Predicted impact of climate change on threatened terrestrial vertebrates in central Spain highlights differences between endotherms and ectotherms

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Abstract

Climate change can induce shifts in species ranges. Of special interest are range shifts in regions with a conflict of interest between land use and the conservation of threatened species. Here we focus on the 94 threatened terrestrial vertebrates occurring in the Madrid region (Central Spain) and model their distributions using data for the whole peninsular Spain to evaluate which vertebrate groups are likely to be more sensitive to climatic change. First, we generated predictive models to quantify the extent to which species distributions are explained by current climate. We then extrapolated the models temporally to predict the effects of two climate-change scenarios on species distributions. We also examined the impact on a recently proposed reserve relative to other interconnected zones with lower protection status but categorized as Areas of Community Importance by the European Union. The variation explained by climatic predictors was greater in ectotherms. The change in species composition differed between the proposed reserve and the other protected areas. Endothermic and ectothermic vertebrates had different patterns of changes in species composition but those of ectotherms matched with temperature departures predicted by climate change. Our results, together with the limited dispersal capacity of herptiles, suggest that trade-offs between different design criteria accounting for animal group differences are necessary for reserve selection.

Introduction

Much effort has been devoted to examine how present-day species distributions relate to current climate (e.g. Guisan & Hofer, 2003), and to develop predictive models to project future distributions under different climate-change scenarios (Pearson & Dawson, 2003).

Predictive models have suggested that climate change might increase extinction risk (e.g. Thomas et al., 2004) and/or species turnover (Peterson et al., 2002) and empirical studies have shown that it has already caused range shifts in many species (Parmesan & Yohe, 2003). Whether traditional, protected area-based conservation approaches will be effective under these circumstances remains uncertain (Hannah, Midgley & Millar, 2002; Araújo et al., 2004; Pressey et al., 2007), particularly in highly populated regions where reserve designs are constrained by urban development. Interestingly, many of these areas are of special interest for conservation, as it has been shown that human population density and species richness tend to be positively associated both in developing (Balmford et al., 2001) and developed regions (Araújo, 2003). Developing solutions for

the preservation of biodiversity in these areas under global warming is complex (Pressey et al., 2007), but it is clear that two first steps are detecting those groups of species that will be more sensitive to climate change (Whittaker et al., 2005), and to evaluate to what extent existing or planned conservation areas will be adequate (Pressey et al., 2007). In particular, threatened species need evaluation of the effects of future climate on their distributions, but relatively few forecast-oriented studies have focused on threatened species (Engler, Guisan & Rechteiner, 2004).

We use the threatened vertebrate species of the Madrid region (Central Spain, 94 species) as a case study and model their distributions across Spain in relation to climate. The annual mean temperature of Spain has increased by nearly 1.6 °C over the last century (Hulme & Sherad, 1999), and a recent, comprehensive study for Europe has shown that Spanish terrestrial ecosystems are among the continent's most strongly affected by climate change (Menzel et al., 2006). The Madrid region harbors a substantial portion of Iberian biodiversity, but is also one of the European regions in which the impact of urban sprawl upon natural areas has became most visible (European Environment Agency,

2006), thus constituting a good example to investigate trade-offs between conservation and urban growth under climate change (Observatorio de la Sostenibilidad de España, 2006).

The focus of our analysis was an evaluation of the plan proposed by the Spanish administrations to raise the protection status of the Guadarrama Mountain range by creating the Guadarrama Natural Reserve (hereafter GNR, Fig. 1). We also considered all areas of the study region and neighboring provinces connected to the GNR that have been categorized as Areas of Community Importance by the European Union; that is the Natura 2000 Network (Council Directive 92/43/EEC). Although these sites are not always devoted to the conservation of fauna, according

to Araújo, Lobo & Moreno (2007) they are necessary for a full representation of the terrestrial vertebrate species within the protected area network in the Iberian Peninsula. We took these relatively well-preserved Natura 2000 sites and compared how species composition may be modified by climate change inside these areas and in the GNR.

We ask three questions: (1) are associations between species distributions and climate different among taxonomic groups?; (2) how will the forecasted changes in species composition due to climate change differ between groups of animals with shared physiological traits?; (3) will the protected areas system of the study region be adequate to accommodate potential alterations regarding different animal groups?
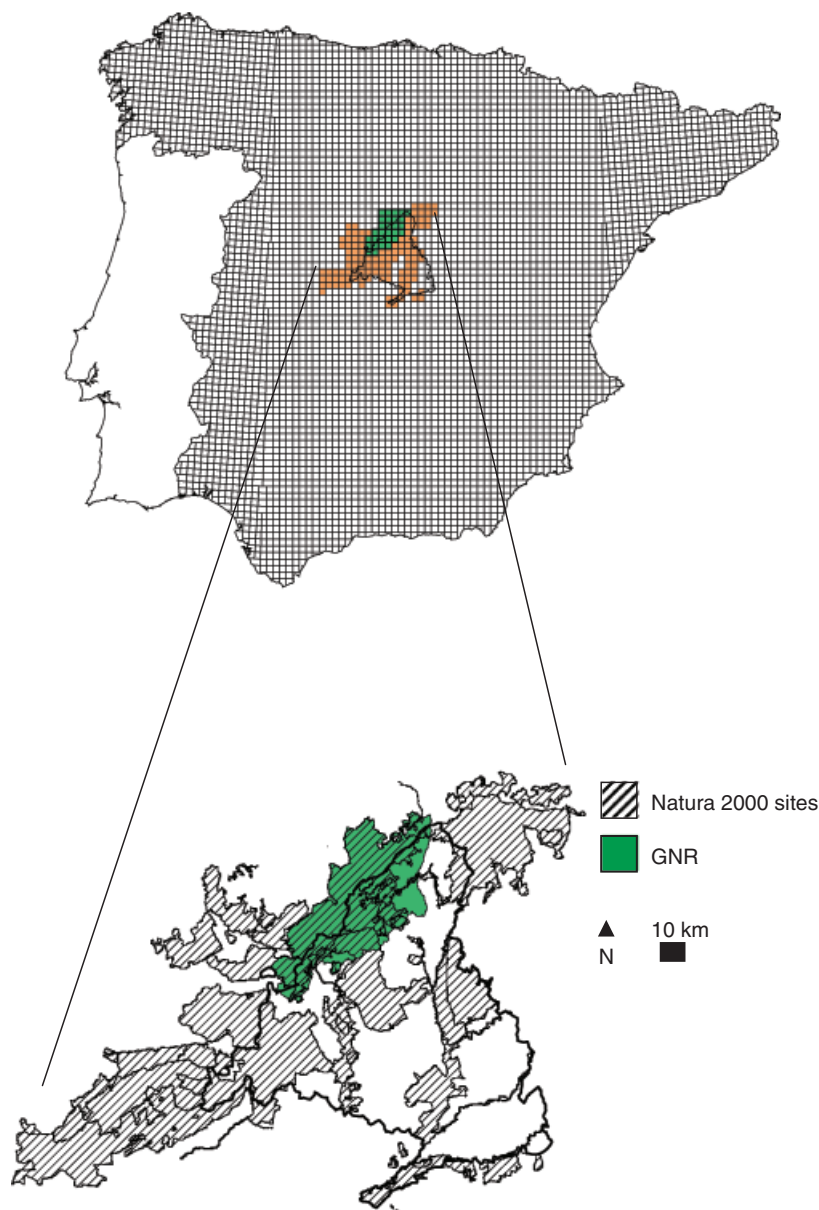
Figure 1 Location of the Natura 2000 sites and the proposed area for the Guadarrama natural reserve (GNR) in the 10 km grid system used in this study. Madrid region is denoted by the bold contour in the zoomed area.

Methods

Species data

Our database comprises all terrestrial vertebrate species inhabiting the Madrid region that had been categorized as critically endangered, vulnerable or near threatened in the IUCN Red List of Threatened Species (IUCN, 2004), and/or as critically endangered, vulnerable, sensitive to habitat change or of special interest in the Regional Catalogue of Threatened Species (http://www.madrid.org, supporting information Appendix S1). This comprises 25 mammals, 56 birds and 13 herptiles, which represent 23% of the terrestrial vertebrate species of peninsular Spain. Observed distributions in all of Spain were obtained from Palomo & Gisbert (2002) for mammals; Martí & del Moral (2003) for birds and Pleguezuelos, Márquez & Lizana (2002) for amphibians and reptiles. All three sources are atlases reporting presence–absence data in UTM-grid cells of a size of 10×10 km. Up to date, this is the highest resolution for presence–absence data of terrestrial vertebrates currently available for Spain.

Current environment data

Water and energy inputs are controlling factors of the physiological processes limiting species distributions, and variables reflecting these environmental characteristics have been widely used in studies on the variation of vertebrate species richness (e.g. Whittaker, Nogués-Bravo & Araújo, 2007) and distributions (e.g. Araújo *et al.*, 2005). We generated six measures of water and energy inputs to represent climatic gradients across peninsular Spain. We also generated six time-invariant predictors (soil and topographical variables) to reduce prediction uncertainty, as it has been shown that excluding non-climatic variables may bias species turnover assessments based on bioclimatic models (e.g. Luoto & Heikkinen, 2008). This is even more important for the resolution of this study (10 km) in comparison with other studies at broader scales (>10 km), because at finer grains both climatic and non-climatic variables may be important in determining species' distributions (Pearson & Dawson, 2003).

We used mean annual temperature, annual potential evapotranspiration and minimum potential evapotranspiration as our energy variables (Rodríguez, Belmontes & Hawkins, 2005). Mean annual temperature was upscaled from a 1 km resolution raster interpolated from 1504 thermometric stations for the period of 1971–2000 (Spanish Agencia Estatal de Meteorología, AEMET). That is, for each cell, we averaged the temperature values of all 1 km raster pixels it comprised. Potential evapotranspiration variables were calculated using Thornthwaite's (1948) formula, which is based on day length and mean annual temperature. Annual potential evapotranspiration reflects the annual sum of monthly values, whereas minimum potential evapotranspiration represents the lowest monthly value.

We used three climate variables to indicate water availability *per se* (annual precipitation) and the combined influence of water and energy inputs on species' distributions (annual actual evapotranspiration and water deficit). Annual precipitation was upscaled from a 1 km resolution raster interpolated from 4835 pluviometric stations for the period of 1971–2000 (INM). For each 10 km cell, we also obtained average values calculated from all 1 km raster pixels they included. Annual actual evapotranspiration is a measure of water–energy balance that has been shown to be the main determinant of the variation of species richness across Europe and at global scale (e.g. Hawkins, Porter & Diniz-Filho, 2003; Rodríguez *et al.*, 2005). This variable was calculated with the Turc–Pike's formula by combining values of annual precipitation and mean annual temperature (Pike, 1964). Water deficit measures dryness levels in the environment, and has been shown to be an important determinant of vertebrate distributions and population trends (Pounds, Fogden & Campbell, 1999; Teixeira, Ferrand & Arntzen, 2001) and habitat structure (Stephenson, 1998). This predictor was calculated as the difference between potential and actual evapotranspiration (Ahn & Tateishi, 1994).

Soil variables were digitized from a lithological map (Instituto Geográfico Nacional, 1995) to reflect the percentage area of each cell that was covered by acidic rock, basic rock, acidic deposits and basic deposits. We used these variables as some species can be influenced by both climate and soil characteristics, as soil pH is important for some vertebrate distributions (e.g. Teixeira *et al.*, 2001). We also generated two topographic variables for each cell, elevation and elevation range, which are considered indirect predictors of animal distributions (Guisan & Hofer, 2003). Range in elevation is often interpreted as a proxy for habitat heterogeneity (Ruggiero & Hawkins, 2008) and has been associated with richness gradients in vertebrates (Rahbek & Graves, 2001). Habitat heterogeneity has been found to be key in determining vertebrate spatial distributions across the Madrid region (Atauri & de Lucio, 2001). These data were extracted from GTOPO30 (http://eros.usgs.gov/#/Find_Data/Products_and_Data_Available/gtopo30_info), a digital elevation model with a resolution of 1 km.

All explanatory variables were standardized ($\bar{X} = 0$ and standard deviation $= 1$) to eliminate the effects of measurement-scale differences. To reduce redundancy and collinearity we used Spearman's correlations among variables to select those explanatory variables to be included in the initial models. Thus, annual potential evapotranspiration was excluded from the analyses because it was strongly correlated with temperature, ($r > 0.96$). Other pair-wise associations between variables included in models ranged from $r < 0.001$ to 0.80, with a mean ± standard error $= 0.30 \pm 0.02$.

Climate-change data

We used two climate-change scenarios: the HadCM2Sa1 scenario (IPCC, 2001) for the year 2020, and the CCM3

scenario for the year 2100. The coupled atmosphere–ocean general circulation model HadCM2Sa1 is a 'business as usual' scenario (Johns *et al.*, 1997), and we used the version generated by Balairón, Martín & Petisco (2001) for Spain at a grain resolution of 56 km, which we spatially downscaled to 10 km following IPCC guidelines (Wilby *et al.*, 2004). First, we calculated average values of elevation, latitude, current mean annual temperature and current annual precipitation at the 56 km grain. Second, for this same grain and each climatic variable, we generated a multiple regression model relating HadCM2Sa1 predictions with observed current values, elevation and latitude. Third, we used these regression models to generate downscaled values of HadCM2Sa1 temperature and precipitation at the 10 km grain. Fourth, to check whether the downscaled HadCM2-Sa1 temperatures and precipitations were accurately reflecting the climatic trends predicted by this scenario, we calculated the averages of these variables at the 56 km resolution to correlate them with the original HadCM2Sa1 predictions. The resulting relationships were very strong in both cases ($r^2 > 0.90$), indicating the adequacy of this procedure.

The CCM3 scenario for the year 2100 is also a 'business as usual' prediction that can be considered as an extreme scenario by assuming duplication of greenhouse-gas emissions, but that is roughly equivalent to the average of the current IPCC scenario families (Dai *et al.*, 2001; Seavy, Dybala & Snyder, 2008). This scenario comes from the results of the highest-resolution simulations of global warming yet performed with an atmospheric general circulation model (Govindasamy, Duffy & Coquard, 2003) and is available at 10 km resolution (http://worldclim.org/fut down.htm). Finally, we generated future values of minimum potential evapotranspiration, annual actual evapotranspiration and water deficit for both scenarios by applying the same procedures described above for current climate variables.

Modelling current species distributions

Presence/absence species data were modelled for peninsular Spain using generalized linear models (GLM) by specifying a binomial distribution and a logit link term (McCullagh & Nelder, 1989). We chose GLMs because their estimates are as reliable as those of other more complex methods (Meynard & Quinn, 2007), and because they are recommended when the goal is transferring predictions to other scenarios (Randin *et al.*, 2006), such as in the present case. In a niche-modelling framework, even if absence data were available, they have to be data regarding absences of the potential distribution area (Jiménez-Valverde, Lobo & Hortal, 2008; Peterson, Papes & Soberón, 2008). Therefore, models were run including all presences and the most probable environmental absences (pseudo-absences), in order to reduce uncertainties in the estimation of species potential distributions (see supporting information Appendixes S2 and S3 for details on the generation of pseudo-absences and their justification).

Modelling consisted of two phases: first, models were fitted including only current climate predictors for peninsular Spain, and then soil and topographical variables were added to obtain the final overall models. Initial models started with linear and quadratic polynomial functions, and the final models were reached through backward stepwise selection in both modelling phases (McCullagh & Nelder, 1989). We transformed the continuous probability values given by each model into predicted presence/absence data using the prevalence of each species (the presence/absence ratio used for modelling) as the threshold value (Liu *et al.*, 2005; Jiménez-Valverde & Lobo, 2006). Additionally, we checked that prevalence was appropriate through a jack-knifing-based resampling procedure (Jiménez-Valverde & Lobo, 2006, 2007) (see results in the supporting information Appendix S4), a technique also used to evaluate our models (Engler *et al.*, 2004; Pearson *et al.*, 2007) (supporting information Appendix S5). Finally, we verified that spatial auto-correlation in model residuals was not significantly different among animal groups (supporting information Appendix S6).

An objective of this study was quantifying the explanatory capacity of climatic predictors on species distributions and testing for differences among taxonomic groups. Therefore, deviances explained by climatic models were calculated and adjusted by the effective degrees of freedom (i.e. by the number of predictors and by the occupancy) used to fit the model (Guisan, Weiss & Weiss, 1999; Engler *et al.*, 2004). To compare adjusted deviances explained by climatic models among animal groups, we used a Kruskal–Wallis test (Quinn & Keough, 2002). To verify that the observed patterns remain the same even after excluding those species with an important part of their range out of the study area, we repeated the analyses using only the 54.25% of the original data base (excluding those species with the broadest range area and few others whose total range area has not yet been totally quantified). In addition, we verified that the result remained the same after correcting by species occupancy (supporting information Appendix S7).

Projected species distributions and range change predictions

The species-specific GLM models were used to project potential future distributions according to the predictions of the HadCM2Sa1 and CCM3 while maintaining those topographical and soil variables when retained by final models. We calculated predicted changes in threatened species composition for each cell assuming two extreme dispersal possibilities, namely no dispersal and universal dispersal (Araújo, Thuiller & Pearson, 2006), as dispersal capabilities are unknown for most species. Specifically, we first utilized the final models to predict current potential threatened species richness (TSR) values using the current climate variables and the topographical and soil predictors included in the models. Then, we computed the numbers of species lost (L) or gained (G) by each cell under each climate-change scenario, and used these values to compute the

turnover of threatened species. The percentage of species turnover assuming no dispersal was calculated for each cell as: $100 \times L/\text{TSR}$, which is an estimate of the proportion of local extinctions caused by climate change. The percentage of species turnover assuming universal dispersal was computed as: $100 \times (L + G)/(\text{TSR} + G)$; which is also an index of dissimilarity between predicted current and future species compositions (Peterson *et al.*, 2002; Thuiller, 2004).

## Assessment of the climate-change impact on protected areas

To examine whether threatened species composition would be at equilibrium with respect to protected areas and climate change, we compared the percentage of species turnover with and without dispersal for the HadCM2Sa1 and CCM3 scenarios between the inside boundaries of both the GNR and the Natura 2000 sites. Among all of the Natura 2000 sites in Spain, we selected those that were located totally or partially in the Madrid region, or connected with the GNR (Fig. 1). To be conservative regarding high variability in dispersal capabilities of the study species, distances of Natura 2000 sites to GNR boundaries were set to be no longer than the maximum length of the GNR (≈ 85 km).

We performed repeated measures analyses of variance (ANOVAs) including the percentages of species turnover with or without dispersal as dependent variables, and type of area (GNR vs. Natura 2000 sites) and type of climate-change scenario as factors. We used the angular transformation for the dependent variables to meet assumptions underlying the linear models (Quinn & Keough, 2002). These analyses were conducted separately for endothermic and ectothermic vertebrates. We proposed this operational framework to examine the role of key limiting physiological properties on species' responses through space and time (Parmesan *et al.*, 2005).

Finally, we examined to what extent temperature variation caused by climate change differs between GNR and Natura 2000 sites, as this could help explain observed differences in species turnover. Thus, we first calculated for each scenario a temperature anomaly variable as the residuals of a simple regression of predicted temperatures on current temperatures (i.e. temperature anomalies reflect within-cell departures of future temperatures from current temperatures), and then performed a repeated measures ANOVA to compare these anomalies between both types of protected areas and climate-change scenarios.

Results

The percentage of adjusted deviance explained by climatic variables differed significantly among groups (Kruskal–Wallis test, $H = 9.16$, $P = 0.010$), being lower for mammals and higher for herptiles (Fig. 2), a pattern that held after correcting for species occupancy (supporting information Appendix S7). This pattern was not due to the number of variables retained in final models because the correlation between the adjusted deviance and the number of variables
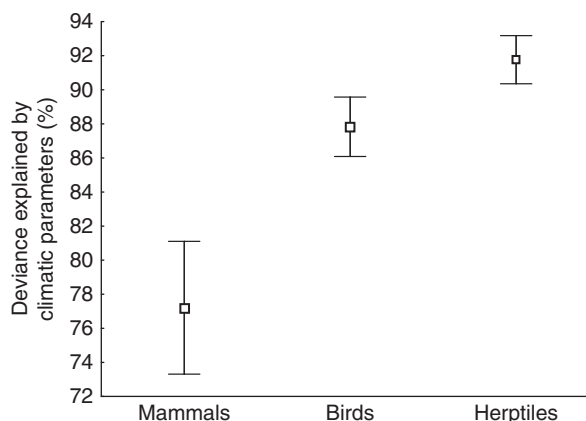

Figure 2 Percentage of deviance explained by climatic variables ($\bar{X} \pm \text{SE}$) for mammal, bird and herptile species modelled for all peninsular Spain and categorized as threatened in the Madrid region.

was not significant (Spearman's correlation: $r = 0.03$, $P > 0.70$). Moreover, the pattern remains the same even after excluding those species with an important part of their range out of Spain (Kruskal–Wallis test, $H = 7.60$, $P = 0.022$).

With respect to climate change-induced turnover of species, we found no significant differences for ectotherms when assuming total dispersal, neither between the proposed reserve (GNR) and Natura 2000 sites ($F_{1,141} = 2.02$, $P < 0.15$; Fig. 3a), nor between climate-change scenarios ($F_{1,141} = 1.22$, $P < 0.27$; Fig. 3a). However, for endotherms, species turnover with total dispersal were significantly higher in Natura 2000 sites ($F_{1,141} = 6.82$, $P < 0.01$; Fig. 3b), and in the CCM3 ($F_{1,141} = 12.86$, $P < 0.001$ Fig. 3b).

In contrast, the ectothermic species turnover without dispersal was significantly higher in the GNR than in the Natura 2000 sites ($F_{1,141} = 18.71$, $P < 0.0001$; Fig. 3c), and was also significantly higher under the CCM3 scenario ($F_{1,141} = 8.30$, $P < 0.01$; Fig. 3c). This pattern closely resembled that found for predicted temperature anomalies (Fig. 4), which were also higher for the GNR areas ($F_{1,141} = 22.63$, $P < 0.001$), and for the CCM3 model ($F_{1,141} = 4.98$, $P = 0.027$). Thus, our results suggest a larger climatic variation for the GNR (a mountainous area), and this variation may cause marked changes in the composition of threatened herptiles of this area when assuming no dispersal. These results highlight the importance of Natura 2000 sites for the conservation of threatened herptiles with limited dispersal abilities.

On the other hand, the percentage of endothermic species turnover assuming no dispersal did not differ significantly between GNR and Natura 2000 sites ($F_{1,141} = 0.83$, $P = 0.36$; Fig. 3d), but continued to be significantly higher in the CCM3 than in the HadCM2Sa1 scenario ($F_{1,141} = 95.00$, $P < 0.0001$; Fig. 3d). Thus, considering both dispersal extremes in endotherms, our results suggest that while the GNR performs better for maintaining the composition when assuming universal dispersal, both GNR and
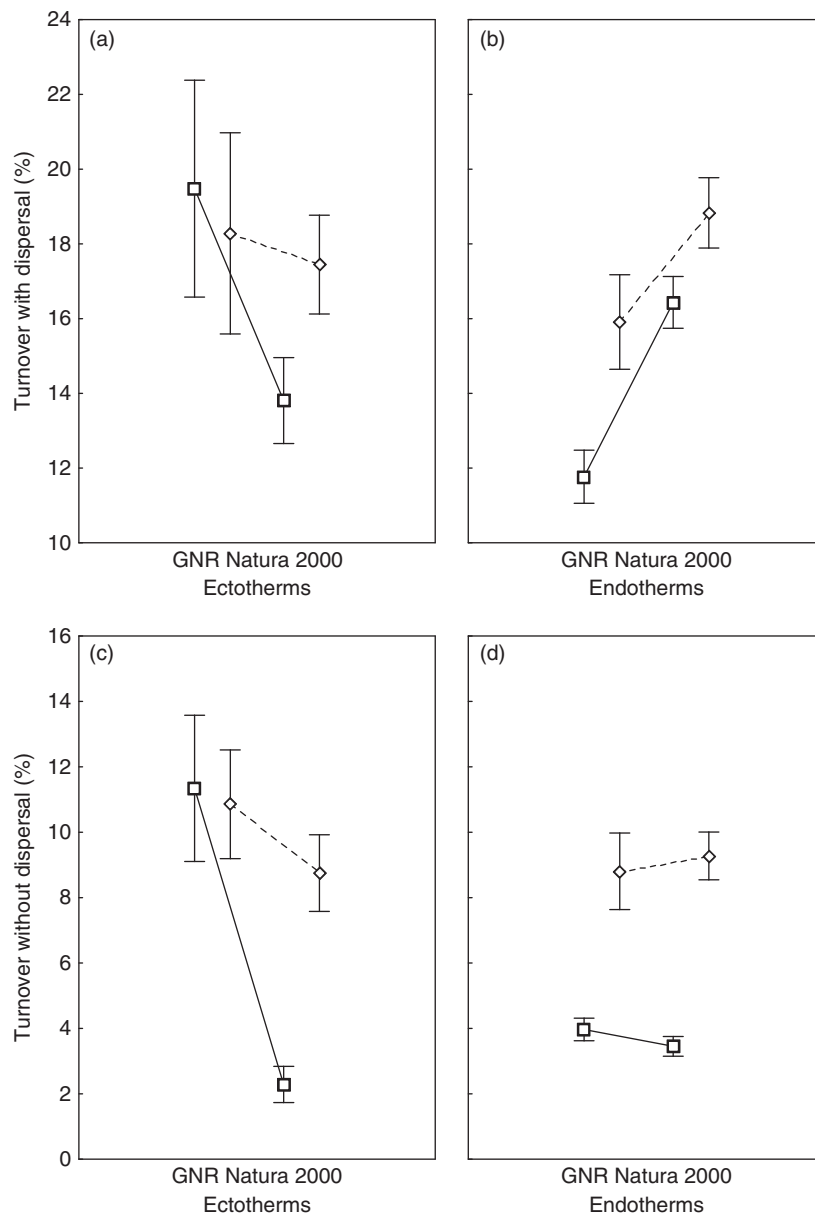
Figure 3 Percentage of species turnover ($\bar{X} \pm$ SE) for the climate scenarios predicted by the HadCM2Sa1 ($\square$) and CCM3 ($\lozenge$) scenarios, in the Natura 2000 sites and in the proposed Guadarrama Natural Reserve (GNR) for (a) ectothermic and (b) endothermic vertebrates assuming total dispersal capability, and (c) ectothermic and (d) endothermic vertebrates assuming null dispersal.

Natura 2000 sites would preserve similarly the composition when assuming no dispersal.

Discussion

We found that, at least at the scale and resolution of this study, potential distributions of threatened herptiles are better explained by climate than in endotherms. In this study, this pattern was not significantly associated with the number of predictors. Also, in the present study the temperature anomaly matched with the percentage of species turnover without dispersal for the two climate scenarios only in the case of herptiles. Additionally, the percentage of species whose final models retained temperature-related factors was also consistent with these results, being lower for mammals and higher for herptiles (supporting information Appendix S8). This is not in contradiction with the fact that water-related factors remained important for all herptile species (supporting information Appendix S8).

Despite the differences among animal groups found here, it is important to note that the variation explained by climatic predictors in endotherms is also high (Fig. 2). A previous study, at this scale and resolution, revealed a stronger direct influence of climate (via physiological constraints) on range distributions of Spanish herptiles and a stronger indirect effect of climate (via plant productivity) on Spanish birds' ranges (Aragón et al., 2010). This does not necessarily imply that other processes may not operate at
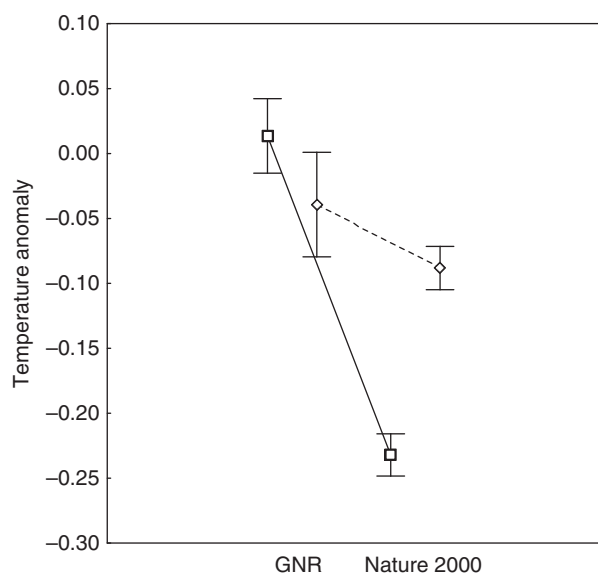
Figure 4 Temperature anomaly (residuals of future temperature on current temperature) ($\bar{X} \pm$ SE) predicted for the HadCM2Sa1 scenario ($\square$) and the CCM3 scenario ($\diamond$) in the Natura 2000 sites and in the proposed Guadarrama Natural Reserve (GNR).

other scales. In fact, it is known that predictions on the impact of climate change on species' distributions may vary depending on the extent, resolution and geographical location (e.g. Trivedi *et al.*, 2008; Randin *et al.*, 2009). Therefore, although for this study we used the finest resolution available, other patterns might emerge at other resolutions, extents and/or geographical locations. The contribution of our study is that at a given resolution and geographic location, different animal groups showed different patterns consistent with differences in their physiology. Whatever the processes involved, there are many empirical studies showing that climate change is influencing different aspects of the biology of both endothermic and ectothermic terrestrial vertebrates, such as population trends (Pounds *et al.*, 1999), phenology and range shifts (Parmesan & Yohe, 2003) and fitness (Reading, 2007). Similarly, studies using envelope modelling have concluded that many species might be imperiled by climate change (Thomas *et al.*, 2004; but see Ladle *et al.*, 2004).

Although the impact of climate change on amphibian populations is receiving attention (Pounds *et al.*, 2006; Whitfield *et al.*, 2007), reptiles are much less well studied. Several nonexclusive mechanisms may explain the impact of climate change on herptiles. Amphibians may respond to a warmer climate by breeding earlier (Parmesan, 2007) and/or reducing their hibernation period (Jørgensen, 1986; Reading, 2007), which might have profound effects on population dynamics. Our results suggesting a potential stronger influence of climate on herptiles are consistent with previous results on the phenological response to global warming. A quantitative comparison among organism taxonomic/functional groups revealed that amphibians had significantly

stronger shift toward earlier breeding than all other groups considered (Parmesan, 2007).

On the other hand, a climate-driven disease is an explanation for the decline of amphibians that is receiving a considerable deal of attention. Several analyses have suggested that global warming may increase the susceptibility of amphibians to infectious diseases in different parts of the globe (Kiesecker, Blaustein & Belden, 2001; Pounds *et al.*, 2006), including our study area (Bosch *et al.*, 2007). On the other hand, other study does not support this hypothesis for amphibian species in Central and South America (Lips *et al.*, 2008).

There are other potential mechanisms that have received less attention for the case of herptiles, but that may be at least as important as those mentioned above. For instance, declines of reptiles and amphibians have recently been attributed to climate-driven changes in microhabitat (Whitfield *et al.*, 2007). Regardless of the mechanisms involved, the dispersal ability of species has profound effects on the ability to track climatic changes (Trakhtenbrot *et al.*, 2005), and in herptiles dispersal is limited in comparison with endotherms (Blaustein *et al.*, 2001).

Taken together, worldwide empirical findings are consistent with results obtained using envelope modelling techniques. Envelope models have shown that temperature-related factors play an important role in the distributions of ectothermic terrestrial vertebrates (Teixeira *et al.*, 2001; Guisan & Hofer, 2003; Ballestero-Barreara, Martínez-Meyer & Gadsden, 2007). Further, our results also agree with an European-scale study that predicted that climate warming will cause significant losses of suitable climate space for herptiles in the Iberian Peninsula (Araújo *et al.*, 2006). However, elucidating which mechanisms are involved in species range shifts is always challenging as information on individualistic responses is limiting for many species. The application of ecophysiological models demonstrated that geographical distributions can be explained by thermal constraints on the egg development in reptiles (Kearney & Porter, 2004) or on the adult locomotor potential in amphibians (Kearney *et al.*, 2008).

Predicted changes in species composition

For endotherms, turnover with dispersal was higher in the Natura 2000 sites than in the proposed GNR for both climate-change scenarios. In contrast, the percentage of turnover without dispersal was similar for both areas, suggesting that the degree of movement of species into new cells is more differentiated between areas than species loss within each cell. Considering only herptiles, we found different trends regarding both the percentage of turnover with dispersal (no differences between areas) and without dispersal (greater changes in the GNR). While the pattern observed for herptiles is consistent with predicted temperature anomalies (Fig. 4) and with the percentage of species ranges associated with temperature-related factors (supporting information Appendix S8), the pattern found for endothermic species seems to be a more complex phenomenon.

The proposed boundaries of the GNR might not favor the persistence of threatened herptiles in the future, as the predicted turnover without dispersal (the degree of local species loss) is higher at the GNR than in other Natura 2000 sites. This emphasizes the importance of Natura 2000 areas for the future conservation of the threatened herptiles with more limited dispersal abilities. On the other hand, considering endothermic species, the area proposed for the GNR would remain more stable, as the turnover with dispersal was predicted to be lower there. However, this can be certain only if we assume no influences of biotic interactions, which seems unlikely (Brooker *et al.*, 2007). For example, time series models with terrestrial endotherms have revealed influences of climate fluctuations on food web structure (Lima, Stenseth & Jaksic, 2002), indicating that impacts of climate change also affect interspecific interactions occurring in ecosystems. Therefore it is necessary to consider that a higher turnover on Natura 2000 sites may provoke readjustments of biotic interactions, which ultimately might affect species composition of two connected areas. Thus, the trend observed for endothermic species, might be also a situation of concern.

Concluding remarks and conservation implications

Previous studies have compared between endothermic and ectothermic species to test biodiversity concordance (Lamoreux *et al.*, 2006) and the effect of climate change on phenology (Parmesan, 2007). To our knowledge, this is the first study quantitatively comparing the influence of current climate and climate change on species' ranges among threatened ectotherm and endotherm species. We selected a study area where there is a strong concordance of high human population density and high species richness, which may be a general problem since similar positive associations have been noted in different continents (Balmford *et al.*, 2001; Araújo, 2003).

Our results agree with those of empirical studies highlighting the sensitivity of the herpetofauna to climate change in different parts of the world, and also suggest that climate-change conservation strategies should make explicit efforts for this animal group.

However, we are still far from this objective. According to the IUCN Red List of Threatened Species, 3.59% of endotherms and 49.44% of vertebrate ectotherms have not been evaluated for their level of threat. Furthermore, of those vertebrate species that have been evaluated, 3.08% of endotherms and 22% of ectotherms are considered insufficiently studied (IUCN, 2007). In fact, the extent of the current amphibian decline is believed to be underestimated (Stuart *et al.*, 2004).

The most challenging aspect in conservation planning is the implementation of dynamic threats, such as climate change, in reserve design selection (Pressey *et al.*, 2007). Our results further support the concept that island-type protected areas with fixed limits are insufficient to afford the effect of climate change. Incorporating species-specific criteria in conservation planning is not always feasible when considering multiple species, because there is insufficient knowledge of many crucial biological aspects, such as dispersal abilities or physiological processes. Alternatively, taxonomic/functional grouping of target species to compare their turnover among areas with different status protection can be a useful tool in the design of conservation strategies. Detecting different trends through time and space among species groups may help to test hypotheses on species' responses (Parmesan *et al.*, 2005) and to determine different design and/or management criteria. The ectothermic and endothermic vertebrates studied here do not follow the same pattern through space and time, probably because there are different mechanisms involved. In addition to the physiological constraints inherent to ectotherms, their limited dispersal ability bears the lower capacity to settle in new suitable climate spaces. Taken all together, our findings suggest that trade-offs between different design criteria regarding taxonomic/functional groups are necessary for reserve selection.

Acknowledgments

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Supporting information

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

Appendix S1. List of species modeled.

Appendix S2. Generation of pseudo-absences.

Appendix S3. Does the use of pseudo-absences increase inter-model consistency regarding potential distributions?

Appendix S4. Threshold to transform continuous probabilities into presence/absence data.

Appendix S5. Evaluation of models.

Appendix S6. Spatial autocorrelation.

Appendix S7. Range size effect on the proportion of deviance explained by models.

Appendix S8. Percentage of species for which a given predictor was retained in the final models.

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Appendix S1: List of species modelled.

Species	Common name
Mammals	
Arvicola sapidus	Southern Water Vole
Barbastella barbastellus	Western Barbastelle
Capra pyrenaica	Spanish Ibex
Chionomys nivalis	Snow Vole
Eliomys quercinus	Garden Dormouse
Felis silvestris	Wild Cat
Galemys pyrenaicus	Pyrenean Desman
Lutra lutra	Common Otter
Lynx pardinus	Iberian Lynx
Microtus cabrerae	Cabrera's Vole
Miniopterus schreibersii	Common Bentwing Bat
Myotis bechsteini	Bechstein's Bat
Myotis blythii	Lesser Mouse-Eared Bat
Myotis emarginatus	Geoffroy's Bat
Myotis myotis	Greater Mouse-Eared Bat
Neomys anomalus	Southern Water Shrew
Nyctalus lasiopterus	Giant Noctule

Nyctalus leisleri	Lesser Noctule
Plecotus auritus	Brown long-eared Bat
Plecotus austriacus	Grey long-eared Bat
Rhinolophus euryale	Mediterranean Horseshoe Bat
Rhinolophus ferrumequinum	Greater Horseshoe Bat
Rhinolophus hipposideros	Lesser Horseshoe Bat
Rhinolophus mehelyi	Mehely's Horseshoe Bat
Sciurus vulgaris	Red Squirrel

Birds

Actitis hypoleucos	Common Sandpiper
Aegypius monachus	Cinereus Vulture
Alcedo atthis	Common Kingfisher
Anas strepera	Gadwall
Apus pallidus	Pallid Swift
Aquila adalberti	Spanish Imperial Eagle
Aquila chrysaetus	Golden Eagle
Ardea purpurea	Purple Heron
Asio flammeus	Short-eared Owl
Bubo bubo	Eurasian Eagle-Owl
Burhinus oedicnemus	Eurasian Thick-Knee
Caprimulgus ruficollis	Red-necked nightjars
Ciconia ciconia	White Stork
Ciconia nigra	Black Stork
Cinclus cinclus	White-Throated Dipper

Circus aeruginosus	Western Marsh Harrier
Circaetus gallicus	Short-Toed Snake-Eagle
Circus pygargus	Montagu's Harrier
Coracias garrulus	Eurasian Roller
Dendrocopos minor	Lesser Spotted Woodpecker
Egretta garzetta	Little Egret
Elanus caeruleus	Black-winged Kite
Emberiza schoeniclus	Reed Bunting
Falco naumanni	Lesser Kestrel
Falco peregrinus	Peregrine Falcon
Falco subbuteo	Eurasian Hobby
Gyps fulvus	Eurasian Griffon
Hieraaetus fasciatus	Bonelli's Eagle
Hieraaetus pennatus	Booted Eagle
Himantopus himantopus	Black-winged Stilt
Ixobrychus minutus	Little Bittern
Jynx torquilla	Wryneck
Lanius excubitor	Great Grey Shrike
Luscinia svecica	Bluethroat
Melanocorypha calandra	Calandra Lark
Milvus milvus	Red Kite
Netta rufina	Red-crested Pochard
Nycticorax nycticorax	Black-crowned night-heron
Oenanthe leucura	Black Wheater

Otis tarda	Great Bustard
Panurus biarmicus	Bearded Parrotbill
Pernis apivorus	Honey Buzzard
Phoenicurus phoenicurus	Common Redstart
Podiceps nigricollis	Black-necked Grebe
Prunella collaris	Alpine Accentor
Pterocles alchata	Pin-Tailed Sandgrouse
Pterocles orientalis	Black-bellied Sandgrouse
Pyrrhocorax pyrrhocorax	Red-Billed Chough
Rallus aquaticus	Water Rail
Riparia riparia	Sand Martin
Saxicola rubetra	Whinchat
Serinus citrinella	Citril Finch
Sylvia hortensis	Orphean Warbler
Tetrax tetrax	Little Bustard
Tyto alba	Barn owl
Vanellus vanellus	Lapwing

Herptiles

Hyla arborea	Common Tree Frog
Rana iberica	Iberian Frog
Pelodytes punctatus	Parsley Frog
Alytes cisternasii	Iberian Midwife Toad
Lissotriton boscai	Bosca's newts
Triturus pygmaeus	Southern Marbled Newt

|	
Mesotriton alpestris	Alpine Newt
Hemorrhois hippocrepis	Horseshoe Whip Snake
Macroprotodon cucullatus	False Smoth Snake
Mauremys leprosa	Spanish turtle
Hemorrhois hippocrepis	European Pond Turtle
Lacerta monticola	Iberian Rock Lizard
Lacerta schreiberi	Schreiber's Green Lizard

Appendix S2: Generation of pseudo-absences

Species distributions are not only constrained by abiotic factors (e.g. climate), but also by biotic interactions, dispersal constrains, anthropogenic effects, stochastic events and other historical, unique and contingent events that may preclude the presence of a given species in *a priori* environmentally suitable places. Thus, if the goal is to predict environmentally suitable areas (i.e. potential distributions regarding environmental suitability), only absences due to unsuitable environmental conditions (i.e. environmental pseudo-absences) should be used to build predictive models (Peterson, Papes & Soberón, 2008; Jiménez-Valverde, Lobo & Hortal, 2008). Here, pseudo-absences were obtained using multi-dimensional niche envelopes over all peninsular Spain (Lobo, Verdú & Numa, 2006 and references therein), in which presence data were used to calculate an environmental range for each species. Pseudo-absences correspond to the observed absences that lay outside each species' environmental range (i.e. outside the maximum and minimum for the variables considered). Lastly, both presences and pseudo-absences were included as a binomial dependent variable in GLMs, in order to estimate the potential species' distributions. GLMs including pseudo-absences generated by the multi-dimensional niche envelope model give predictions closer to the potential species' distributions (Chefaoui and Lobo, 2008). Assuming that there is not a strong methodological bias in the presence data, as in the present study, this procedure enables to reduce the effect of factors, such as dispersal constraints, that preclude the characterization of the entire species' potential distribution.

Appendix S3: Does the use of pseudo-absences increase inter-model consistency regarding potential distributions?

This investigation pursues generating models able to predict species' potential distributions (i.e. environmentally suitable areas) through space and time, for which we combined observed presences and pseudo-absences under the expectation that pseudo-absences would reduce prediction errors (Chefaoui and Lobo, 2008). To investigate this, we took into account that predictions often vary among different modelling techniques (e.g. Araújo *et al.*, 2005), and assumed that the most robust results should be those that are less dependent on the technique used for modelling. Specifically, we compared the results provided by our General Linear Models (GLMs) when using all observed absences or only pseudo-absences, with the results generated by other two widely employed modelling techniques: Neural Networks (NNTs) and Classification Tree Analyses (TREEs). That is, for each species and technique we obtained two sets of probabilities over all peninsular Spain (modelling either with all absences or only with pseudo-absences), and then examined to what extent the degree of agreement of GLMs with the other models was dependent on the type of data used. Thus, for each species we performed Pearson's correlations between the obtained probabilities using GLMs and those obtained using the alternative technique (either NNTs or TREEs) for both types of data separately. We compared between the two types of data used, the correlation coefficients obtained for each species. We found that the use of pseudo-absences increased inter-model consistency for the set of species modeled (repeated measures ANOVA; GLM *vs*. NNT: $F_{1,93} = 42.72$, $P < 0.000001$; GLM *vs*. TREE: $F_{1,93} = 104.38$, $P < 0.000001$; Fig. B). This indeed supports that pseudo-absences give more robust results in this case.
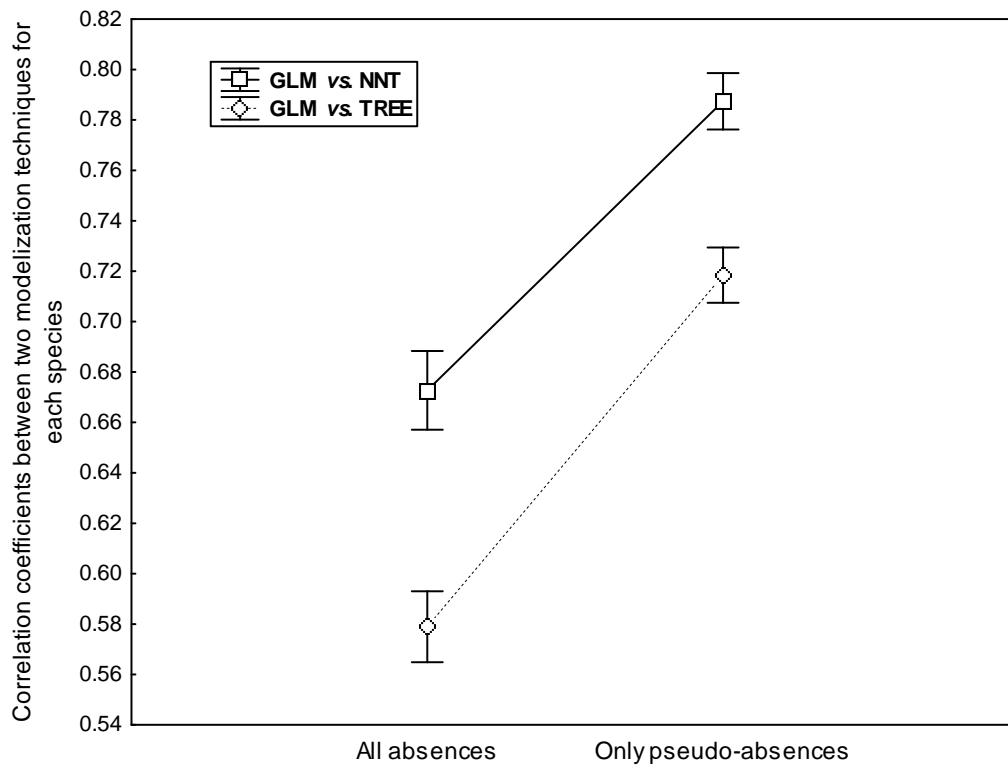
Fig. S3 - Pearson correlation coefficients ($\overline{X} \pm SE$) between the probabilities obtained using Generalized Linear Models and Neural Networks (GLM *vs*. NNT: □) or Classification Trees (GLM *vs*. TREE: ◊), for each species modelled for all of peninsular Spain.

Appendix S4: Threshold to transform continuous probabilities into presence/absence data

Logistic models generate continuous probabilities of species presences, and a specific threshold is needed to transform the probability data to presence/absence data. Among the different approaches to determine such threshold, we used the prevalence (presence/absence ratio used for modelling), a method that has already been shown to be effective for plants (Liu *et al.*, 2005), aquatic invertebrate families (Manel, Williams & Ormerod, 2001), and simulated species (Jiménez-Valverde and Lobo, 2006). Additionally, we also followed Jiménez-Valverde and Lobo (2006; 2007) to check whether this approach worked well for the case of threatened terrestrial vertebrates analyzed here. We first conducted a jack-knifing resampling technique (Vaughan and Ormerod, 2005; Pearson *et al.*, 2007) to estimate the fractions of correctly predicted presences (sensitivity) and correctly predicted absences (specificity) by our GLM models. The resampling is executed in an iterative way. That is, we excluded one observation at each time and rebuilt the model with the remaining data to predict the response of the excluded observation. Then we re-entered this observation into the dataset and repeated the operation until all observations were predicted. Sensitivity and specificity were computed for each model based on these predictions, and these were used to establish the cut-off level that minimizes model prediction error (i.e. the threshold probability value that minimizes the sensitivity-specificity difference). The correlation between these cut-off level values and species' prevalences was nearly one (Pearson's correlation: $R = 0.960$, $F_{1,92} = 1086.09$, $P < 0.000001$; Fig. C), thus supporting prevalence as an appropriate reference to transform model probabilities into predicted presence/absence data.
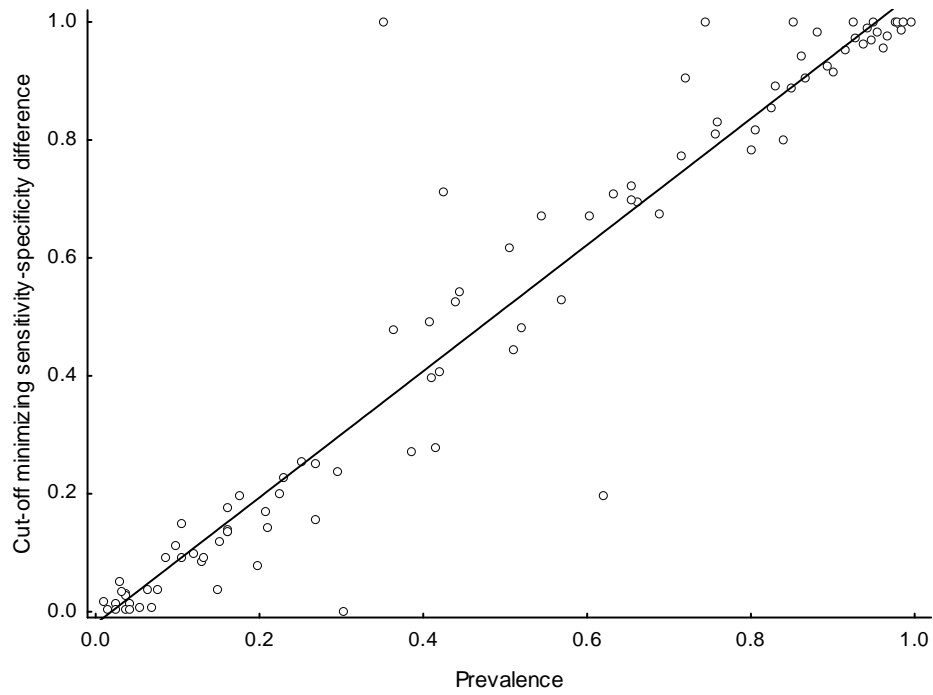
Fig. S4 - Relationship between the cut-off that minimized the prediction error (measured as the minimized sensitivity-specificity difference) and prevalence.

Appendix S5: Evaluation of models

Often, threatened species exhibit low numbers of presences, including some of the species considered in this study, thus preventing to split the data into training and validation datasets. Alternatively, model stability can be estimated by comparing sensitivity and specificity values obtained from direct model predictions with those provided by the jack-knifing resampling technique described above (Vaughan and Ormerod, 2005; Pearson *et al.*, 2007). We also calculated for each model the area under the curve (AUC) of the Receiver Operating Characteristic (ROC) plot of sensitivity against 1-specificity (Fielding and Bell, 1997), in order to use this estimate as an additional index of the overall stability of the models. Specifically, we used simple regressions to perform paired comparisons of the species' values obtained before and after jack-knifing for sensitivity, specificity and AUC. All relationships were strong, positive and highly significant (sensitivity: $R = 0.945$, $F_{1,92} = 766.47$, $P < 0.000001$; specificity: $R = 0.890$, $F_{1,92} = 350.22$, $P < 0.000001$; AUC: $R = 0.751$, $F_{1,92} = 118.78$, $P < 0.000001$), thus denoting small overall bias.

Additionally, to examine whether there were differences in terms of model stability among animal groups, we took the residuals from the former regressions as measurements of model stability for each species relative to the other species, and then compared them among animal groups using one-way ANOVAs. We only compared the residuals of sensitivity and specificity, since the AUC approach is not recommended to perform among-species accuracy estimations (Lobo, Jiménez-Valverde & Real, 2007). Residuals of sensitivity and specificity did not differ significantly among animal groups (sensitivity: $F_{2,91} = 0.53$, $P = 0.58$; specificity: $F_{2,91} = 0.88$, $P = 0.41$), for which we concluded that there were no biases toward any particular taxa.

Appendix S6: Spatial autocorrelation

It has been shown that the parameter estimation of models is not seriously affected by the spatial autocorrelation in the residuals of models (Hawkins *et al.*, 2007; Diniz-Filho *et al.*, 2007). However, since the aim of our study is to examine differences among animal groups, it is worthwhile to test whether spatial autocorrelation in the residuals of models differs among them. For this purpose we generated spatial correlograms of Moran's I using the spatial analysis in macroecology (SAM) software (Rangel, Diniz-Filho & Bini, 2006). Specifically, we identified for each species the maximum distances at which positive spatial autocorrelation remained statistically significant in the data. We then compared among animal groups and found no significant differences (one-way ANOVA: $F_{2,91} = 0.48$, $P = 0.62$).

Appendix S7: Range size effect on the proportion of deviance explained by models

It has been shown that the fit or performance of models can be associated with species occupancy (Manel *et al.*, 2001; Segurado and Araújo, 2004; Schwartz *et al.*, 2006), therefore we examined this possibility using a Pearson correlation between deviance explained and species occupancy (number of presences). In fact, even the adjusted deviance, weighted by the effective degrees of freedom used to fit the model (Guisan *et al.,* 1999; Engler *et al.,* 2004), significantly correlated with species occupancy (Pearson's correlation: $R = 0.32$, $F_{1,92} = 10.67$, $P < 0.01$). Then, we took the residuals of this regression as a measurement of range-corrected deviance to verify that the observed patterns of deviances through functional groups were still the highest for herptiles (one-way ANOVA: $F_{1,91} = 4.52$, $P = 0.03$).

Appendix S8:

Table S8 - Within-group percentage of species for which a given predictor was retained in the final models after the backward selection procedure (see Methods section). T, mean annual temperature; mPET, minimum potential evapotranspiration; P, annual precipitation; tpAET, Turc-Pike's actual evapotranspiration; WD, water deficit.

Predictors included in models	Animal Groups		
	% Mammals	% Birds	% Herptiles
Temperature-related predictors			
T	68	73.2	76.9
mPET	64	76.7	53.8
T+mPET	80	96.4	100
Water-related predictors			
P	80	55.3	84.6
Temperature- and water-related predictors			
tpAET	72	55.3	76.9
WD	92	73.2	69.2
tpAET+WD	96	91	100
Soil predictors			
Acidic deposits	52	35.7	46.1
Basic deposits	44	46.4	23.1
Acidic rocks	48	44.6	53.8
Basic rocks	44	37.5	46.1
Topographical predictors			
Average elevation	48	51.7	53.8
Range of elevation	40	69.6	53.8

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