RESEARCH PAPER

The contribution of contemporary climate to ectothermic and endothermic vertebrate distributions in a glacial refuge

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ABSTRACT

Aim Climatic factors are known to influence species distributions. However, elucidating the underlying mechanisms is challenging because direct and indirect effects of climatic and non-climatic factors are correlated. In the absence of this covariation and at fine-grain resolutions the direct effect of climate via physiological constraints should be stronger on the distributions of ectothermic organisms. So far, no comprehensive study has explicitly tested the influence of climate on species distributions by quantitatively comparing ectothermic and endothermic vertebrates.

Location Peninsular Spain.

Methods Presence–absence data of native terrestrial vertebrates in Peninsular Spain were modelled using generalized additive models to disentangle the influence of climate and other contemporary correlated factors (topography and plant cover). We performed partial regressions to partition the deviance explained by climatic and non-climatic effects into independent and shared components. We compared the independent contributions of climatic and non-climatic effects between ectothermic and endothermic vertebrates, and among mammals, birds, reptiles and amphibians.

Results After reducing the covariation with non-climatic factors, climate explained a greater proportion of deviance in ectotherms than in endotherms. Also, the contribution of temperature was highest for reptiles, and the contribution of precipitation was highest for amphibians, after extracting their overlaps with precipitation and temperature, respectively. The contribution of topography and plant cover remained high for birds after extracting the overlap with climate.

Main conclusions Our results are consistent with the prediction that, at fine resolutions, the direct influence of climate (via physiological constraints) on range distributions is stronger in ectothermic vertebrates. Also, at least for birds, indirect effects of climate (via plant productivity) and other habitat characteristics remained relatively important once their covariation with climate was reduced. This study shows that controlling the direct effects of climate by their indirect effects and/or other correlated factors, combined with comparisons among functional groups, can be a useful approach to elucidate causal links with the spatial patterns of organisms.

Keywords

Climate, covariation, ectotherms, elevation, endotherms, generalized additive models, Iberian Peninsula, productivity, terrestrial vertebrates.

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INTRODUCTION

A major goal in ecology is to understand the underlying mechanisms by which environmental factors affect variations in species distributions and population dynamics. Many predictive models of the association between climate and vertebrate distributions have focused on birds (e.g. Jetz *et al.*, 2007) and mammals (Dunbar, 1998; Lawler *et al.*, 2006), whereas ectothermic terrestrial vertebrates have received less attention (Guisan & Hofer, 2003; Kearney & Porter, 2004; Araújo *et al.*, 2006). More importantly, comprehensive studies quantitatively comparing the influence of climate on species distributions between endothermic and ectothermic vertebrates are still lacking. Moreover, whereas there is a publication bias toward significant trends associated with environmental factors, the exclusion of non-responsive species might affect the inference of overall patterns from meta-analyses (Parmesan, 2007).

Despite the fact that the predictive power of models has been substantially improved, understanding the underlying mechanisms is always challenging (Shipley, 1999). Among the potential challenges, at least two remain important for many species. (1) Climatic and non-climatic factors are often correlated. Thus, it is difficult to establish whether climatic factors have a causal relationship with the physiology of the organisms or have an indirect influence through habitat structure and/or biotic interactions. It is expected that the more the covariation of climate with non-climatic factors is reduced, the clearer will be the signal of direct climatic effects operating on physiological requirements. (2) For many species it is not possible to test specific hypotheses about physiological processes because of a lack of data on species-specific physiological parameters or processes (Kearney, 2006). However, specific comparisons and contrasts between taxonomic or functional groups of species may provide a powerful tool to test more general physiological hypotheses of species distributions (Guisan & Thuiller, 2005; Parmesan *et al.*, 2005). A useful approach to allow comparisons is to examine the extent to which a priori proposed meaningful predictors regarding ecological theories can explain species distributions. This is facilitated by examining whether some animal groups are better modelled than others, and the ecological reasons for such patterns (Guisan & Thuiller, 2005; Voigt *et al.*, 2007).

While ectotherms maintain their body temperature by thermal exchange with the environment, endotherms control their temperature by shifts in their metabolic rates. Another key difference is that in ectotherms most of the energy obtained from food is devoted to biomass production, whereas endotherms allocate part of the energy from food to maintaining their body temperature (Pough, 1980). Also, whereas endotherms regulate embryo temperature, through viviparity in mammals or parental care in birds, ectotherm embryos are often more directly subjected to environmental variations. Thus, the influence of climate on species distributions should be different for ectothermic and endothermic species because they are differently constrained by physiological threshold responses to temperature and water-related factors. Several aspects of interactions with the environment are more readily apparent in ectotherms. In the absence of covariation with other factors, temperature should reveal a major role in reptiles as their body temperature depends on the absorption of heat energy from the environment (Gans & Pough, 1982). In the case of amphibians, water availability is considered a key determinant for their life cycles (Carey & Alexander, 2003), especially in areas where water is a limited resource. This is the case for Spain, which is dominated by hot/warm and dry summers (Kottek *et al.*, 2006). As well as being ectotherms, amphibians have a permeable body covering, and the majority of water loss occurs via evaporation from the skin. Therefore their physiological constraints are compounded by thermoregulatory and water/moisture requirements (Duellman & Trueb, 1986). Taking all this together, we hypothesized that physiological constraints should have a stronger influence on the distribution of ectothermic terrestrial vertebrates. Under this scenario, it is predicted that the direct effects of climate (i.e. once extracted from its covariation with other factors) on species distributions should be stronger in ectotherms than in endotherms at fine-grained resolutions.

The aim of this study was to estimate the direct effects of climate on the distribution of terrestrial vertebrates by reducing the covariation of climate with its indirect effects and other correlated factors. Once we reduced this covariation, we compared the extent to which contemporary climate explains species distributions of ectothermic and endothermic terrestrial vertebrates in Peninsular Spain at a fine-grain resolution (10 km). Thus, we propose to make use of what can be seen as a natural experiment in a glacial refugium in southern Europe, where it is expected that species distributions are closer to equilibrium with contemporary climate because they were beyond of the influence of previous glaciations (e.g. Hawkins & Porter, 2003; Montoya *et al.*, 2007; Svenning & Skov, 2007). The equilibrium postulate is an important assumption that is not always fulfilled (Guisan & Thuiller, 2005), especially for species with limited dispersal abilities, because of their lower capacity to track previous climate changes (Svenning & Skov, 2004; Araújo *et al.*, 2008). It is also important for conservation purposes, since glacial refugia in southern Europe support most of the current intraspecific genetic variation (Hewitt, 1999).

We used generalized additive models (GAMs) to determine the explanatory capacity of climatic and non-climatic factors, which were modelled both separately and jointly to disentangle the direct effects of temperature and precipitation from other correlated environmental factors. The purpose of this study was not to project our models onto other scenarios; rather we aimed to detect simple and general patterns through comparisons among animal groups. Therefore, characterizing the entire realized species niches by explaining all of the variation was not necessary to establish comparisons regarding target questions. Thus, we estimated the relative weight of climatic variables among animal groups after correcting for covariations with other non-climatic factors. After distinguishing between the independent contributions of climatic and non-climatic effects, we compared the degree of association between temperature and water-related factors and species distributions for native

mammals, birds, reptiles and amphibians of Spain. Our procedure also gave us the opportunity to compare the independent contributions of non-climatic factors. Taking into account that, at finer resolutions, other factors in addition to climatic ones often become relevant in determining the distribution of species (Pearson & Dawson, 2003), habitat variables may emerge as important after extracting their covariance with climate depending on the animal group and the variables considered.

METHODS

Species data

Presence–absence maps over Peninsular Spain were obtained from Palomo & Gisbert (2002) for mammals, Martí & Moral (2003) for breeding birds and Pleguezuelos *et al.* (2002) for amphibians and reptiles, which were referenced onto 4945 10 × 10 km grid cells. These atlases correspond mainly to the period from the 1980s to the current decade. Those species that were introduced during the last century were excluded from the analyses because their distributions are probably farther from the equilibrium with environmental variables than those of native species. Thus, we modelled a total of 384 species of terrestrial vertebrates in Spain (84 mammals, 233 breeding birds, 41 reptiles and 26 amphibians).

Environmental data

Temperature predictors

To test the relative effect of temperature-related factors, we used mean annual temperature (°C), maximum summer temperature (°C) and winter minimum temperature (°C). Temperature variables were scaled up from a 1 × 1 km resolution raster interpolated from 1504 thermometric stations for the period of 1971–2000 (provided by the Spanish Instituto Nacional de Meteorología, INM).

Precipitation predictors

To test the relative effect of water-related factors, we used annual precipitation (mm), monthly minimum precipitation (mm) and monthly maximum precipitation (mm). These variables were scaled up from 1 × 1 km resolution rasters (INM), which were generated from 4835 pluviometric stations for the period of 1971–2000.

Non-climatic predictors

We used one habitat and two topographic variables as non-climatic predictors that, although correlated with climatic variables, can influence species distributions for reasons not directly linked with climate. As a habitat variable, we used the Global Vegetation Index (GVI), which is derived from radiometer data from the NOAA Polar Orbiting Environmental Satellites (NCDC Satellite Data Services Division, 1985–1988; http://

www.ngdc.noaa.gov/ecosys/fliers/gutavhrr.shtml). The GVI is a measurement of the density and greenness of the plant canopy, total standing biomass, green leaf-area index and percentage vegetation cover. This variable is often included in studies in which animal distributions are potentially influenced by the conversion of environmental energy to plant production, and is known to be relevant at a wide range of spatial scales (Mittelbach *et al.*, 2001). We used the average elevation and range of elevation as topographic variables. The first variable is usually included in models as a predictor of animal distributions (e.g. Guisan & Hofer, 2003; Muñoz *et al.*, 2005) because it is a proxy for climatic and non-climatic factors. The range of elevation, or analogous predictors, is a surrogate for habitat heterogeneity, being frequently associated with animal distributions and richness gradients in vertebrates (Rahbek & Graves, 2001; Muñoz *et al.*, 2005; Ruggiero & Hawkins, 2008). More generally, it can be argued that topographic variables may influence spatial variation of diversity by means of primary productivity, and/or by other non-climatic factors such as area, geometric constraints and human impact (Nogués-Bravo *et al.*, 2008).

There are other environmental variables, such as actual evapotranspiration (AET), that have frequently been found to explain geographical patterns in diversity for a variety of vertebrate groups at broader scales (e.g. Hawkins *et al.*, 2003; Rodríguez *et al.*, 2005). In spite of AET being calculated from a temperature–water-related formula (Pike, 1964), it has been argued that AET is likely to be more indicative of water availability in Mediterranean Europe (Whittaker *et al.*, 2007). In fact, in Spain the correlation of AET with precipitation is much more apparent than with temperature (see Appendix S1 in Supporting Information). Also, it has been suggested that spatial patterns of biodiversity associated with AET operate via plant productivity (Hawkins *et al.*, 2003). Thus, in Spain AET is also correlated with our measure of plant productivity (GVI) (Appendix S1), precluding interpretations about direct (physiological mechanisms) or indirect (habitat characteristics) effects of AET. Therefore, the inclusion of GVI in models seems more appropriate for examining the indirect effect (via plant productivity). Since AET in Spain is well represented by precipitation, a picture of the direct effect of climate (via physiological constraints) can be explored by comparing the magnitude of the effects of original climatic variables depending on which other variables are used as controlling factors for a given taxon.

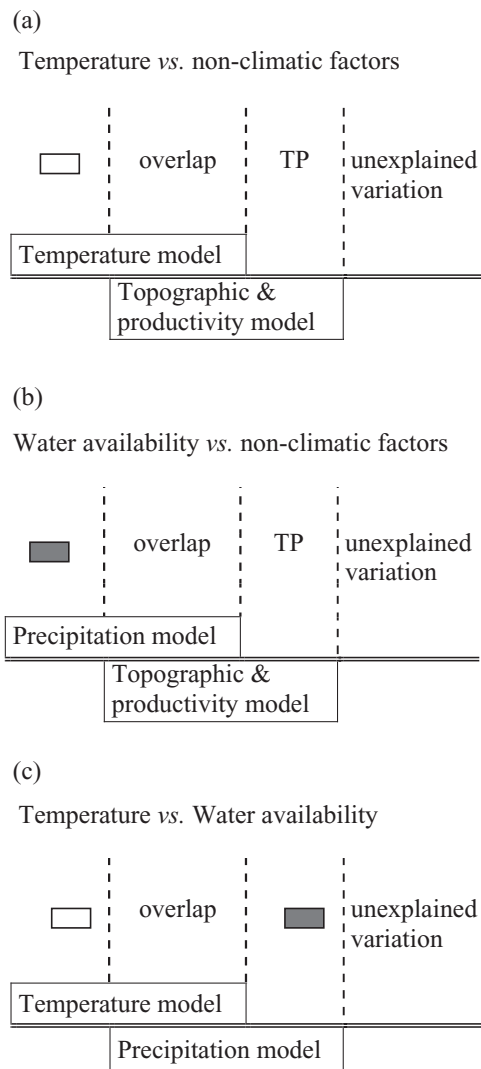### Species distribution models

For each of the 10 × 10 km Universal Transverse Mercator (UTM) grid cells, we managed the set of climatic and non-climatic descriptors using ARCGIS 9.2 (ESRI, 2002). We used a modelling technique extensively used in species distribution modelling, namely GAMs. In comparison with other family regression techniques, GAMs are more flexible because they do not require a specific response curve to be fitted to the predictors (Hastie & Tibshirani, 1990), and are preferable when the testing of ecological theory is central, as in this study (Guisan & Thuiller, 2005). For each species, presence–absence data were

Table 1 Simple and combined generalized additive models (GAMs) preformed to examine the influence of current climate on the geographical distributions of terrestrial vertebrates in Spain. We ran 2304 models (six models per 384 species) to obtain the proportion of deviance explained for each species.

Generalized additive models	Predictors included in models
Simple models	
Temperature models	Mean annual temperature, winter minimum temperature, summer maximum temperature
Precipitation models	Annual precipitation, monthly minimum precipitation, monthly maximum precipitation
Non-climatic models	Average elevation, range in elevation, global vegetation index
Combined models	
Climatic models	Temperature and precipitation predictors
Temperature extended	Temperature and non-climatic predictors
Precipitation extended	Precipitation and non-climatic predictors

(a)

Temperature *vs.* non-climatic factors

(b)

Water availability *vs.* non-climatic factors

(c)

Temperature *vs.* Water availability

Figure 1 Conceptual framework to test the energy or water availability hypotheses for the distributions of terrestrial vertebrates in Spain. Partial generalized additive models (GAMs) partitioning the deviance into independent contributions of temperature (white), precipitation (grey) or habitat (TP), and the overlap between (a) the temperature and habitat models, (b) the precipitation and habitat models and (c) the overlap between temperature and precipitation models.

included as a binomial dependent variable to estimate the fit of its distribution with regard to the predictors. The order of splines was limited to four degrees of freedom to prevent overfitting (Wood & Augustin, 2002). GAMs were carried out using the mgcv package, implemented in R software (Ihaka & Gentleman, 1996).

A common difficulty when examining direct and indirect effects of environmental factors in models of species distributions is that environmental variables are often correlated. To examine the independent contributions of temperature, precipitation and non-climatic variables, their effects should be disentangled. Therefore, to assess the extent to which different sets of three temperature, three precipitation and three non-climatic variables can explain species distributions independently of the other two sets of variables, we calculated from GAMs the shared and independent proportions of deviance explained by models. Partial regression analyses (Legendre & Legendre, 1998) were used to discriminate between single and shared effects. Thus, for each species, we performed three simple models (Table 1; Fig. 1) and three combined models (Table 1) to partition the deviance explained by temperature, precipitation and non-climatic variables into independent and shared components (see Legendre & Legendre, 1998, for a detailed description of the procedure). In all, 2304 models were run (six models per 384 species) to obtain the proportions of deviance explained. This procedure substantially reduced the covariation among temperature, precipitation and non-climatic models (see Appendix S2 for the relationships between the explanatory capacity of models before and after the extraction of their shared components). The scheme of our procedure was as follows: we used three sets of variables (A, B and C) and each set was composed of three variables of the same nature (say A, three temperature variables; B, three precipitation variables; and C, three non-climatic variables). For A we estimated two different measurements of its independent contribution, first controlling by the set B and then controlling by the set C. In the same way, two different independent contributions were also estimated for B and another two for C. Although the independent contributions were calculated through both simple and combined models, this procedure ensured a balanced design regarding the number of variables whose independent contribution was estimated and the number of controlling variables; otherwise it might bias the estimation of explanatory capacity. This approach allows the examination of whether the explanatory capacity changes or not and how, depending on which controlling factors are used. There are other variables

specific to each species that surely would explain part of the variation; however, we used the same meaningful and representative variables through all species to allow comparisons. As this study is proposed as a natural experiment, a requirement for the experimental design is keeping constant some factors while manipulating others to detect changes in response variables (here the explanatory capacities).

Comparisons among animal groups

Effects of temperature and precipitation, independent of non-climatic factors

The independent components of the deviance explained by temperature, precipitation and non-climatic models obtained from GAMs were compared as response variables among animal groups. To compare the independent contributions of climate to endotherms and ectotherms we used the contributions of both temperature and precipitation after extracting their overlap with the non-climatic factors (Fig. 1a, b). For this analysis, we used one-way MANOVA (Quinn & Keough, 2002), because although the overlap with the non-climatic model was extracted in each case, the contributions of temperature and precipitation were still significantly correlated (regression analyses: $F_{1,382} = 1578.7$, $R = 0.89$, $P < 0.0001$). Thus, we included the animal group as a four-level factor and, when a significant effect was found, we compared endotherms and ectotherms.

Effects of temperature and precipitation, independent of each other

To compare the contribution of temperature independently of precipitation and vice versa, we used one-way ANOVAs with the proportion of deviance explained as response variable and the animal group as a four-level factor. For these analyses we used the explanatory capacity of temperature and precipitation after extracting the shared component between them (Fig. 1c). While a more direct effect of energy input can be argued for reptiles (e.g. Rodríguez *et al.*, 2005; Whittaker *et al.*, 2007), water availability is expected to be a major environmental factor determining amphibian distributions (Carey & Alexander, 2003). After the verification of an overall significant effect with ANOVAs, we used planned comparisons (Quinn & Keough, 2002) of reptiles versus the remaining animal groups for temperature, and between amphibians versus the remaining animal groups for precipitation.

Effects of non-climatic factors, independent of temperature and precipitation

Here, we aimed to test whether distributions of animal groups could be explained differently by the independent contributions of topography and plant productivity obtained in the non-climatic models (Table 1). We used a one-way MANOVA, including as response variables the explanatory capacity of the non-climatic models either independently of temperature or

independently of precipitation. Then, we tested each variable separately using protected one-way ANOVAs. When a significant effect was found, we used Tukey's honestly significant difference (HSD) test to perform *post hoc* comparisons (Quinn & Keough, 2002). Response variables were log-transformed to meet assumptions underlying linear models (Quinn & Keough, 2002).

Finally, we performed additional analyses to verify that the patterns resulting when controlling by the covariation with the other sets of variables simultaneously (see Appendix S3) remain the same as those patterns resulting after the extraction of each shared component separately (see Results). On the other hand, we challenged the robustness of our results by assuming an extreme scenario where the shared component between habitat and climate is entirely attributed to the habitat effect (see Appendix S4).

Range size

It has been documented that the range size can be associated with model fit (e.g. Schwartz *et al.*, 2006). Therefore, we performed regression analyses to test for this potential effect. We found that the number of cells occupied by each species was negatively associated with the explained deviances, although the strength of these associations was not strong ($-0.33 < R < -0.13$). Thus, we took the residuals of this regression as a measurement of explained range-corrected deviance to verify that the observed patterns of deviances through animal groups (see Results) did not change after this correction (see Appendix S5).
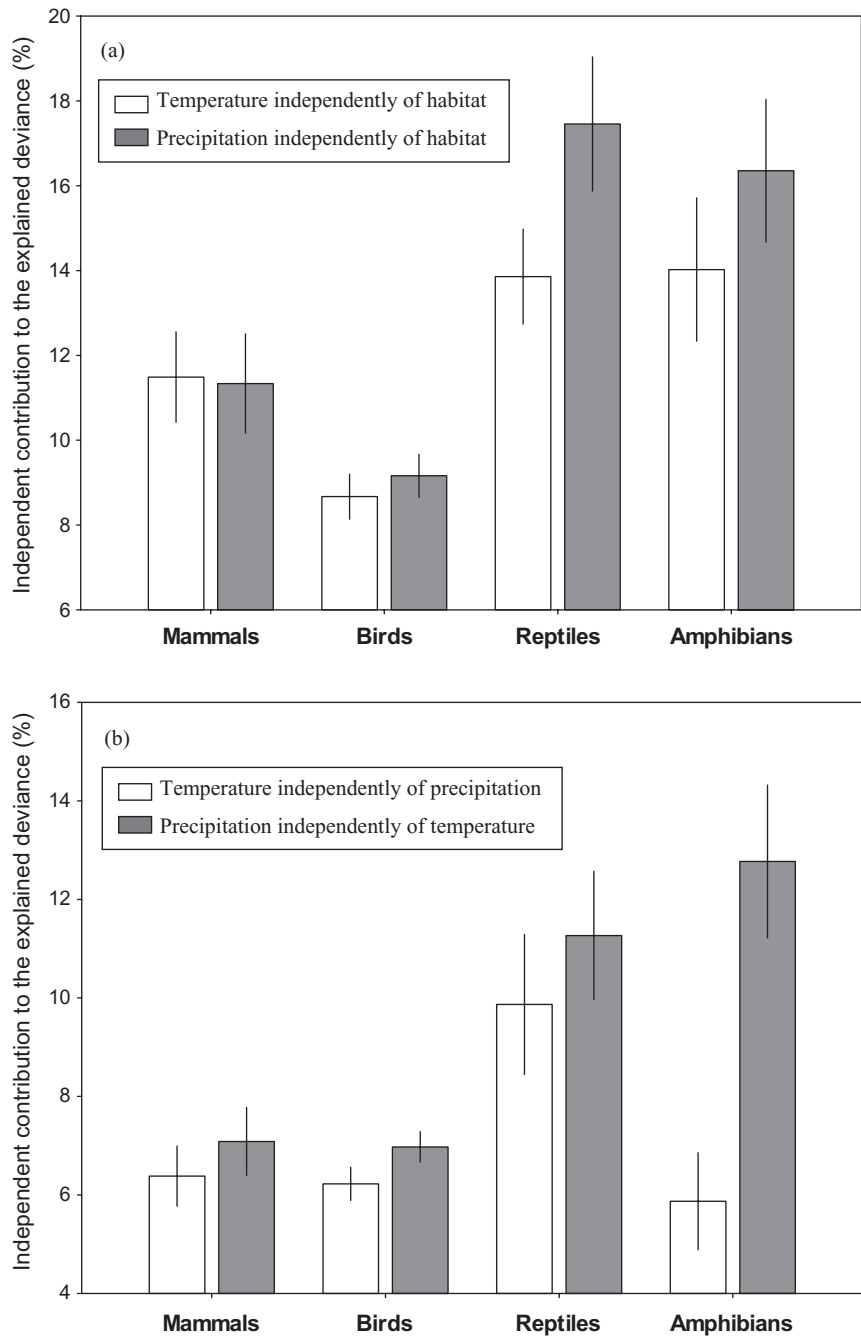
RESULTS

Effects of temperature and precipitation independently of topography and productivity

There were significant differences among animal groups with respect to temperature and precipitation independent of habitat (MANOVA: Wilk's $\lambda = 0.86$, $F_{6,758} = 9.38$, $P < 0.000001$; Fig. 2a), and the proportions of deviance explained by temperature and precipitation were higher in ectotherms than in endotherms (Wilk's $\lambda = 0.90$, $F_{2,379} = 19.74$, $P < 0.000001$).

Effects of temperature and precipitation, independent of each other

There were significant differences among the animal groups in the proportion of deviance explained by temperature independent of precipitation (one-way ANOVA: $F_{3,380} = 3.25$, $P = 0.021$; Fig. 2b). The contribution of temperature was significantly higher in reptiles than in the other animal groups ($F_{1,380} = 9.28$, $P = 0.0024$). There were also significant differences among the animal groups in the proportion of deviance explained by precipitation independent of temperature (one-way ANOVA: $F_{3,380} = 11.37$, $P < 0.000001$; Fig. 2b). The contribution of
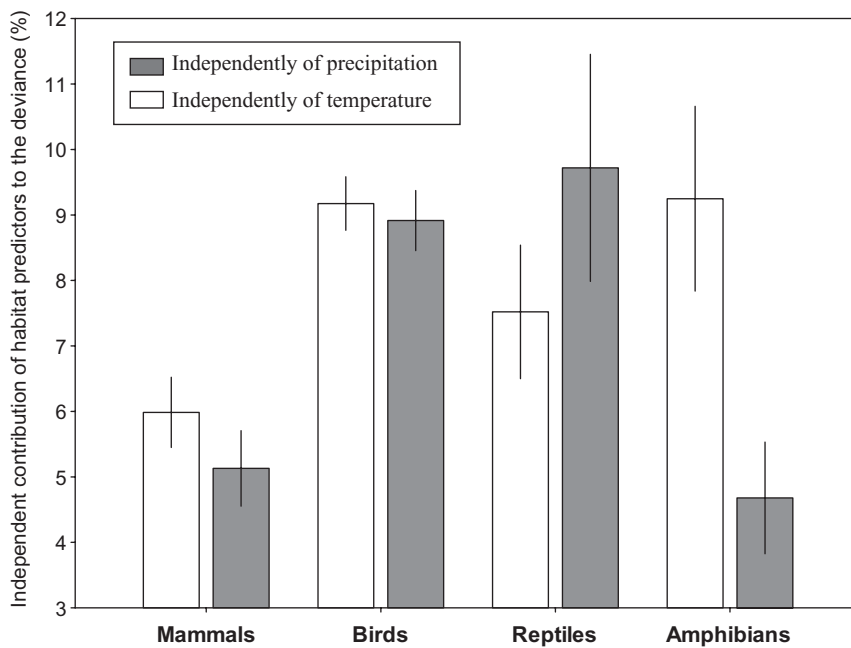
Figure 2 Independent components of variation explained (mean deviance ± SE) by temperature (white) and precipitation models (grey) for the geographical distributions of mammals, birds, reptiles and amphibians: (a) after the extraction of the overlap with the habitat models and (b) after the extraction of overlap between precipitation and temperature.

precipitation was significantly higher in amphibians than in the other animal groups ($F_{1,380} = 13.16$, $P = 0.0003$).

Effects of non-climatic factors, independent of temperature and precipitation

There were significant differences among the animal groups in the proportions of deviance explained by topographic and plant productivity predictors, independent of temperature or precipitation (MANOVA: Wilk's λ = 0.87, $F_{6,758} = 8.63$, $P < 0.000001$; Fig. 3). The univariate analyses showed significant differences among animal groups for the deviance explained by non-climatic models, both independent of temperature (one-way ANOVA: $F_{3,380} = 8.70$, $P < 0.0001$) and precipitation ($F_{3,380} = 11.87$, $P < 0.000001$). *Post hoc* comparisons revealed that the proportion of deviance explained by these non-climatic models independently of temperature was higher in birds than in mammals (Tukey's HSD test: $P < 0.001$), whereas there were no significant differences for the rest of the comparisons ($P > 0.05$ in all cases). The proportion of deviance explained by the non-climatic models independent of precipitation was higher in birds than in mammals ($P < 0.00001$) and amphibians ($P < 0.01$). Also, this proportion was significantly higher in reptiles than in mammals ($P = 0.031$), whereas there were no

Figure 3 Independent components of variation explained (mean deviance ± SE) by the habitat models after the extraction of the overlap with the temperature (white) and the precipitation models (grey) for the geographical distributions of mammals, birds, reptiles and amphibians.

significant differences for the rest of the comparisons (*P* > 0.05 in all cases).

DISCUSSION

In this study, we tested whether the relative influence of climate on species distributions is different among animal groups of terrestrial vertebrates. To test our prediction, we compared the explanatory capacity of models for endothermic and ectothermic vertebrates of Spain, including either climatic or non-climatic predictors. Because environmental factors are correlated in nature, we partitioned the variation into independent and shared contributions, which substantially reduced the covariation. While our procedure was useful for reducing covariation to test the main effects of variables, the interaction between temperature and precipitation was not explicitly tested. However, this was partially achieved by including in the models an indirect effect of such interaction, a plant productivity index. We found that the proportion of variation explained by climate, independent of non-climatic variables, was higher in ectotherms than in endotherms. Once the covariation between temperature and precipitation was reduced, our results also revealed that there is a stronger association between reptile distributions and temperature, and between amphibian distributions and precipitation, relative to the other animal groups. On the other hand, the contribution of topography (average elevation and range in elevation) and plant productivity to bird distributions remained relatively important after reducing the covariation with either temperature or precipitation.

Finally, our results are not a by-product of species occupancy, since we obtained the same results when analysing the range size-corrected variables (Appendix S5). In the same way, our results remain consistent when controlling simultaneously by the corresponding shared effects (Appendix S3), or even when

assuming an extreme scenario where the shared effect between climatic and non-climatic factors is entirely attributed to non-climatic factors (Appendix S4). On the other hand, we have previously verified that for a reasonable proportion of the Spanish terrestrial vertebrates (25%) there was no bias due to autocorrelation toward any animal group (Aragón *et al.*, unpublished data). In this previous study, devoted to another specific question of conservation regarding park and off-park changes in species turnover forecasts, we ran models that also included variables of precipitation, temperature and topography, and also for all Peninsular Spain. We found that the amount of spatial structure of the unexplained variability was not significantly different among animal groups (Aragón *et al.*, unpublished data).

The stronger association of herptile distributions with temperature and precipitation, independent of topography and plant productivity, is compatible with predictions of both thermal and water dependence. This result is consistent with previous analyses of species richness in a province of southeastern Spain, which revealed that climate explains much more variance in ectothermic than in endothermic vertebrates (Moreno-Rueda & Pizarro, 2007).

In the case of reptiles, the prediction of thermal dependence is doubly supported by the fact that the variation explained by temperature, after reducing the covariation with precipitation, remained higher in this animal group than in the others. Both results together support the important influence of energy on reptile distributions via, at least in part, physiological requirements affecting autoecological aspects such as activity or egg development. Previous results suggest that richness gradients (Schall & Pianka, 1978; Rodríguez *et al.*, 2005; Whittaker *et al.*, 2007) and distributional limits (Guisan & Hofer, 2003; Ballestero-Barreara *et al.*, 2007) of reptile species can be predominantly set by temperature-related factors. Furthermore, it

has been demonstrated that the effect of temperature on egg development in lizards can modulate their geographical distributions (Kearney & Porter, 2004).

Interestingly, in the case of amphibians, while the variation explained by temperature, independent of habitat predictors, is higher than in endotherms, this effect decreased considerably after extracting the shared component with precipitation. This suggests that temperature and water availability have interacting effects, at least for some aspects of amphibian ecology (see also Buckley & Jetz, 2007). In fact, temperature regulation in amphibians is complicated because it may be compromised by demands of water economy, revealing the importance of the joint effects of temperature and water (Duellman & Trueb, 1986). Since water availability is a limiting resource in the Iberian Peninsula (Kottek *et al.*, 2006), where higher temperatures are associated with lower precipitation levels (see Appendix S1), it is congruent that water availability is critical along a physiological trade-off. The mechanisms involved in temperature maintenance and water economy in amphibians cannot be dissociated (Duellman & Trueb, 1986). However, the contribution of our study is that precipitation *per se* (i.e. after extracting the variation shared with elevation/productivity or temperature) can also be an important predictor of amphibian distributions. This result does not imply that the direct effect of precipitation is the single factor influencing amphibian distributions but that it represents an important contribution that can act in addition to and/or in interaction with other types of influences. Also, at the global scale, when water availability is considered singly it appeared to be the strongest constrain of amphibian richness (Buckley & Jetz, 2007). This is consistent with previous studies on population trends revealing that the strongest predictor of amphibian decline is water availability (Pounds *et al.*, 1999; Lips *et al.*, 2003). In fact, amphibians are water dependent for key factors of fitness such as reproduction or larval development (Carey & Alexander, 2003). Like many other amphibian species around the globe, most Iberian species can be associated with temporal water sources and/or moisture fluctuations owing to precipitation levels (Pleguezuelos *et al.*, 2002; García-Paris *et al.*, 2004). Therefore, Iberian amphibians can be imperilled not only by dryness due to global warming but also by inappropriate land uses that prevent access to water sources or contaminate them (Blaustein *et al.*, 2003; Collins & Storfer, 2003; Becker *et al.*, 2007).

Regarding terrestrial endotherms, it has been shown that their distributions may also be influenced by climate via physiological constraints, at least at broader environmental ranges. On a broad scale, the winter ranges of a large number of passerines are limited by the energy expenditure necessary to compensate for colder ambient temperatures (Root, 1988). Our results show a relatively weaker association of endothermic distributions with the independent contributions of climate. This picture is compatible with the hierarchical framework proposed by other authors, where different processes are more important at different scales. That is, at finer data resolutions, other factors in addition to climatic ones, such as topography, landscape and biotic interactions, become increasingly important in explaining species distributions (e.g. Pearson & Dawson, 2003; Soberón, 2007). In fact, we found an important association of bird species distributions with both topography and plant productivity, independently of temperature or precipitation. Thus, our results suggest that, at least at this extent and grain resolution, part of the association between climate and endotherm distributions might be mediated through biotic interactions, topography or other habitat characteristics, which in turn can be influenced by or correlated with climate. In agreement, a study on bird population dynamics in Spain at the same scale as used here, showed that population trends are much better explained by landscape characteristics than by climatic factors. Authors have concluded that changes in plant productivity might explain the observed trends (Seoane & Carrascal, 2008). Other studies have shown that global warming may cause a pervasive mismatch between insectivorous bird reproduction and insect productivity, which in turn depends on plant productivity (Vissier & Both, 2005). As an example of the complexity of biotic interactions, a study on time-series models with terrestrial endotherms revealed the influence of climate fluctuations on the food web (Lima *et al.*, 2002). This study showed that climate fluctuations affected population dynamics of small mammals via plant and/or insect productivity, which in turn affected the population dynamics of their bird predators. Moreover, it has been suggested that the strong association of bird diversity patterns with actual evapotranspiration at a global scale operates via plant productivity (Hawkins *et al.*, 2003). In agreement, seasonal vegetation cover has been shown to play an important role in seasonal spatial patterns of birds at broad scales (H-Acevedo & Currie, 2003). These scenarios are compatible with the fact that endotherms need to transform part of the food supply to their energetic demands for temperature maintenance (Pough, 1980).

In conclusion, our study reveals that, after reducing the covariation with non-climatic factors, there is a stronger effect of climate on the distributions of ectothermic than endothermic terrestrial vertebrates operating directly via physiological constraints. Also, at least at our scale and resolution, an indirect effect of climate operating via plant productivity together with topography remained important for bird species after reducing the covariation with climate. This study shows that to address ecological hypotheses it is crucial to disentangle the direct effect of climate and indirect and/or other correlated effects, combined with comparisons among functional groups. Other more cryptic processes operating on species ranges might be elucidated by applying analogous procedures with target variables and specific designs.

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SUPPORTING INFORMATION

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

Appendix S1 Correlation coefficients of the environmental variables.
Appendix S2 Relationships between the explanatory capacity of models before and after the extraction of their shared components.
Appendix S3 Patterns of deviances corrected simultaneously by their shared components through functional groups.
Appendix S4 Testing the robustness of the main results.
Appendix S5 Associations between range size and explained deviances. Patterns of range-corrected deviances through taxonomic/functional groups.

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BIOSKETCH

Pedro Aragón is currently interested in searching for and interpreting spatial patterns of terrestrial vertebrates according to ecophysiological differences among species groups.

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