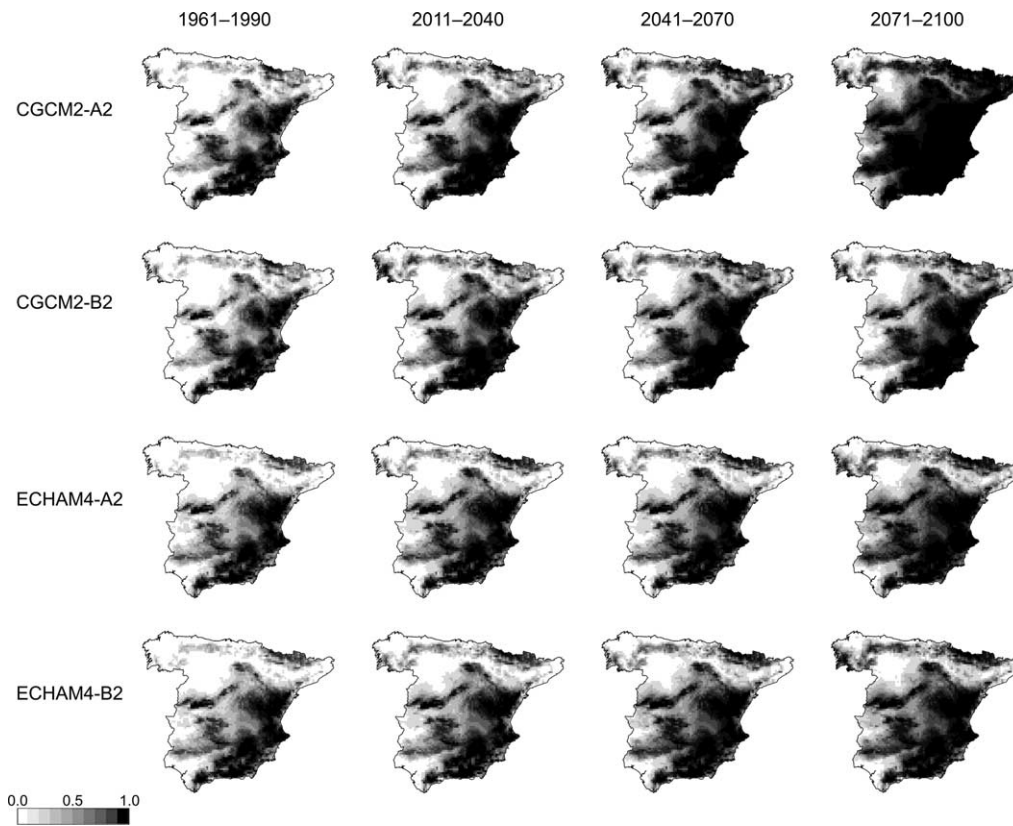


Figure 4. Favourability predicted at each 10×10 km UTM square of mainland Spain for *C. pyrenaica* according to each climatic model and for each period.

society, can affect and, thus, is of value to emission policy planning. If the expected responses of species to different SRESs were similar, then uncertainty would be low, but this would imply that the way we control our gas emissions will not affect species distributions much. This may be useful information for policy-making, but not for greenhouse emissions policy planning, as the policy maker would have

no reason to prefer, by including the expected effect of the emissions scenarios on species distribution in the cost/benefit balance, one SRES to another. Consequently, species distribution models will be more informative in this respect if coincidences are lower.

In areas with great spatial variability of climate, such as the Iberian Peninsula, it is particularly important to use reliable AOGCMs to forecast future climate change (Sánchez et al. 2004). Although our analyses did not evaluate the reliability of AOGCMs, in order for general knowledge on the effects of oceans and atmosphere to be considered reliable it is a necessary, although not sufficient, requirement that the uncertainty associated with the differences between AOGCMs to be low. In our case, competing AOGCMs differ in their simulation of average climate values, thus generating a kind of uncertainty which is implicit in the climate variables used in our models and which is transmitted to our analyses. This adds to the methodological uncertainty associated with the modelling procedures (Thuiller et al. 2008), which the modelling community can deal with through the analysis of different modelling alternatives. Given that we used the same methodology to produce all the models, it is unlikely that our modelling procedure biased the uncertainty associated with AOGCMs and SRESs. In this way, the uncertainty associated with disagreements between different AOGCMs could be assessed and compared to that associated with the existence of different SRESs. The latter should be higher than the former, as policy planners can only affect the emission of gasses producing global warming. If uncertainty

Table 6. Coincidences between predictions using different SRESs for each circulation model and consistencies between predictions for each emission scenario using different AOGCMs.

Species	Period	Coincidences		Consistencies	
		CGCM2	ECHAM4	A2	B2
<i>A. dickhilleni</i>	2011-2040	0.873	0.776	0.720	0.638
	2041-2070	0.735	0.532	0.507	0.667
	2071-2100	0.434	0.587	0.333	0.444
	Mean	0.680	0.632	0.520	0.583
<i>V. latasti</i>	2011-2040	0.532	0.872	0.511	0.624
	2041-2070	0.824	0.670	0.582	0.532
	2071-2100	0.492	0.882	0.496	0.669
	Mean	0.616	0.808	0.530	0.609
<i>A. fasciata</i>	2011-2040	0.863	0.839	0.872	0.803
	2041-2070	0.881	0.867	0.629	0.729
	2071-2100	0.884	0.756	0.801	0.841
	Mean	0.876	0.821	0.767	0.791
<i>C. pyrenaica</i>	2011-2040	0.915	0.964	0.791	0.812
	2041-2070	0.902	0.871	0.772	0.800
	2071-2100	0.563	0.918	0.691	0.775
	Mean	0.794	0.918	0.751	0.796
Total mean	0.738	0.787	0.635	0.688	

about the future distribution of areas favourable to a species is not clearly associated with the different SRESs, then choosing between them is not likely to produce the difference desired for the future distribution of the species.

The use of fuzzy logic to assess the effect of climate change on species distribution bypassed the loss of information implicit in the use of a threshold for converting model output values into predicted presences and absences to be compared with actual data (Parra and Monahan 2008, Randin et al. 2009). The fact that the favourability function is a membership function was essential to calculate the increment, overlap, maintenance, shifting, expansion, and net loss of the predicted favourability for every species preserving all the information included in the individual favourability values. In this respect, our results are meant to exemplify a useful way to assess the comparative effects of AOGCMs and SRESs on simulations of future species distributions.

The expected response to climate change tends to be species-specific (see, for example, Levinsky et al. 2007, Seoane and Carrascal 2008, Virkkala et al. 2008). Our results suggest a negative effect of climate change on the areas favourable to the ectotherm species *A. dickhilleni* and *V. latasti*, whereas the other two species, *A. fasciata* and *C. pyreniaca*, could benefit from a regional increase in temperature (Table 4, Fig. 1, 2, 3 and 4). Although these results concern too few species to warrant any generalization, they agree with those of Aragón et al. (2010), who found that the influence of climate on Iberian species distributions is stronger in ectothermic vertebrates. In addition, coincidences were lower in ectotherms when compared with endotherms, which seems to indicate that the distribution of areas favourable to the more sensitive amphibians and reptiles are more likely to be affected by emission policy decisions than those of the endothermic birds and mammals. However, our consistence values were also lower in ectotherms and, thus, the overall informative value was not really higher.

In summary, uncertainties related to the AOGCM employed were bigger than those related to the SRES used for every species analysed. This adds to accumulating evidence that agreement between projections using different AOGCMs is currently insufficient. Variation among different AOGCMs was found to be larger than the expected impact of the different SRESs when predicting crop growth (Audsley et al. 2006), regional climatic features (Rowell 2006, Déqué et al. 2007, Paeth et al. 2008) or river flow regimes (Prudhomme and Davies 2009). An improvement in knowledge on the effect of oceans and atmosphere on climate is needed if really informative models are to be produced. Our conclusion is that species distribution models in climate warming scenarios are still not useful for informing emission policy planning, although they have great potential as tools once consistencies become higher than coincidences.

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